Savanna aliens

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Thesis
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Savanna aliens

2009 Mhosisi Masocha

To

my son Farirai and daughter Kundisai

&

in memory of my father and young brother Edwin

Table of contents

Abstract

The invasion of alien plants into African savannas poses a threat to native biodiversity and alters ecosystem functioning. Our current understanding of the factors and mechanisms causing invasion in these ecosystems is poor. Yet, this knowledge is critical for the development of successful strategies for controlling invasive species and conserving native biodiversity. In this thesis, field measurements, a greenhouse experiment, field experiments, a long-term burning experiment, remote sensing, and Geographical Information System (GIS) techniques were used to understand the mechanisms of invasion and ecological factors controlling the susceptibility of African savanna systems to invasion by alien species (invasibility). In a nutrient-limited Zimbabwean savanna (southern Africa), native termites, which are widely distributed in the tropics, enhanced alien plant invasion by boosting nutrient concentrations in top soils around their mounds and creating spatial heterogeneity in microsite availability. This is the first time that the role of termites in facilitating alien plant invasion in a savanna has been reported. In a semi-arid savanna in southern Zimbabwe, the rate of spread of an invasive alien shrub was controlled by rainfall. During years of above-average rainfall, the mean annual rate of spread of the invasive shrub *Lantana camara* was at least twice that of native shrub encroachers, whereas in other years natives spread at the same rate as the alien shrub. This is a novel finding suggesting that in water-limited African savanna systems, pulses in rainfall may accelerate the spread of invasive alien species. In a humid savanna in central Zimbabwe, frequent burning promoted invasion by alien plant species. The interaction of human disturbance and overgrazing by cattle increased the level of invasion of a degraded savanna in southern Zimbabwe. These results combined lead to the general conclusion that the invasibility of an African savanna system tends to increase when the availability of key limiting resources (water and nutrients) coincides with disturbances like cattle grazing and fire, which open up an intact plant assemblage to colonisation by alien plant invaders. This is consistent with ecological theory and implies that manipulating resource availability and reducing the level of disturbance may be the keys to controlling the spread of invasive alien species and conserving native biodiversity in African savannas.

Acknowledgments

Life in Africa is a perpetual struggle, and pursuing a career in science is considered to be a luxury by many. This is ironic. I am one of the few lucky Africans who got the chance to understand that through science we can solve most problems confronting Africa. I thus start by expressing my sincere gratitude to the Netherlands Organisation for International Cooperation in Higher Education (NUFFIC) for funding this doctoral study. I also thank many people, who shaped my thinking as I wrestled to understand why there are so many 'aliens' in African savannas.

Let me start by acknowledging the contributions of my doctoral thesis supervisors Andrew Skidmore, Herbert Prins, and Milena Holmgren, who helped me to understand the problem better and sharpen the logic. To Andrew, I am perpetually indebted. You helped me to write the research proposal when I was in Zimbabwe, which resulted in the award of this PhD fellowship. Because we hardly made acquaintance at that time your trust and confidence in my ability made a big difference to me. I thank you for your mentorship. I must admit that I have lost count of the number of fruitful scientific discussions we had over the last four years in your office. But I still remember the famous question you used to ask each time I came to your office for a discussion: "Is everything under control?". May I answer it one more time with a broad African smile, "Yes Prof!". I learned a lot about science and the art of scientific writing from you. One thing stands out, and I quote 'because one can always be parsimonious, less is more in science'. I cannot list all the things I learned from you here otherwise I will be violating one of your mottos: "less is more" and going against what your mother taught you, which is "everything should be done in moderation, always". My mother taught me the same when I was young.

To Herbert Prins, your contribution and encouragement were also critical to the successful completion of this doctoral thesis and my career development. Allow me to quote a few lines from two emails out of many, which clarify what I mean and save me words. Firstly, "…I advise, I show possible roads, I cajole, I support, I steer but I want YOU to decide simply because I think making choices and facing all the uncertainties associated with it, is a part of your training towards becoming an independent scientist". I could not have expressed it better. Secondly, "…Indeed, weaning is the right term: I

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Chapter 1

General introduction

Alien species invasions

Invasions of managed and natural systems by alien species pose the second greatest threat to biodiversity after habitat loss worldwide (Elton 1958; Vitousek et al. 1996; Lonsdale 1999; Mack et al. 2000). Alien plant invasions occur when non-native plants or their propagules which are moved by humans either deliberately or by accident across major biogeographical barriers, overcome abiotic and biotic filters to survive, reproduce, and establish new self-sustaining populations (Richardson et al. 2000; Kolar and Lodge 2001). Not all naturalised alien plant species will have profound adverse impacts on native biota and ecosystems (Martin et al. 2009). In fact, many show no detectable impact at all (Simberloff 1988). In some cases, introduced alien plants may play a beneficial role, for example, by providing critical habitats to some endangered native fauna (Sax 2002). But this is not always the case. Many introduced alien plant species gain the ability to reproduce offspring, often in large numbers and are able to disperse rapidly over extensive areas (Pyšek and Richardson 2008). These invasive alien species can out-compete native species, alter ecosystem functioning, and cause considerable economic damage (Chapin et al. 1997; Pimentel et al. 2001; Yurkonis et al. 2005). For instance, the economic losses caused by invasive species in the United States of America have been estimated to run into billions of United States dollars (Wilcove et al. 1998; Pimentel et al. 2000; Pimentel et al. 2005). Estimates for South Africa also exceed several billions of United States dollars (Van Wilgen et al. 2001).

Statement of the problem

Savannas are a unique biome characterised by the coexistence of trees and grasses (Scholes and Walker 1993; Jeltsch et al. 2000). They cover approximately 12 % of the world's total land area but support the largest diversity of mammal herbivores on the planet and as much as half of the total human population in Africa (Scholes and Archer 1997). The invasion of African savannas by numerous alien plant species is a key environmental problem confronting natural resource managers (Foxcroft and Richardson 2003; Henderson 2007). Invasive alien plants can alter the structure, diversity and functioning of African savanna ecosystems by modifying fire regimes (Brooks et al. 2004), nutrient cycling (Ehrenfeld 2003), causing the loss of native

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biodiversity (Levine et al. 2003), as well as by changing river flow regimes thus exacerbating water scarcity (Enright 2000; Le Maitre et al. 2002). Removing invasive plants or controlling their further spread is therefore crucial for conserving native biodiversity, maintaining ecosystem functioning and ensuring that savannas continue to provide goods and services.

Two major obstacles hinder the management of invasive alien species in African savannas. Firstly, our understanding of the mechanisms of invasion operating in these ecosystems is poor (Pyšek et al. 2008). Secondly, very little is known about how and why the distribution of invasive aliens change over time (Foxcroft et al. 2009). Because the ecological impacts of invasive plants are directly correlated with their spread and abundance (Hejda and Pyšek 2008), understanding how invasibility varies within and across savanna landscapes is crucial for optimising the allocation of resources to control invasive alien species.

It has been suggested that rainfall, soil nutrient availability, grazing, and fire are the four principal determinants of vegetation structure, composition, and dynamics in African savannas (Jeltsch et al. 1996; Scholes and Archer 1997; Van Langevelde et al. 2003; Sankaran et al. 2005). What is unclear, though, is whether these factors play a similar role in the invasion of alien plant species in these ecosystems. Therefore, the main aim of this thesis was to investigate and gain an understanding of how these four co-determinants of vegetation structure and composition govern the invasibility of savanna systems in Africa. My initial main hypothesis was: how an alien plant species responds to rainfall, soil nutrient availability, fire, and grazing, including their spatiotemporal variation, determines its ability to invade. For example, many termite species are known to boost nutrient concentrations in the top soil around their mounds in savannas (Lee and Wood 1971). Since plant distribution and growth in African savannas tend to be limited by the low availability of soil nutrients, one would expect that these insects may enhance the invasibility of these savannas. Throughout this thesis, savanna invasibility is defined as its susceptibility to invasion by alien plant species (Lonsdale 1999) and is variously indexed by the diversity of alien taxa present, number of alien species relative to total plant species richness present, frequency of occurrence, abundance of alien invaders as well as the proportion of the habitat invaded.

Methods

A range of approaches consisting of field measurements, a greenhouse experiment, field experiments, a long-term burning experiment, remote sensing, and Geographical Information System (GIS) techniques were used to understand how the availability of two key resources limiting primary productivity in African savannas (water and nutrients) as well as major disturbances (i.e., fire and grazing) determine the invasibility of these systems. Also, to improve invasive species mapping, traditional image classifiers were combined with a simple GIS expert system, yielding a robust hybrid algorithm capable of mapping the cover of a target invasive species across the entire landscape from satellite imagery more accurately than either the traditional classifiers or GIS expert system could by themselves.

Study sites

The study was conducted in the 44 km^2 Kyle Game Reserve and the adjacent 344 km^2 Mutirikwi communal area (Fig. 1). They are located between the latitudes 20° 06$'$ and 20° 20$'$ south and the longitudes 30° 58$'$ and 31° 08$'$ east in Zimbabwe (southern Africa). Precipitation is low and erratic, with a long-term annual mean of 635 mm (100-year period: 1906-2006, Masvingo weather station). Soils are predominantly coarse-textured sandy loams of low nutrient status, derived from granite (Nyamapfene 1991). The vegetation consists of a mosaic of broad-leaved deciduous woodland, bushland thickets, and open grassland. *Brachystegia spiciformis* and *Julbernardia globiflora* dominate the woodland, whereas the bushland is dominated by *Dodonaea viscosa*, *Dichrostachys cinerea*, and the invasive *Lantana camara*. Open grassland areas are dominated by *Hyparrhenia filipendula* and *Hyperthelia dissoluta* (Vincent and Thomas 1960).

The study sites border onto each other, but their land tenure, management practices, and disturbance regimes differ. The game reserve is a relatively pristine savanna, which is fenced off primarily to conserve biological diversity. It is managed by the Parks and Wildlife Management Authority of Zimbabwe. In contrast, the communal area is a degraded savanna (Whitlow 1988; Scherr 1999; Masocha and Kariaga 2001) with a high human population density averaging 45 people per km^2 (CSO 2004) and an

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open access tenure regime (Chenje et al. 1998). Subsistence agriculture and continuous heavy grazing by cattle are the main disturbances. The juxtaposition of these study sites with similar soil types, rainfall conditions but different disturbance regimes makes them ideal for testing the effects of anthropogenic disturbance on alien plant invasion in a savanna system.
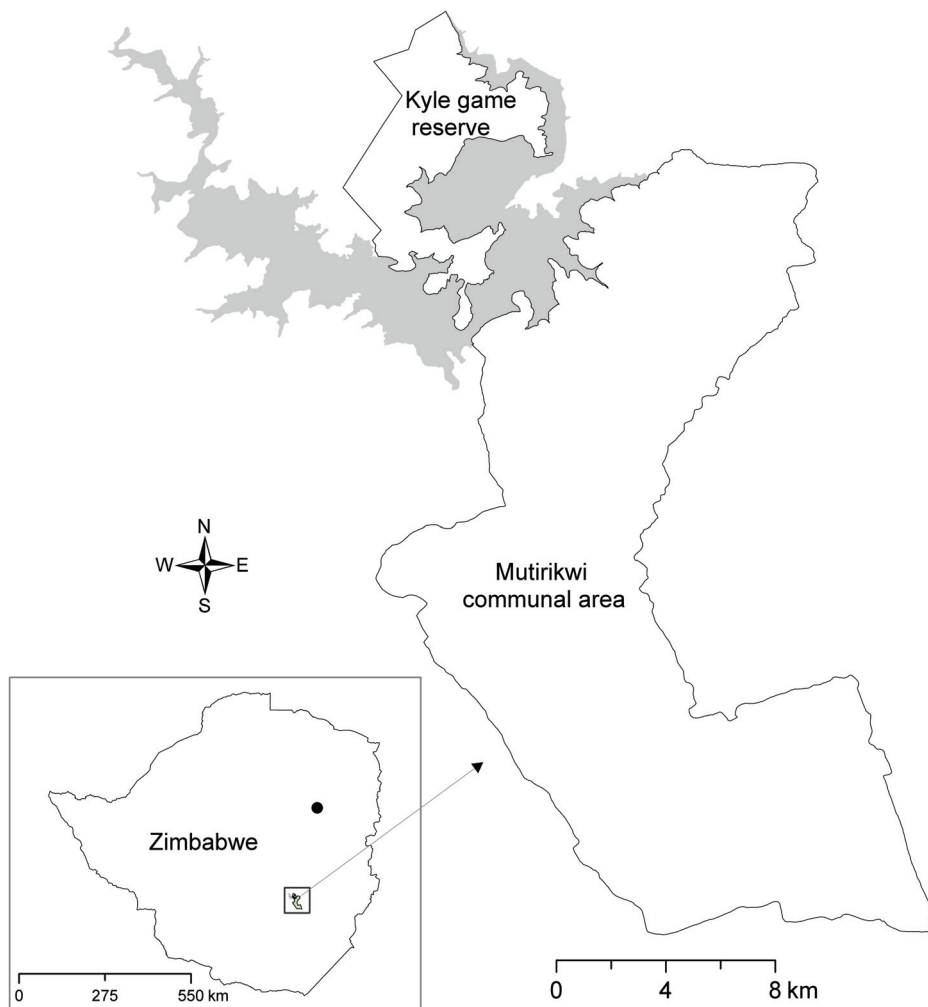
Fig. 1. Location of the study sites in Zimbabwe. The study sites are separated by Lake Mutirikwi (grey shading). The black circle in the insert represents the location of the experimental site at Grasslands Research Station near Marondera town.

Experimental site

The effects of frequency of burning on alien plant invasion were assessed in a humid savanna. The experimental site is located at the Grassland Research Station (18° 65′ S, 31° 15′ E; altitude 1,630 m) near Marondera town in Zimbabwe (Fig. 1). The climate is humid with precipitation averaging 885 mm per year, falling between mid-October and mid-April. Mean monthly temperatures range from 12.3^o C in June to 19.7^o C in October (Grundy et al. 1994). The soils are coarse-textured sandy loams derived from granite (Barnes 1965). The vegetation is deciduous savanna woodland with *Brachystegia spiciformis* and *Julbernardia globiflora* as the dominant trees. The herbaceous layer is dominated by *Hyparrhenia filipendula*, *Heteropogon contortus*, and *Nidorela uricrata* (Campbell et al. 1988; Furley et al. 2008). The botanical nomenclature for the flora in the study sites and at the experimental site corresponds with authorities in Mapaura and Timberlake (2004).

Outline of the thesis

This thesis consists of several coherent chapters contributing to the understanding of the ecological mechanisms and factors controlling the susceptibility of African savanna ecosystems to invasion by alien plant species (invasibility). Chapter 2 investigates how termites, which modulate the availability of nutrients to plants and create patchiness in microsite availability in the landscape, facilitate the invasion of savannas by alien plants. The hypothesis tested is: by concentrating soil nutrients around their mounds and disturbing the soil, termites create spatial environmental heterogeneity, which may promote alien plant invasion in nutrient-limited savannas.

Chapter 3 assesses the relative importance of germination and seedling survival phases to explain the abundance of invasive alien shrubs on termite mounds. This is the first time field experiments have been performed to evaluate the effects of termite mound soils on alien shrub recruitment in African savannas.

In Chapter 4, the rates of spread of invasive and native encroaching shrub species are quantified over a relatively long period and the link with rainfall variation tested in a semi-arid savanna. In these savannas, rainfall is the primary factor

controlling vegetation dynamics but whether the response of invasive alien species to rainfall variation differed from the response of native, functionally similar species, was unknown.

Chapter 5 evaluates whether the frequency of burning has any impact on the invasion of a humid savanna by alien plant species. Fire is one of the key disturbances influencing vegetation structure and composition in savannas, yet its role in promoting or limiting alien invasions of these systems is poorly understood.

Chapter 6 deals with the joint effects of human and livestock disturbance on savanna invasibility. The hypothesis tested is: high human disturbance and continuous heavy grazing by livestock may favour alien plant invaders especially those with a ruderal strategy and/or those which are unpalatable to domestic herbivores.

In Chapter 7, traditional image classifiers are integrated with a simple GIS expert system in order to improve invasive species mapping. It is demonstrated for the first time that the resultant hybrid classifier can detect and map invasive species across the entire landscape from satellite imagery with greater accuracy than either the standard classifiers or the GIS expert system alone.

Finally, in Chapter 8, the main results from the previous chapters are brought together in order to gain a better understanding of the major factors controlling the invasibility of African savannas. The mechanisms of invasion are highlighted and the applicability of our results to other terrestrial ecosystems is discussed. Ultimately, two suggestions are made for future research.

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Chapter 2

Native termites facilitate alien plant invasion in a southern African savanna

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and Herbert H.T. Prins

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Abstract

Numerous alien plant species currently invade African savannas, threatening native biodiversity and ecosystem functioning. Yet, the mechanisms that cause the widespread invasion of savannas are not clear. We tested whether native termites, through disturbing the soil and increasing nutrient concentrations, enhance alien plant invasion in savannas. We registered the occurrence of all native and alien plant species at randomly selected termite mounds and the surrounding non-mound locations in a Zimbabwean savanna. Furthermore, we mapped the distribution of two common invasive shrub species in African savannas, *Lantana camara* L. and *Duranta erecta* L., and determined whether their occurrence was associated with termite mounds. We also performed a greenhouse experiment to test whether the growth of these two species was enhanced in mound soils compared to non-mound soils. Here, we show that alien plant species richness increased threefold on termite mounds compared to the surrounding non-mound areas. Moreover, both *L. camara* and *D. erecta* clustered around termite mounds with no individuals occurring farther from the mound peripheries. These invasive shrubs grew more rapidly and doubled dry matter production in termite mound soils compared to the surrounding non-mound soils. We hypothesise that the increased diversity and enhanced performance of alien species was due to higher nutrient concentrations in mound soils. By disturbing the soil and boosting soil nutrient concentrations, native termites appear to facilitate alien plant invasions in this savanna ecosystem. To our knowledge, this is the first evidence that termites facilitate the invasion of savannas by alien plant species.

Key words: disturbance, invasive species, resource availability, seedling growth, spatial clustering

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Introduction

Savannas are characterised by the coexistence of grasses and trees. They cover approximately 12 % of the world's total land area but support one fifth of the world's human population and most of its large wild herbivore biomass (Scholes and Archer 1997; Sankaran et al. 2005). Numerous alien plant species currently invade African savannas (Henderson 2007; Van Wilgen et al. 2007), and some, such as the common *Lantana camara* L.*,* are becoming locally dominant, thereby posing a threat to native biodiversity and natural ecosystem functioning (Richardson and Van Wilgen 2004). Understanding the ecological mechanisms explaining the invasion of savannas is crucial for sustainable natural resource management and biodiversity conservation, yet it remains poorly addressed (Lonsdale 1999).

Alien plant invasions are often associated with disturbances and consequent increased resource availability (D'Antonio et al. 1999; Davis and Pelsor 2001; Huston 2004; Rose and Hermanutz 2004). Davis et al. (2000) predicted that a plant assemblage becomes more susceptible to invasion by alien plants if disturbances increase the amount of unused resources, since for an alien species to invade successfully it has to survive and capitalise on resources left unconsumed by native plants (Seabloom et al. 2003). Disturbances may enhance an ecosystem's invasibility by increasing the availability of the most limiting resources such as soil nutrients (Shea and Chesson 2002).

Across African savannas (with the exception of some East African savannas where soils are rich in nutrients) plant growth is limited by low soil nutrient availability, especially nitrogen and phosphorus (Sankaran et al. 2005). In these ecosystems, termite species, such as *Macrotermes natalensis* Haviland and *Macrotermes michaelseni* Sjöstedt, are important disturbing agents that modify savanna soils via the construction of large mounds built to create a suitable microclimate environment and protect their nests (Anderson and Wood 1988). These mounds tend to have higher nutrient concentrations than the surrounding soils (Konate et al. 1999; Jouquet et al. 2005). Nutrient enrichment occurs for two reasons. First, termites construct mounds using soil from deeper layers with a higher proportion of clay minerals and a higher cation exchange capacity than the coarser textured soils from the surface (Lee and Wood 1971).

Second, termites import and incorporate nutrient-rich organic matter into their mounds (Wood 1988; López-Hernández et al. 2005). Termite mounds are also prone to further disturbance by foraging animals such as aardvarks (*Orycteropus afer* Pallas), which feed on termites, and by mammalian herbivores attracted by the high forage quality of plants growing on mounds (Dangerfield et al. 1998).

We propose that by increasing the availability of soil nutrients to plants and disturbing the soil, native termites facilitate the invasion of African savannas by alien plant species. To test this hypothesis, we focused on termite mounds constructed by *M. natalensis* - a widespread termite species in African savannas occurring in both deciduous woodlands and open savanna grasslands (Uys 2002; Mitchell 2007). We registered the occurrence of all native and alien plant species at randomly selected termite mounds and the surrounding non-mound locations in a protected savanna of southern Zimbabwe. Furthermore, we mapped the distribution of two common invasive alien shrub species in southern African savannas, *L. camara* and *Duranta erecta* L., and determined whether their occurrence was associated with the presence of termite mounds. Finally, we performed a greenhouse experiment to test whether the growth of these two invasive shrubs differs between mound soils and non-mound soils.

Methods

Study site

The 44 km^2 Kyle Game Reserve is situated at 20° 13$'$ S and 31° 03$'$ E about 38 km southeast of Masvingo town in southern Zimbabwe. It is a relatively flat plain (averaging 1,060 m a.s.l.) that stretches northwards from Lake Mutirikwi to the Beza mountain range. The climate is semi-arid with three distinct seasons: hot and wet (November to April), cool and dry (May to mid-August) and hot and dry (mid-August to October). The Masvingo weather station situated about 30 km northwest of the game reserve has a long-term (1899 - 2000) average annual rainfall of 635 mm. Summer rains (November-April) often fall sporadically and long dry spells are common. The mean maximum daily temperature ranges from 21° C in June to 29° C in October and the mean daily minimum temperature ranges from 5° C in July to 17° C in January.

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Our study site is located at the southern part of the game reserve dominated by shallow, coarse and nutrient-poor sandy soils derived from granite (Nyamapfene 1991). This site is an open savanna grassland dominated by *Hyperthelia dissoluta* (Steud.) Clayton, *Hyparrhenia filipendula* (Hochst.) Stapf. and *Themeda triandra* Forssk. Woody species dominated by *Schotia brachypetala* Sond. and *Diospyros mespiliformis* Hochst. ex A. DC., growing mostly at termite mounds, are scattered throughout the continuous open grassland matrix. The botanical nomenclature follows Oudtshoorn (2006) for grasses and Palgrave (2002) for woody species. The main disturbances are fire and herbivory by large grazers and browsers particularly the zebra (*Equus burchellii* Gray) and giraffe (*Giraffa camelopardalis* L.).

Focal invasive shrub species

We mapped the spatial distribution of two alien shrub species, *L. camara* and *D. erecta,* both considered aggressive invaders of some African savannas (Henderson 2007) to determine whether they were associated with native termites. *Lantana camara* is a multi-stemmed perennial shrub with recurved spines that usually grows up to 2 m tall. Mature *L. camara* plants can produce up to 12,000 seeds per m^2 (1995). Seed scarification in bird guts (Day et al. 2003) and probably baboons (*Papio ursinus* Kerr) improve germination. *Lantana camara* was introduced from Central and South America into southern Africa in 1858 as an ornamental shrub. It has since escaped and invaded a wide range of habitats including watercourses, forest and plantation margins, roadsides, pastures, and degraded land (Palgrave 2002).

Lantana camara invasion poses a threat to native biodiversity and agro-ecosystems in many countries. Stands of *L. camara* form dense and prickly monospecific thickets with interlocking crowns. These thickets suppress the germination and growth of native plants through shading and allelopathy (Gentle and Duggin 1998). In addition, *L. camara* thickets diminish the amenity values of recreational parks because they restrict human access and vehicle movement (Fensham et al. 1994). *Lantana camara* clusters are also known to harbour insects including tsetse flies and mosquitoes which spread diseases such as trypanosomiasis and malaria to livestock and humans, respectively (Syed and Guerin 2004). *Lantana camara* leaves

contain toxic phenolic compounds such as triterperne lantadenes which poison livestock and can result in death if ingested (Sharma et al. 1988). For example, in Australian savannas, it is estimated that annual losses attributed to *L. camara* poisoning are about 1,500 cattle deaths, at a cost of 7.7 million Australian dollars (ARMC-ANZ 2001).

Duranta erecta is an evergreen or semi-deciduous shrub with spiny branches that can grow up to 6 m in height. It usually forms a multi-stemmed clump of trailing branches. Although it is reported that the berries are poisonous, they are eaten and dispersed by birds (Palgrave 2002). *Duranta erecta* was also introduced from Central and South America into southern Africa as an ornamental shrub but has naturalised and invaded savannas and urban open areas (Palgrave 2002). However, little information exists about the spatial extent as well the economic and ecological consequences associated with its invasion.

Data collection

To determine whether alien plant species diversity and cover differ between termite mounds and non-mound areas, we conducted a field survey in March 2008 (during the peak of the growing season). A total of sixteen 20 m x 5 m plots were randomly selected out of 163 identified in aerial photographs. Half of the plots (8) were centred on existing termite mounds while the other half (8) were situated in the surrounding areas without termite mounds. One non-mound plot was placed about 60 m away from the outer-edge of each of the eight selected termite mounds. Previous research has shown that the foraging galleries of many termite species radiate outwards in various directions for up to 50 m but tend to be concentrated within 30-40 m from the mound (Lee and Wood 1971; Ferrar 1982).

Vegetation and soil data were collected using the modified-Whittaker plot (Barnett and Stohlgren 2003), which had one central 10-m^2 (5 m x 2 m) sub-plot and four 1-m^2 (2 m x 0.5 m) sub-plots located at each side. The occurrence of all native and alien plant species was registered in each 1-m^2 sub-plot. In addition, the percentage cover of each plant species was estimated visually in the four sub-plots by three observers with the aid of a graduated rectangular wooden frame and averaged. Plant

species that were not detected in the 1-m^2 sub-plots but were present in the 100-m^2 plot were also recorded.

Relative richness and abundance of alien plant species

Plant specimens and records kept at the National Herbarium and Botanical Garden in Harare (Zimbabwe), as well as local vegetation checklists and regional floras, were used to determine whether the plant species identified in the sampled plots were native or alien, i.e., those plant species not indigenous to southern Africa (Pyšek et al. 2008). We calculated the relative richness of aliens as the number of alien plant species present in a plot divided by the total number of plant species present in that plot. We similarly calculated the relative cover of aliens.

Soil nutrient analysis

Soil samples were collected from the upper 20 cm of the soil at five random locations in the 1-m^2 and 10-m^2 sub-plots. For each plot, soil samples were mixed to form a composite sample and analysed for nitrogen (N), phosphorus (P), calcium (Ca) and magnesium (Mg). To estimate the total amount of N that would normally be available under field conditions, soil samples were first incubated at 35° C for 14 days. After incubation, the acid extraction method was used to estimate total N (ppm). Total P (ppm) was measured using the resin extraction method. The atomic absorption method was used to measure the total amount of Ca (me/100g of soil) and Mg (me/100g of soil). For details of these procedures, see Anderson and Ingram (1989).

Mapping the distribution of invasive shrub species

The distribution of two common invasive shrub species, *L. camara* and *D. erecta,* in relation to termite mounds was mapped in a 1,000 m by 300 m randomly selected study site, using a global position system unit to locate the centre of every *M. natalensis* mound. For each *L. camara* and *D. erecta* plant, the distance and bearing to the centre of the nearest mound were measured in order to calculate their position relative to the

nearest mound. Maps showing the distribution of the two invasive shrub species relative to the location of termite mounds were generated using the ILWIS Geographical Information System software (version 3.3).

Spatial analysis

The *K* function (Ripley 1977) was used to test the hypothesis that a significant spatial association exists between the distribution of termite mounds and that of *L. camara* and *D. erecta*. The modified version of the *K* function, which takes into account spatial variation in the densities of mapped point patterns (Diggle 2003), was used to calculate and compare the observed and expected number of *L. camara* and *D. erecta* plants at given distances from the termite mounds. To stabilise the variance and make the results easier to interpret, $\hat{K}_{12}(r)$ was divided by π, square root-transformed and plotted against *r* (Stoyan and Penttinen 2000). Since the underlying distribution of most spatial point processes is not known, Monte Carlo computer simulations were performed to generate 95 % confidence envelopes. All spatial point pattern analyses were undertaken using Spatstat (Baddeley and Turner 2005), which runs under the open source R statistical software version 2.9.1 (R Development Core Team 2009).

Greenhouse experimental design

A greenhouse experiment was performed to test whether termite mound soils enhance the growth of *L. camara* and *D. erecta* compared to the surrounding non-mound soils. Soil samples were collected from eight selected termite mounds and eight surrounding non-mound (control) locations in the Kyle Game Reserve, using the methods described above. Each soil sample was air-dried and, after removal of all visible plant material, thoroughly mixed to form one composite sample. A total of 20 pots (20 cm wide and 20 cm deep) were allocated to each of the two study species, ten filled with mound soil and ten filled with non-mound soil.

Seeds of *L. camara* and *D. erecta* were collected from different adult shrubs in the Kyle Game Reserve and germinated in a greenhouse. In each pot, a one-week old seedling was transplanted and allowed to grow for 13 weeks at a day temperature of 26°

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C and a night temperature of 21° C. To mimic the average rainfall in the study site during the growing season (November to March), each seedling was irrigated with 100 ml of water every week. Pots were randomly distributed on a bench and randomly shifted after every two weeks.

We measured seedling height weekly and calculated relative height growth changes between the first and 13th weeks using the log-transformed height measurements (Hoffmann and Poorter 2002). To evaluate plant biomass at week 13, pots were cut open, plants were carefully removed and their roots washed. Shoots and roots were then dried in an oven at 70° C for 48 hours and weighed separately.

Statistical analysis

Paired *t*-tests were used to evaluate whether termite mounds and the surrounding non-mound areas differed in native species richness, alien species richness, relative richness of aliens, the absolute cover of natives, the absolute cover of aliens, and the relative cover of aliens as well as nutrient concentrations (N, P, Ca, and Mg). For the greenhouse experiment, *t*-tests were used to compare the growth (stem height) and biomass of seedlings grown in mound and non-mound soils. Data were transformed where necessary to normalise them. Statistical analyses were performed with Statistica version 7.0 (StatSoft, Inc.) and data are presented as means ± 95 % confidence level.

Results

Alien species richness and abundance at mounds vs. non-mound areas

We found seventeen alien plant species belonging to eight families in the sampled areas, 65 % of which occurred more frequently at termite mound plots than in the non-mound plots (see Appendix 1; $t = 2.78$, df = 16, $P < 0.05$). Termite mounds had significantly greater numbers of both native and alien plant species compared to the surrounding non-mound areas (Table 1). The mean number of alien and native species was 2.7 and 1.3 times higher respectively in mound plots than in non-mound plots. Consequently, the mean proportion of alien species relative to that of total species was significantly higher

at termite mounds compared to non-mound plots. Similarly, the mean absolute cover of natives and aliens were significantly higher at mounds compared to non-mound plots, and alien species accounted for a significantly higher proportion of total vegetation cover than in mound plots (Table 1).

Table 1: Native and alien plant species richness and their cover (mean ± 95 % confidence level, n = 8) on termite mounds and the surrounding non-mound areas in the Kyle Game Reserve (data on percentage cover were arcsine-transformed to normalise them).

Variable	termite mound	non-mound area	$t_{(d.f=7)}$
native species richness	43.4 ± 8.1	32.3 ± 5.1	2.49*
alien species richness	7.5 ± 1.9	2.8 ± 1.3	4.04**
relative richness of aliens	0.15 ± 0.04	0.07 ± 0.03	3.21*
absolute cover of natives	1.17 ± 0.07	0.70 ± 0.20	4.80**
absolute cover of aliens	0.13 ± 0.04	0.03 ± 0.01	5.12**
relative cover of aliens	0.11 ± 0.04	0.03 ± 0.01	4.93**

significance levels: $* < 0.05$; $** < 0.01$

Both *L. camara* and *D. erecta* clustered on termite mounds, with no individuals occurring farther from the mound peripheries (Fig. 2a, b). Results of spatial analyses also indicate significant clustering of these invasive alien shrubs around termite mounds (Fig. 3a, b).

(a) *Lantana camara*
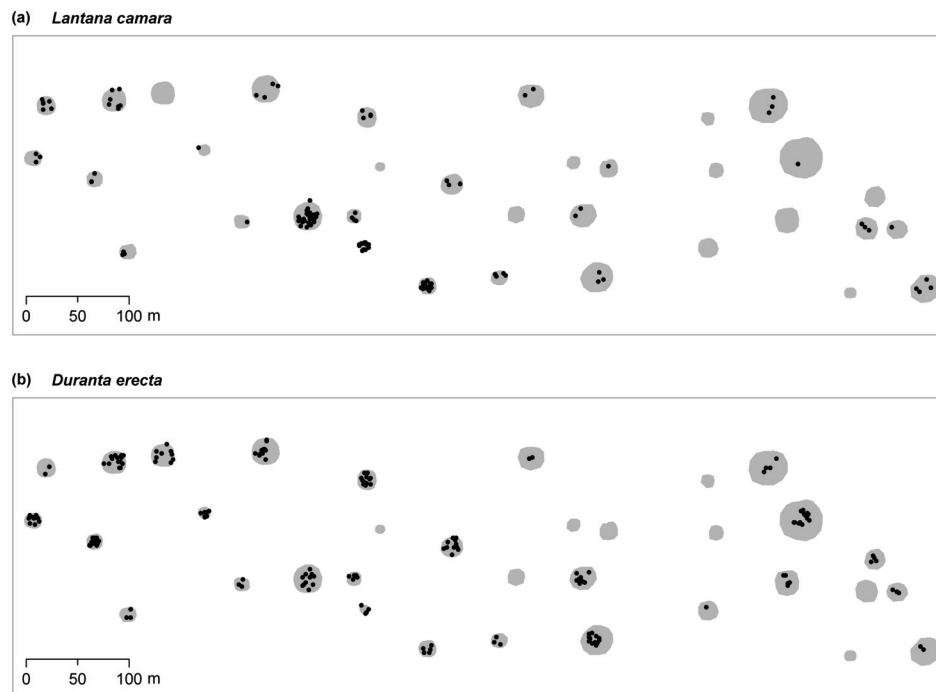
(b) *Duranta erecta*

Fig. 2. Spatial clustering of two invasive shrubs, *Lantana camara* and *Duranta erecta* (black circles) on termite mounds (grey shaded polygons) in a 30-ha study site located in the Kyle Game Reserve, Zimbabwe. The size of polygons corresponds with the areal extent of mounds while the bounding rectangle represents the spatial extent of the study site. The average diameter of termite mounds at base was 19 m ± 6 m standard deviation.

(a) *Lantana camara*
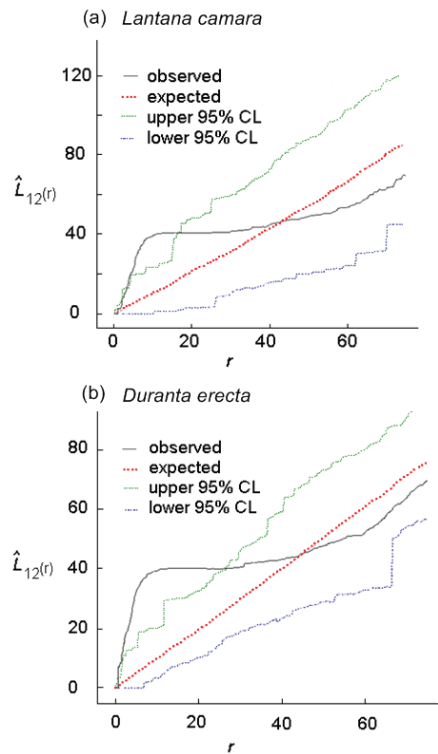
(b) *Duranta erecta*

Fig. 3. *L* functions for two invasive shrub species, *Lantana camara* and *Duranta erecta*, mapped in a 30-ha study site located in the Kyle Game Reserve of southern Zimbabwe. Observed values of *L. camara* (bold line) are greater than the expected (dotted line) and outside the 95 % confidence envelopes up to a distance (*r*) of 18 m from the centre of the nearest termite mound (Fig. 3a). This indicates significant clustering of this invasive shrub at termite mounds. Similarly, observed values of *D. erecta* (bold line) are greater than the expected (dotted line) and outside the 95 % confidence envelopes up to a distance of 25 m from the nearest mound (Fig. 3b). This again indicates significant aggregation of this invasive shrub at termite mounds.

Nutrient concentrations at termite mounds versus non-mound areas

Termite mound soils had consistently higher concentrations of macro-nutrients (N and P) and exchangeable bases (Ca and Mg) than the surrounding non-mound soils (Table 2). The relative magnitude of the increase was larger for the exchangeable bases than macro-nutrients.

Effects of mound soil on seedling growth

Both *L. camara* and *D. erecta* seedlings growing in mound soil increased in height twice as fast and accumulated significantly more dry matter (i.e., shoot and root biomass) than seedlings growing in non-mound soil. Seedlings of *D. erecta* but not *L. camara* produced relatively more root biomass in non-mound soil (Table 3).

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Table 2: Nutrient concentrations (mean ± 95 % confidence level, $n = 8$) in termite mound soils and the surrounding non-mound soils in the Kyle Game Reserve, Zimbabwe (ppm: parts per million; me: milligram equivalents per 100 grams of soil).

Nutrients	termite mound soil	non-mound soil	$t_{(d.f=7)}$
N (ppm)	4.01 ± 0.33	3.05 ± 0.19	5.23**
P (ppm)	2.76 ± 0.62	1.50 ± 0.20	3.99**
Ca (me/100g)	8.89 ± 5.91	0.86 ± 0.20	7.29***
Mg (me/100g)	2.96 ± 1.12	0.61 ± 0.13	5.36**

significance levels: * < 0.05; ** < 0.01; *** <0.001

Table 3: Relative height growth rate (RHGR) and dry matter (mean ± 95 % confidence level, $n = 10$) of *Lantana camara* and *Duranta erecta* grown in mound soil and non-mound soil after 13 weeks.

Species	growth indicator	mound soil	non-mound soil	$t_{(d.f. =18)}$
L. camara	RHGR (cm cm^{-1} per week)	0.16 ± 0.02	0.08 ± 0.02	5.48***
	shoot biomass (g)	2.10 ± 0.38	0.74 ± 0.33	6.13***
	root biomass (g)	1.77 ± 0.48	0.91 ± 0.55	2.66*
	root/shoot biomass ratio	0.92 ± 0.13	0.99 ± 0.18	-0.93^{ns}
D. erecta	RHGR (cm cm^{-1} per week)	0.16 ± 0.02	0.07 ± 0.02	6.76***
	shoot biomass (g)	1.35 ± 0.21	0.23 ± 0.10	10.78***
	root biomass (g)	0.89 ± 0.20	0.27 ± 0.10	6.44***
	root/shoot biomass ratio	0.65 ± 0.08	1.32 ± 0.47	-3.25**

significance levels: * < 0.05; ** < 0.01; *** < 0.001; ns = not significant.

Discussion

Our results reveal that in a savanna ecosystem, native termites can facilitate the establishment of both native and alien plant species, but the relative effects are stronger among alien species. Alien species richness increased threefold on termite mounds, while native species richness was on average only 30 % higher on the mounds compared to the surrounding non-mound areas. This increased diversity of plant species was related to high nutrient concentrations in mound soils, which had consistently

higher concentrations of macro-nutrients and exchangeable bases than the surrounding non-mound soils. Nutrient enrichment caused by native termites was also associated with higher abundance of alien invaders. We showed that the absolute cover of alien species was significantly higher at mounds compared to non-mound areas. Moreover, the results of our greenhouse experiment confirmed that dry matter production and the growth of two invasive shrub species (*Lantana camara* and *Duranta erecta*) doubled in mound soils compared to the surrounding non-mound soils.

Termite mounds go through a construction phase in which the insects deposit fresh soil at their mounds, which has been reported to suppress the growth of native vegetation (Rogers et al. 1999). This increases the availability of microsites, with reduced competition of native flora, that are suitable for the germination and survival of seedlings of invaders (Eriksson and Ehrlen 1992). Termite disturbance might further enhance the diversity of alien species especially of those small-seeded 'ruderal' alien species that establish on bare mineral soil at open sites (Fridley et al. 2007). The microsite effect together with nutrient enrichment may combine to create a positive feedback enhancing the invasion of alien plant species. This might have implications for the invasion success of alien invaders at mounds because the ability of an alien plant species to rapidly increase its biomass at environmentally favourable locations is a trait associated with successful invasion (Grotkopp and Rejmánek 2007; Melbourne et al. 2007).

In the greenhouse, seedlings of two invasive shrub species survived when grown in non-mound soils, yet, in the field these invasive shrubs were restricted to termite mounds. This suggests that other mechanisms, interacting with the high nutrient concentrations at termite mounds, must facilitate invasion. Due to high nutrient availability at mounds, plants growing there tend to be of higher forage quality than those growing in the surrounding non-mound areas and this attracts vertebrate herbivores searching for high quality forage (Dangerfield et al. 1998; Loveridge and Moe 2004). Defecation by these herbivores may further increase nutrient concentrations and trigger a positive feedback for nutrient enrichment (Augustine et al. 2003). Also, increased grazing pressure at mounds compared to non-mound areas may affect native and alien plants differently (Holdo and McDowell 2004; Loveridge and Moe 2004). Recently it has been claimed that novel phytochemicals with anti-herbivore properties

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explain partly the invasion success of alien species (Cappuccino and Arnason 2006). Such novel phytochemicals may tilt the outcome of competition in favour of some aliens with stronger anti-herbivore adaptations, an effect expected to increase with herbivory intensity (Callaway et al. 1999). Indeed, some of the alien species that were dominant at mounds, like *L. camara,* possess toxic phenolic compounds that are poisonous to most vertebrate herbivores (Sharma et al. 1988). We did not measure and compare differences in herbivore damage between alien and native species in this study, but it is documented that some invasive species suffer less herbivore damage than natives (Callaway and Ridenour 2004; Cappuccino and Arnason 2006). Hence, the evidence of findings so far indicates that it might be plausible that termites, while attracting herbivores, increase selection pressure against native plants.

Also, different impacts of fire on mounds and non-mound areas could further accentuate the patterns we found and may explain why both *L. camara* and *D. erecta* individuals were not found farther away from termite mounds. Reduced fire severity at mounds compared to non-mounds areas can contribute to maintaining the spatial clumping of woody plants at mounds in African savannas. For example, Barot et al. (1999) attributed the spatial aggregation of palm trees (*Borassus aethiopum* Mart.) in west African savannas to reduced fire severity at termite mounds, which translate into higher survival rates for seedlings growing on mounds compared to those that recruit in the surrounding non-mound locations. Similarly, in east African savannas, Bloesch (2008) identified fire protection as one of the main factors facilitating the growth of thickets around mounds built by termite species of the *Macrotermes* genus.

To our knowledge, this is the first time that a significant association between termite mounds and increased alien diversity and abundance in an African savanna has been reported. These results improve our understanding of the spatial variation in the invasibility of savannas by alien plant species and are consistent with studies in the Americas which assessed the association between ant nests and plant invasion. Farji-Brener and Ghermandi (2008) found that two invasive herbs (*Carduus nutans* L. and *Onopordum acanthium* L.) accumulated more leaf and root biomass when grown in soils collected from nests of a leaf-cutting ant species (*Acromyrmex lobicornis* Emery) compared with the surrounding soils. This explained the association between the invasion of roadsides by these two invasive herbs and occurrence of ant nests in a

protected area in Patagonia (Argentina). Similarly, Wagner and Jones (2006) found that in the arid regions of North America, the seed-harvesting ant (*Pogonomyrmex rugosus* Emery) increased soil nutrient concentrations favouring the growth of an invasive grass species (*Schismus barbatus* (Loefl. ex L.) Thellung**)**. These studies provide further evidence that soil invertebrates may drive invasion through constructing nests and modulating the availability of limiting resources to alien plants.

Overall, our results suggest that for African savannas, where nutrients are known to limit plant production, soils modified by termites tend to be richer in soil nutrients than non-mound soils. Both native and alien plant species profit from these favourable termite mound conditions, but some invasive shrub species appear to benefit more from soil disturbance and increases in nutrient concentrations caused by termites. This is consistent with the fluctuating resource hypothesis proposed to explain invasions (Davis et al. 2000).

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Appendix 1: Frequencies of occurrence of 17 alien plant species found at sampled termite mounds and the surrounding non-mound plots (*n* = 8 paired sample plots) in the Kyle Game Reserve of Zimbabwe. Nomenclature follows Pooley (1998) for herbs and Palgrave (2002) for shrubs and trees.

Species	family	mound	non-mound	difference
herbs				
Acanthospermum australe	Asteraceae	1	0	1
Acanthospermum hispidum	Asteraceae	0	1	-1
Ageratum conyzoides	Asteraceae	4	1	3
Bidens pilosa	Asteraceae	6	2	4
Conyza sumatrensis	Asteraceae	1	3	-2
Schkuhria pinnata	Asteraceae	5	1	4
Sonchus oleraceus	Asteraceae	1	1	0
Tagetes minuta	Asteraceae	5	3	2
Gomphrena celosioides	Amaranthaceae	1	1	0
Richardia scabra	Rubiaceae	4	3	1
Solanum incanum	Solanaceae	8	3	5
Verbena bonariensis	Verbenaceae	0	1	-1
shrubs				
Duranta erecta	Verbenaceae	8	0	8
Lantana camara	Verbenaceae	7	0	7
trees				
Jacaranda mimosifolia	Bignoniaceae	2	0	2
Melia azedarach	Meliaceae	1	0	1
Psidium guajava	Myrtaceae	0	1	-1

Nomenclature:

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Chapter 3

Enhanced alien shrub recruitment on termite mounds in a southern African savanna

Mhosisi Masocha, Andrew K. Skidmore and Milena Holmgren

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Abstract

Encroachment of savanna ecosystems by alien shrub species can profoundly alter the structure, functioning and diversity of these ecosystems. Understanding which habitats are favourable to the germination and seedling recruitment is important because these two life stages are the most critical for successful invasion. We conducted a field experiment in a protected semi-arid savanna in Zimbabwe, southern Africa, to test the hypothesis that seed germination and survival of the invasive alien shrub *Duranta erecta* is enhanced by increased microsite availability around termite mounds. Seeds and seedlings were introduced to experimental plots located both at termite mounds and away from mounds. The germination rate of *D. erecta* in termite mound soils was twice as high as in the surrounding soils. Also the seedling survival rate was significantly higher at termite mounds than away from mounds. These results show that termite mounds in southern African savannas have increased propensity to invasion by alien shrubs.

Key words: disturbance, *Duranta erecta*, germination, Kyle Game Reserve, *Macrotermes*, plant invasion, seedling survival, shrub encroachment, Zimbabwe

Introduction

Increased shrub abundance has been documented in savannas worldwide (Archer et al. 1988; Brown and Archer 1999; Van Auken 2000; Roques et al. 2001; Rodger and Twine 2002). Encroachment by invasive alien shrubs is particularly problematic since these shrubs can profoundly alter the structure and functioning of these ecosystems (Mack and D'Antonio 1998; Mooney and Cleland 2001; Ehrenfeld 2003; Levine et al. 2003). Little is understood about the mechanisms causing the spread of invasive shrubs across savanna ecosystems (Lonsdale 1999; Pyšek et al. 2008). It has been suggested that alien plant invasion is often associated with disturbances and the consequent increased resource availability (Hobbs 1989; D'Antonio et al. 1999; Sher and Hyatt 1999; Blumenthal 2005). Davis et al. (2000) predicted that an ecosystem becomes more susceptible to invasion by alien species if disturbances increase the amount of unused resources such as soil nutrients, since for an alien species to invade successfully, it has to capitalise on resources left unused by resident species (Seabloom et al. 2003; Melbourne et al. 2007; MacDougall et al. 2009). Disturbances may further enhance an ecosystem's invasibility by increasing the availability of the most limiting resources such as soil nutrients (Shea and Chesson 2002).

In African savannas, plant growth is often limited by low soil nutrient availability, in particular nitrogen and phosphorus (Huston 1993; Sankaran et al. 2005). In these ecosystems, termite species, such as *Macrotermes natalensis* Haviland, are important disturbing agents modifying savanna soils by constructing large mounds with higher nutrient concentrations than the surrounding soils (Lee and Wood 1971; Konate et al. 1999; Jouquet et al. 2005). Consequently, termite mounds tend to harbour a high diversity of alien taxa with some invasive alien shrubs clustering at the mounds while occurring less frequently beyond their outer edges (Chapter 2 in this thesis).

Several mechanisms may potentially contribute to this clustering of alien shrubs on mounds. Termites may enhance seed germination through exposing bare mineral soil to the surface around their mounds (Rogers et al. 1999; Fridley et al. 2007), and also nutrient-rich mound soils may be favourable for the establishment of seedlings. We designed a field experiment in order to assess the relative importance of germination and seedling survival phases to explain the abundance of alien shrubs on

termite mounds. To our knowledge, this is the first time field experiments have been performed to evaluate the effects of termite mound soils on alien shrub recruitment in African savannas.

Methods

Study site

The study was conducted in the Kyle Game Reserve (20° 13′ South, 31° 03′ East; altitude 1,060 m) located about 38 km southeast of Masvingo town in Zimbabwe. Precipitation averages 635 mm annually and falls mostly between November and March (*c.a.* 85 %). Mean monthly temperatures range from 19° C in June to 29° C in October. In 2008, the year the field experiment was performed, total annual rainfall was 668 mm. The study site is located at the southern part of the game reserve dominated by coarse-textured sandy soils derived from granite (Nyamapfene 1991). The vegetation comprises open savanna grassland, dominated by the perennial grasses *Hyperthelia dissoluta* (Steud.) Clayton, and *Hyparrhenia filipendula* (Hochst.) Stapf, with the woody species *Schotia brachypetala* and *Duranta erecta* scattered throughout the open grassland matrix.

Study species

Duranta erecta L. (Verbenaceae) is a bird-dispersed semi-deciduous shrub growing up to 6 m tall (Navarro and Medel 2009). It was introduced from Central and South America into southern Africa as an ornamental garden species but is now one of the most widespread terrestrial invaders in the region posing a threat to both natural and agro-ecosystems (Palgrave 2002).

Experimental design

Two field experiments were performed to test whether the recruitment of *D. erecta* differed between termite mound and non-mound habitats. The response variables were

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the proportion of seedlings emerging and seedling survival time. In December 2007, we located sixteen termite mounds where *D. erecta* plants were absent. The mounds had been built by *Macrotermes natalensis* and were evenly distributed across the study site. At each termite mound, two 1-m^2 plots were placed. At a distance of about 60 m but not more than 75 m away from the outer-edge of each selected mound, two other 1-m^2 plots were located in a randomly assigned direction (north, north-east, east, south-east, south, south-west, west, north-west). Previous research has shown that the foraging galleries of mound-building termites radiate outwards in various directions for up to 50 m but tend to be concentrated within 30-40 m from the mound (Ferrar 1982; Dangerfield et al. 1998). Therefore, it was assumed that beyond 60 m from the mound, these insects would have little effect on the recruitment success or failure of invasive shrub species. In total, 64 plots were established; half (32) of which were located at termite mounds while the other half (32) were situated in the surrounding non-mound areas (Fig. 4). Experimental plots were situated in open places away from the canopy of any resident trees or shrubs to avoid the confounding effect of shading.

Experiment 1: *seed germination*

Fresh seeds of *D. erecta* were collected during December 2007 from more than 60 shrubs, found at the study site. Seeds were prepared by being dried in the sun for three days, scarified between sandpaper and soaked in water for 24 hours prior to sowing to break dormancy (Hagenah et al. 2009). Pilot trails revealed a high germination rate of about 80 % regardless of the scarification method (i.e., soaked in concentrated sulphuric acid, soaked in boiling water for 20 minutes or just soaked in water for 24 hours).

In mid-December 2007, 30 scarified seeds were sown approximately 1 cm deep in one of the two 1-m^2 plots established at 16 selected termite mounds. The same protocol was followed in one of the two reference plots established at the 16 off-mound locations. Each treatment was replicated 16 times, yielding a total of 960 seeds, half sown in mound plots, the other half in non-mound (control) plots. Sowing was done during the rains, which continued for three days after sowing. No artificial irrigation was used.
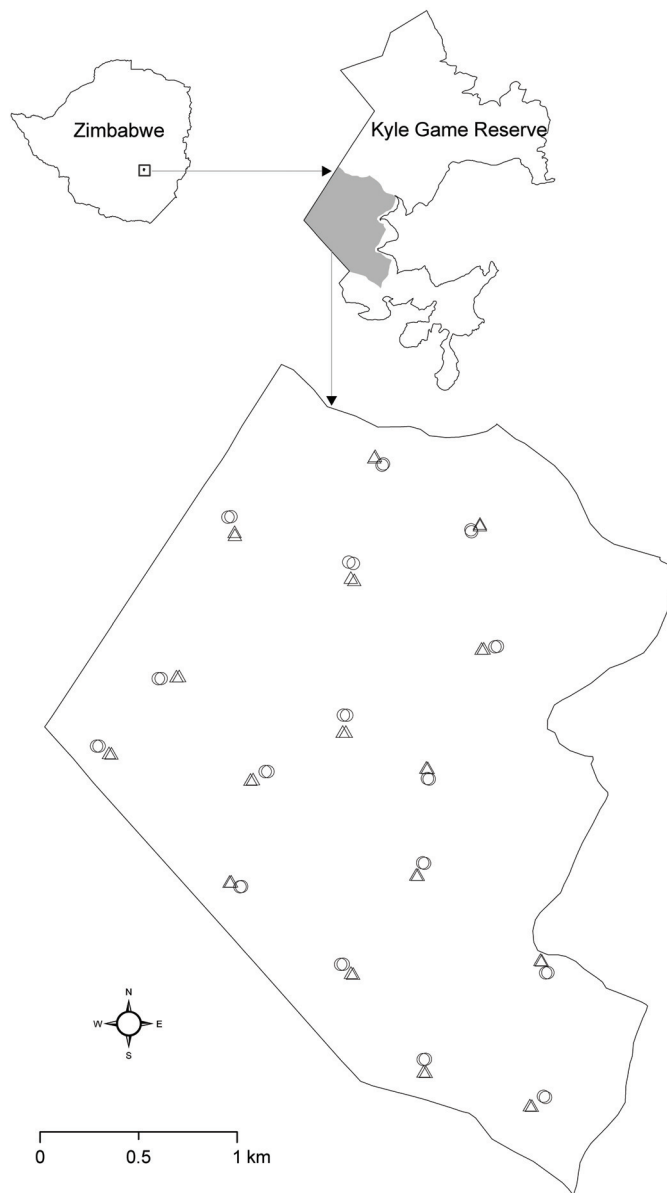
Fig. 4. Distribution of experimental plots in the study site situated in the Kyle Game Reserve in Zimbabwe. Open triangles represent the location of plots at the sixteen selected termite mounds (i.e., 2 plots per mound) and open circles represent the location of control plots situated away from the mounds (i.e., 2 plots for each non-mound location).

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Monitoring started three weeks after sowing because germination trials conducted in a greenhouse revealed that this was the average seedling emergence time. Emergence was monitored every ten days between January and March 2008.

Experiment 2: *Seedling survival*

In January 2008, 256 two-week old *D. erecta* seedlings (8 per plot) were planted in 32 experimental plots; half (16) of which were located at termite mounds while the other half (16) were located at off-mound locations. The seedlings were planted in those plots where *D. erecta* seeds had not been sown. Seedlings were not watered as transplanting was done on a rainy day. The rains continued to fall for three days after transplanting. The transplanted seedlings had germinated *ex-situ* in a greenhouse from seeds collected from plants growing at the study site as described above. Seedlings were surveyed every 10 days from April to June during the first dry season when drought can severely limit tree seedling survival in savannas (Scholes and Archer 1997). At each survey, a seedling was recorded to be either alive or dead. At the end of the experiment, all surviving seedlings were destroyed.

Statistical analysis

A *Z*-test was used to compare whether *D. erecta* seedling emergence differed between termite mounds and non-mounds. It was hypothesised that because termites expose bare mineral soil of higher nutrient status, the proportion of seeds germinating would be higher in mound soil than in non-mound soil.

To compare seedling survival rates between mound and non-mound locations a repeated measures analysis of variance (ANOVA) was performed. Prior to performing ANOVA, data on the proportion of seedlings alive at a given census interval were arcsine-transformed and tested for normality as well as for homogeneity of variance using the Shapiro-Wilk's test and Levene's test of equality of variance respectively and found to satisfy ANOVA assumptions. Statistical analyses were performed using Statistica version 7.0 (StatSoft, Inc.).

Results

Seedling emergence and survival on termite mounds vs. away from mounds

Seed germination under field conditions was relatively low (< 30 %), but the proportion of seeds that emerged relative to the total number of seeds sown was significantly higher in mound plots than in off-mound plots (Z-test, $Z = 4.25$, $P < 0.01$; Fig. 5a). Seedling survival also differed significantly between termite mounds and off-mound areas with seedlings planted in termite mound soil having a longer survival time than those planted in non-mound soil (repeated measures ANOVA; $F_{1, 30} = 55.2$, $P < 0.01$; Fig. 5b).
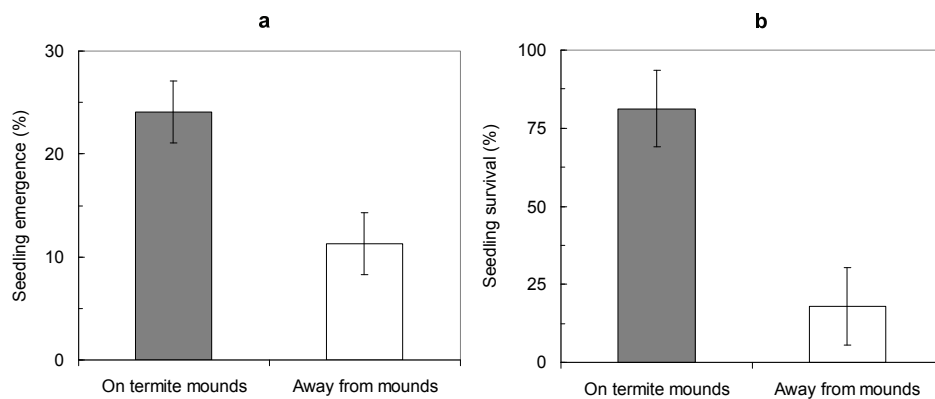
Fig. 5. Seedling emergence and survival rates of *Duranta erecta* on termite mounds and away from mounds in the Kyle Game Reserve in Zimbabwe: (**a**) proportion of seedlings emerging from seeds sown in mound soil and non-mound soil during the growing season; and (**b**) final proportion of seedlings surviving on mounds and away from mounds at the end of the third month of the first dry season (June). For both **a** and **b**, bars represent mean percentages, and whiskers represent 95 % confidence intervals ($n = 16$).

Discussion

The results of this study indicate that the clustering of alien shrub species around termite mounds in southern African savannas may be attributed to higher germination and seedling survival on the mounds than in the surrounding off-mound areas. Germination rate of the invasive alien shrub *Duranta erecta* in mound soils was twice as high as in soils in the surrounding areas undisturbed by termites. In addition, seedling survival was consistently higher on termite mounds than away from mounds. These findings suggest that some alien woody species may recruit more successfully at termite mounds than in the surrounding non-mound areas.

Termite mounds tend to harbour a higher diversity of alien species than the surrounding non-mound areas and invasive alien shrubs spatially aggregate at mounds without individuals occurring in the surrounding open grassland areas (Chapter 2 in this thesis). The experimental results of this study demonstrate that successful germination and survival of alien shrub species are important mechanisms to explain the higher diversity and spatial clumping of alien shrubs at termite mounds. Seed dispersal may also be a contributing factor, but clearly seeds of alien shrub species reaching termite mounds have a higher chance of germinating and growing than seeds dispersed into areas away from mounds.

The enhanced recruitment success of *D. erecta* at mounds is likely to result from higher nutrient concentrations. That mound soils tend to be richer in soil nutrients than non-mound soils has been demonstrated throughout tropical savannas (Wood 1988; Lobry de Bruyn and Conacher 1990; Dangerfield et al. 1998; López-Hernández et al. 2005). Consequently, once seedlings germinate in mound soil, they are more likely to grow fast and survive the subsequent dry seasons than seedlings growing in non-mound soils. Lack of water during the dry season does severely limit seedling survival in tropical savannas, representing a major bottleneck in shrub recruitment (Scholes and Archer 1997; Bond 2008). Environmental conditions that favour reaching a safe plant size become crucial to escape from subsequent drought-induced mortality (Scheffer et al. 2008).

Alien shrubs which establish at mounds are likely to produce more seeds than plants in non-mound soils. For instance, in a protected national park in northern

Patagonia (Argentina), alien plants growing at nutrient-richer dumps created by leaf-cutting ants produce as much as 300 % more seeds than nearby plants growing in non-nest areas (Farji-Brener and Ghermandi 2008). Clearly, if this is also the case with alien shrubs in southern African savannas, a positive feedback mechanism between enhanced recruitment and increased fecundity may result in the spatial clustering of alien woody species at mounds.

Conclusion

To our knowledge, this study provided the first field experimental evidence that termites may enhance the invasion of southern African savannas by constructing mounds with favourable environmental conditions for recruitment of alien shrubs. This contributes towards the understanding of the spatial variation in invasibility of savannas by alien plant species and suggests that environmental heterogeneity created by termites plays a more important role in facilitating alien plant invasions into savannas than previously thought.

Acknowledgments

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Chapter 4

High rainfall accelerates alien shrub encroachment in a Zimbabwean savanna

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Abstract

Understanding the environmental factors governing the spread of alien shrubs is crucial for conserving native biodiversity. In the semi-arid savannas of Africa, alien shrub invasion often occurs simultaneously with native shrub encroachment, but it is currently unknown whether factors affecting native shrub encroachment, especially rainfall, have the same effect on invasive alien shrubs. A combination of historical aerial photographs and field measurements was used to compare the spread of the invasive shrub *Lantana camara* L. with that of native encroaching shrubs over a 31-year period in a protected semi-arid savanna in Zimbabwe (southern Africa). We tested whether the response of this invasive alien shrub to rainfall differs from that of native shrub encroachers. Both the invasive shrub *L. camara* and native encroaching shrubs spread significantly faster during high rainfall years than in dry years. However, the response of *L. camara* to annual rainfall was stronger than the response of native encroaching shrubs. During years of above-average rainfall, the mean annual rate of spread of *L. camara* was at least twice that of native shrub encroachers, whereas in other years natives spread at the same rate as the alien shrub. This is a novel finding suggesting that in water-limited savannas, pulses in rainfall may accelerate the spread of some invasive alien species. Since climate change will likely alter the precipitation patterns of savanna regions, understanding the link between rainfall and the spread of invasive species in savanna ecosystems is important to predict the potential changes in savanna species composition, structure and dynamics.

Key words: invasive, *Lantana camara*, Kyle Game Reserve, patch dynamics, rainfall variability, shrub invasion

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Introduction

Increased shrub abundance has been documented in savannas worldwide. Encroachment by alien shrubs is particularly problematic since it can profoundly alter the structure and functioning of these ecosystems (Archer 1995; Lonsdale 1999; Mack et al. 2000) by modifying fire regimes (Brooks et al. 2004) and nutrient cycling (Ehrenfeld 2003) as well as by accelerating the loss of native species richness (Levine et al. 2003). Surprisingly, little is known about the rates of invasion and the mechanisms causing the spread of invasive alien shrubs across savanna ecosystems (Lonsdale 1993; With 2002; Pyšek et al. 2008). Understanding these key aspects of the invasion process is crucial for managing invasive species and conserving native biodiversity.

Water availability limits plant growth and productivity in savannas (Prins and Loth 1988; Scholes and Archer 1997; Dube and Pickup 2001; Sankaran et al. 2005; Bond 2008). Although average rainfall is low and the pattern of precipitation very variable, large rainfall pulses can trigger massive tree and shrub recruitment (Holmgren and Scheffer 2001; Chesson et al. 2004; Sankaran et al. 2004; Schwinning and Sala 2004). Successful tree and shrub establishment occurs when seedlings grow fast enough to reach a safe size to escape subsequent droughts or 'topkill' by herbivores and fire (Bond and Midgley 2000; Scheffer et al. 2008). Episodic tree and shrub recruitment events caused by rainfall pulses have been observed across semi-arid savannas in Africa (Sankaran et al. 2008), North America (Swetnam et al. 1999; Brown and Wu 2005; Knapp et al. 2008), South America (Holmgren et al. 2006a; Holmgren et al. 2006b), and Australia (Austin and Williams 1988). From these studies, it can be hypothesised that in dry savannas, high rainfall facilitates the spread of invasive alien shrubs.

In semi-arid savannas in Africa, alien shrub invasion often occurs simultaneously with native shrub encroachment (Trollope 1974; Prins and Van der Jeugd 1993; Jeltsch et al. 1997; Shackleton 2000; Roques et al. 2001; Van Gils et al. 2006; Wigley et al. 2009). Understanding whether environmental factors play a similar role in the spread of invasive alien shrubs and native encroaching shrubs may yield insights into alien shrub invasion dynamics, leading to better decisions in invasive species management. It has been hypothesised that successful alien and native plant species respond in a similar manner to fluctuations in resource availability (Thompson

et al. 1995; Daehler 2003; Huston 2004; Meiners 2007). However, since invasive alien plants are probably not hindered by their specialist herbivores, parasites or pathogens, they may respond more strongly to increases in resource availability (Davis et al. 2000; Keane and Crawley 2002; Schumacher et al. 2008; Edward et al. 2009).

We hypothesised that: (1) since rainfall is the main factor limiting plant growth in dry savannas, shrub spread would be significantly higher in wetter periods than drier ones, whether species were indigenous to southern Africa or not; and (2) during high rainfall years, invasive alien shrubs would spread faster because, less hindered by their specialist herbivores, they would suffer less damage. To test these predictions, a combination of historical aerial photographs and field measurements was used to retrospectively quantify and compare the spread of an invasive shrub and native encroaching shrubs during a 31-year period characterised by variable annual rainfall in a protected semi-arid savanna in Zimbabwe. This is the first time that, over a relatively long period of time, the spatio-temporal patterns of spread of invasive and native encroaching shrub species have been quantified in savanna systems and the link with rainfall availability tested. Because climate change will likely alter the precipitation patterns of extensive savanna regions (Hulme et al. 2001; Christensen et al. 2007), understanding the link between rainfall and alien woody species establishment in savanna ecosystems is important to be able to predict spread.

Methods

Study site

The study was conducted in the 44 km^2 Kyle Game Reserve (20° 13′ S, 31° 03′ E). It was proclaimed a nature reserve in 1961 and fenced off, primarily to conserve biodiversity. The climate is sub-tropical, with a mean daily maximum temperature ranging from 21° C in June to 29° C in October. The long-term average annual rainfall is 635 mm (100-year period: 1906-2006, Masvingo weather station) but annual rainfall is variable (Table 4).

The vegetation consists of a mosaic of open savanna grassland, broad-leaved deciduous woodland, and bush thickets. The open grassland is dominated by

Hyparrhenia filipendula (Hochst.) Stapf*, Hyperthelia dissoluta* (Steud.) Clayton, and *Themeda triandra* Forssk., whereas the deciduous woodland is dominated by *Brachystegia spiciformis* Benth. and *Julbernardia globiflora* (Benth.) Troupin*.* Bush thickets are dominated by *Acacia karroo* Hayne, *Dichrostachys cinerea* (L.) Wight & Arn. and *Ziziphus mucronata* Willd. as well as the invasive alien shrub *Lantana camara* L. In the study site, these shrubs typically encroach on open grasslands. The botanical nomenclature follows Oudtshoorn (2006) for grasses and Palgrave (2002) for woody species.

Table 4: Deviation from the long-term mean annual precipitation (635 mm) during the study period (1975 - 2006) at the Kyle Game Reserve, Zimbabwe. Census interval boundaries represent the years in which the aerial photographs used to calculate the changes in the areal extent of encroaching shrubs were made.

census interval (years)	mean annual rainfall (mm)	rainfall deviation (mm)
1975 - 1980	761	126
1980 - 1985	764	119
1985 - 1996	539	-0.71
1996 - 2006	585	-0.50

Since its establishment more than 45 years ago, livestock has been excluded from the reserve and human interference has been minimal. Browsing by giraffe (*Giraffa camelopardalis* L.), kudu (*Tragelaphus strepsiceros* Pallas) and mixed feeders like impala (*Aepyceros melampus* Lichtenstein), forms the main disturbance which may potentially suppress shrub encroachment, but this does not affect *L. camara* because it is poisonous. This protected game reserve provides an ideal case study for testing the effect of rainfall on alien shrub encroachment without the confounding effects of human and livestock disturbance.

Field measurements

A field survey was undertaken in October 2006 to identify monotypic patches of the invasive shrub *L. camara* easily distinguishable on aerial photographs. Each *L. camara*

patch located in the field was assigned a unique number and a total of 24 patches were randomly selected for detailed measurement. Selected patches were evenly distributed over the game reserve. They were checked for spatial autocorrelation and found to be uncorrelated (Moran's test; I value = 0.03, $P > 0.5$). For each selected *L. camara* patch, a reference patch dominated by a mixture of native encroaching shrubs was selected. To ensure that environmental conditions were relatively similar, the reference patches were located at least 30 m but not farther than 60 m from each *L. camara* patch. The direction was randomly selected. At each selected patch, a 30 m x 30 m plot was positioned centrally, yielding a total of 48 plots half of which were dominated by *L. camara* (> 85 % canopy cover), while the other half contained a mixture of native encroaching shrub species, but no *L. camara*.

In this study, a shrub patch was defined as a discrete cluster of vegetation dominated by overlapping canopies of either *L. camara* or a mixture of two or more native shrub species surrounded by herbaceous vegetation (Archer et al. 1988). Native shrub patches contained 5 to 20 woody species, dominated by *A. karroo*, *Acacia rehmanniana* Schinz, *D. cinerea*, *Diospyros lycioides* Desf., *Lippia javanica* (Burm F.) Spreng., and *Z. mucronata*. These shrub species are indigenous to southern Africa, whereas *L. camara* was introduced from South and Central America into southern Africa as an ornamental shrub during the 19th century and has since become invasive (Cronk and Fuller 2001; Henderson 2007).

Patch dynamics

In the field, a global positioning system unit was used to map sample plots as well as the areal extent of shrub patches within plot boundaries. These two maps were used as input to a Geographical Information System (GIS). To monitor and quantify changes in the areal extent of shrub patches, maps of plot boundaries and the patches they contained were overlaid on top of scanned and orthorectified stereo-pairs of black and white aerial photographs obtained for the years 1975 (1: 20 000), 1980 (1: 25 000); 1985 (1: 25 000); and 1996 (1: 40 000) from the Surveyor General's Office (Harare). The Integrated Land and Water Information System GIS software (version 3.5) was used to process aerial photographs and calculate the area covered by each patch.

Annual rate of spread

To convert changes in the areal extent of patches between each census interval into a mean annual rate of spread the following formula was used:

$$mean\ annual\ rate\ of\ spread = \frac{\log A_2 - \log A_1}{t_2 - t_1} \qquad (1)$$

where $\log A_2$ and $\log A_1$ are the natural-logarithm transformed patch sizes at times t_2 and t_1 (in years), respectively. This formula takes into account differences in the relative growth rate of patches attributed to differences in patch size (Archer 1989; Hunt et al. 2002).

Statistical analysis

To assess the effect of rainfall on the rate of spread of shrubs, each census interval was classified as either dry or wet depending on whether the average annual rainfall during that census interval was higher or lower than the long-term mean annual rainfall plus or minus one standard deviation respectively (Table 4).

Repeated measures analysis of variance (ANOVA) was used to test whether rainfall had a significant effect on the rate of shrub spread. Species origin was the between-group factor. Prior to statistical analyses, data on annual rate of spread were tested for normality using the Shapiro-Wilk's test and for homogeneity of variance using the Levene's test of equality of variance and found to satisfy ANOVA assumptions. Following a significant rainfall effect, Tukey's difference tests were performed to detect significant pairwise differences between groups. Statistical analyses were performed using the open source R statistical software version 2.9.0 (R Development Core Team 2009).

Results

Rainfall had a significant positive effect on the rate of spread of shrubs (Fig. 6). During wet periods, both the invasive shrub *L. camara* and native encroaching shrubs spread significantly faster than during dry periods ($F_{3, 44} = 30.2$, $P < 0.01$). However, the response of *L. camara* to rainfall was stronger than that of native encroaching shrubs ($F_{1, 44} = 22.7$, $P < 0.01$). During wet periods (i.e., those of above average annual rainfall), the mean annual rate of spread of *L. camara* was at least twice as high as the rate of spread of native encroaching shrubs (Fig. 6). However, during dry periods (i.e., those of below-average rainfall), natives and the alien shrub spread equally fast. Overall, during this 31-year period, shrub cover consistently expanded into the savanna (Fig. 7).
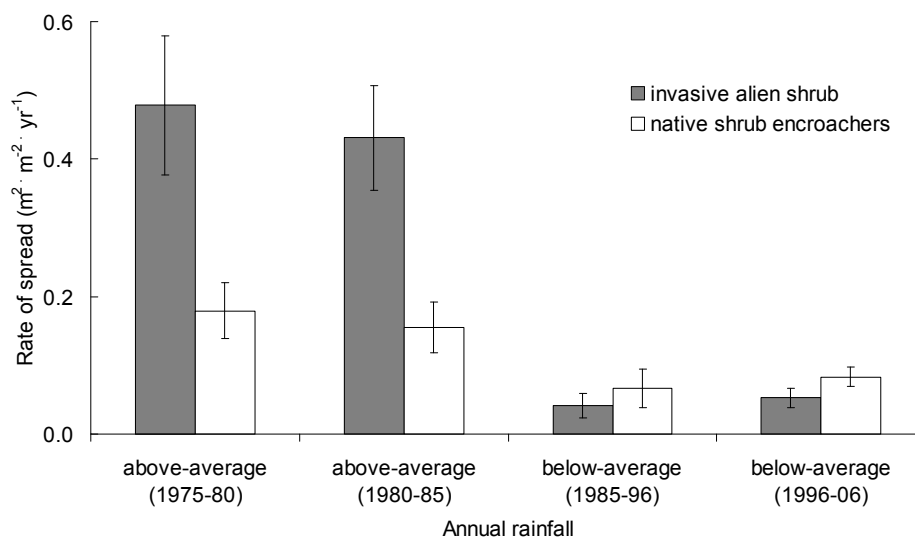
Fig. 6. Effects of annual rainfall on rates of spread of an invasive alien shrub *Lantana camara* (grey bars) and native encroaching shrub species (open bars) during a 31-year study period in the Kyle Game Reserve, Zimbabwe. Bars represent means and the whiskers represent ± 95 % confidence interval ($n = 24$ for each species type).
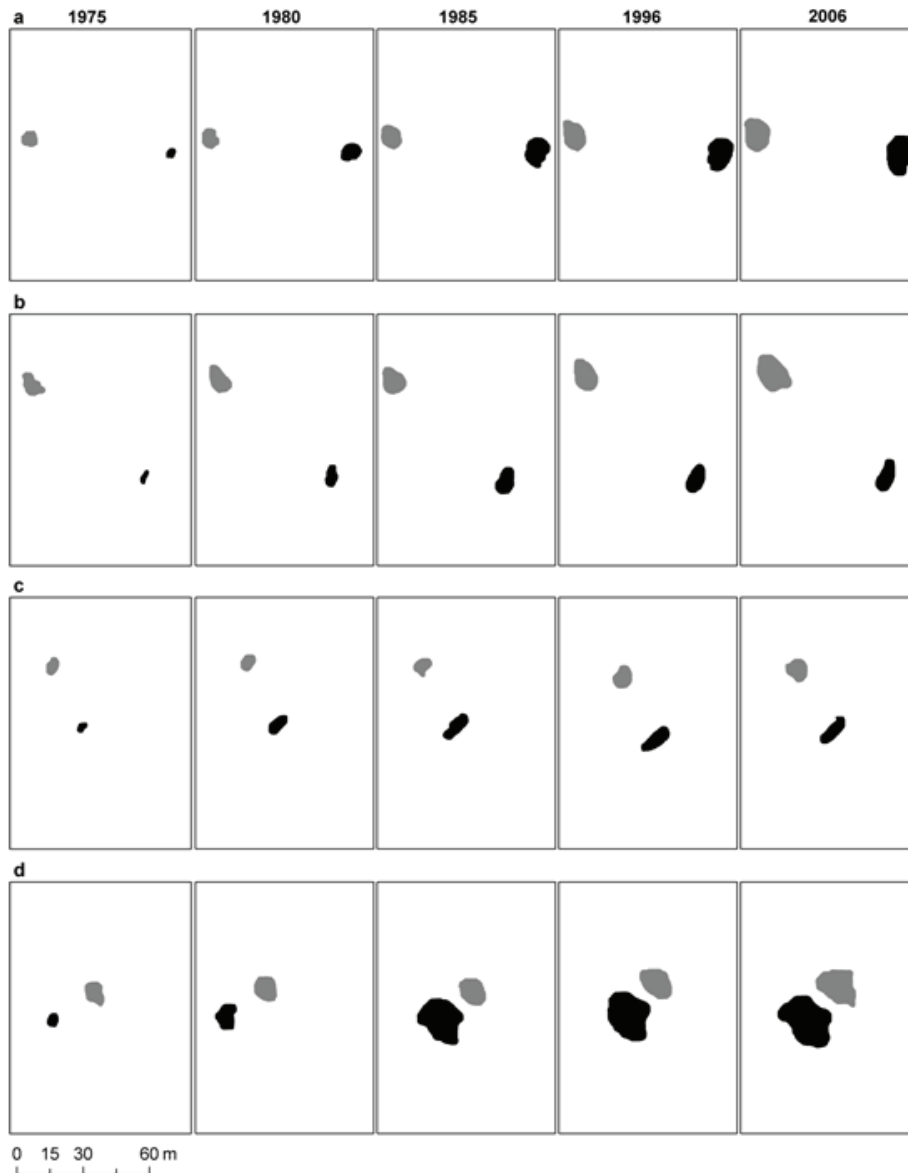
Fig. 7. Spatio-temporal changes in the size of patches dominated by the invasive shrub *Lantana camara* (black) or native encroaching shrub species (grey shading) at four locations (**a** - **d**) in the Kyle Game Reserve, Zimbabwe. Patch size was calculated from digitised aerial photographs for 1975, 1980, 1985, 1996 and from field measurements for 2006.

Discussion

The results of this study reveal that rainfall pulses facilitate shrub encroachment in semi-arid savannas of southern Africa. Shrubs, whether alien or indigenous to southern Africa, spread significantly faster during high rainfall years. This finding is consistent with the hypothesis that rainfall determines shrub recruitment and establishment in dry savannas (Roques et al. 2001; Sankaran et al. 2008) as in other arid and semiarid ecosystems around the world (Asner et al. 2003; Chesson et al. 2004; Holmgren et al. 2006a; Donohue et al. 2009). We found that during years of above-average annual rainfall, the annual rate of spread of the invasive shrub *Lantana camara* averaged at least twice that of native encroaching shrubs whereas in other periods, natives and the alien shrub spread equally fast. This result is inconsistent with the observation in temperate terrestrial systems that alien species and native species had comparable rates of landscape spread (Thompson et al. 1995).

The faster spread of *L. camara* relative to native colonising shrubs during high rainfall years may be attributed to the lack of natural enemies including mammal herbivores (Masocha et al. under review). *Lantana camara* has unique secondary metabolites, such as lantadene A, which are absent in native taxa, rendering it unpalatable to large mammal browsers (Swarbrick et al. 1998; Sharma et al. 2005). In contrast, most native encroaching shrubs, such as *D. cinerea* and *A. Karoo,* do not have an effective chemical defence against browsing by resident herbivores, like kudu and giraffe (Augustine and McNaughton 1998; Bond and Loffell 2001; Hagenah et al. 2009). These herbivores select palatable species in a landscape first (Senft et al. 1987; Augustine and McNaughton 2004), and they could be avoiding *L. camara* and consuming native palatable shrubs by preference. Such selective browsing may favour *L. camara* growth and facilitate its fast spread, while suppressing the growth and reducing the spread of native palatable species.

Understanding how rainfall variability affects the spread of invasive alien shrubs in savannas is critical for predicting and ultimately controlling this spread. As shown here, in high rainfall years, the annual rate of spread of the invasive shrub *L. camara* averaged at least twice that of native shrub encroachers. This finding sheds light on the dynamics of alien shrub invasion in protected semi-arid savannas and suggests

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that accelerated spread triggered by rainfall pulses explains why some invasive aliens become widespread and locally dominant in these water-limited systems. Predicted changes in precipitation patterns induced by global and regional climate changes will likely change the species composition and structure of extensive savanna regions.

Acknowledgments

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Chapter 5

Frequent burning promotes invasions of alien plants into a mesic savanna

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Abstract

Fire is a key disturbance factor, influencing vegetation dynamics and ecosystem functioning in mesic savannas. Without disturbances such as fire or grazing, tree cover can increase at the expense of grass cover and dominate mesic savannas. Consequently, repeated burning is widely used to suppress tree recruitment and control bush encroachment. However, the effect of regular burning on invasion by alien plant species is little understood. Here, vegetation data from a long-term fire experiment, which began in 1953 in a mesic Zimbabwean savanna, were used to test whether the frequency of burning promoted alien plant invasion. The fire treatments consisted of late season fires, lit at 1-, 2-, 3-, and 4-year intervals, and these burnt areas were compared with unburnt areas. Results show that alien plant species accounted for a significantly higher proportion of vascular plant species richness in regularly burnt plots compared with unburnt (control) plots. The proportion of alien plant species was highest in the annually burnt plots, followed by plots burnt biennially, triennially, and quadrennially. Plots protected from fire contained the lowest proportion of alien invaders. Moreover, alien forbs occurred more frequently in regularly burnt plots than in the unburnt control plots and their abundance increased as the intervals between fires became shorter. All together, these results suggest that frequent burning of a mesic savanna enhances invasion by alien plants, with short intervals between fires favouring alien forbs. Therefore, reducing the frequency of burning may be a key to minimising the risk of invasion, which is important because invasive plants are known to threaten native biodiversity and alter ecosystem functions.

Key words: exotic forbs, fire, Grasslands Research Station, long-term experiment, Zimbabwe

Introduction

Fire is one of the major factors controlling vegetation structure, composition, and dynamics as well as ecosystem functioning in humid African savannas (Scholes and Archer 1997; Bond et al. 2005; Savadogo et al. 2008). Without disturbances such as fire or grazing, tree cover can increase at the expense of grass cover and dominate these mesic savannas (Van Langevelde et al. 2003; Sankaran et al. 2005). Because tree-grass coexistence is essential for savanna functioning, managers of these savannas use fire to control bush encroachment (Jeltsch et al. 2000; Govender et al. 2006). The use of fire to manage savannas is justified by managers on the grounds that most savanna vegetation evolved in the presence of fire and is thus adapted to, or tolerant of, fire (Bond and Midgley 2001; Andersen et al. 2005). However, despite decades of research, there is still uncertainty and disagreement among ecologists regarding the appropriate fire regimes natural resource managers should employ to manage savannas (Trollope 1974; O' Connor 1985; Bond et al. 2003; Van Wilgen et al. 2004; Archibald et al. 2009).

For example, based on current understanding of the relationship between fire intensity, its frequency and tree mortality, some ecologists recommend regular burning during the dry season to limit tree recruitment and control bush encroachment (Trollope 1974; Roques et al. 2001). Other fire ecologists, however, suggest that the imposition of regular fires of similar intensity can lead to the dominance of grasses. Hence these ecologists recommend fires of variable intensities, and they further stress that flexible burning is required to promote tree-grass coexistence (Higgins et al. 2000; Bond and Archibald 2003). At present, regular burning remains the most popular tool for managing savannas, despite the fact that the effects of fire frequency on species composition are little understood. Frequent fires in savanna ecosystems may promote invasion by non-indigenous (alien) species, since disturbance is known to increase the invasibility of plant communities (Hobbs and Huenneke 1992; Valery et al. 2008). Yet, this issue remains poorly addressed in fire ecology studies.

Empirical evidence suggests that in savannas, different fire regimes promote particular traits in plants (Bond and Keeley 2005; Watson et al. 2009). For example, 'ruderalism', that is, the specialisation associated with a short life cycle and high seed production (Grime 1977), and having pole-like stems are important traits, enabling

plants to establish and persist in frequently burnt savannas. These traits are known to facilitate rapid colonisation (Lavorel et al. 1997; Hayes and Barry 2008) and bolting towards a height that is out of reach of surface fires before the next burn (Bond and Keeley 2005).

The purpose of this study is to test the hypotheses that frequent burning favours ruderal alien species and that short intervals between fires select for alien species with a short life history. To test these hypotheses, vegetation data from a long-term fire experiment, which began in 1953 at a mesic Zimbabwean savanna site, were used. The fire treatments applied were annual, biennial, triennial, and quadrennial burning late in the dry season, and these treatments were compared with an unburnt control. This burning experiment was designed to assess the effects of fire on tree growth and dominance, but may shed light on the impact of fire on alien plant invasion, going beyond the original scope of the study, because the treatments have been applied for a more than 50 years.

Methods

Study site

The study was conducted at the Grassland Research Station (18° 65′ S, 31° 15′ E; altitude 1,630 m), located 8 km west of Marondera town (see Fig. 1) and about 55 km southeast of Harare in Zimbabwe. The climate is seasonal with most of the precipitation, averaging 885 mm per year, falling between mid-October and mid-April. Mean monthly temperatures range from 12.3° C in June to 19.7° C in October (Grundy et al. 1994). The soils are coarse-textured sandy loams derived from granite (Barnes 1965). The vegetation is deciduous savanna woodland with *Brachystegia spiciformis* and *Julbernardia globiflora* as the dominant trees. The herbaceous layer is variable in composition, but the dominant grasses are *Hyparrhenia filipendula*, *Melinis minutiflora*, and *Heteropogon contortus*. Botanical nomenclature follows Palgrave (2002) for woody species and Oudtshoorn (2006) for grasses.

Experimental design

In 1953, experimental burning began at the Grassland Research Station to investigate the effectiveness of fire as a management tool for controlling coppice regrowth of the woody vegetation (Barnes 1965). Before the start of the experiment, all the woody vegetation was cut to ground level. A total of 22 experimental plots each measuring 36 m x 60 m were then established. A 3 m wide firebreak was established around each plot and livestock grazing was excluded. The main treatment was burning with late season fires lit at 1-, 2-, 3-, and 4-year intervals, to be compared with no burning (control). Treatment plots were subdivided into two equal parts (each 18 m x 60 m) and given two sub-plot treatments, namely burning after cutting woody growth to ground level (slashing), and burning without preliminary slashing. The effects of slashing before burning were not considered in this study. The different treatments were replicated as follows: burning once every four years was replicated eight times; burning once every three years six times; burning once every two years four times; burning once every year and the unburnt control twice each. Replication was biased in favour of treatments with longer intervals between fires to ensure that for each fire frequency at least one plot was burnt every year. Further details about the history of the experiment and its design can be found in Strang (1974) and Furley et al. (2008).

Vegetation sampling

In 2007 during the growing season, vascular plant species composition was recorded along two diagonal transects (50 m in length and 5 m in width) established in each experimental plot. For each species, the number of individuals was counted and averaged. National vegetation checklists and regional floras were used to classify plant species identified in the experimental plots as natives or aliens (i.e., those species not indigenous to southern Africa). The proportion of aliens was calculated as the number of alien plant species present in a plot divided by the total number of plant species present in that plot.

Statistical analysis

One-way analysis of variance (ANOVA) was used to test whether the frequency of fire had a significant effect on the proportion of alien species and the abundance of common alien forbs. Prior to performing ANOVA, data on the proportion of alien species were arcsine-transformed to normalise them and to correct for skewness in the distribution arising from the fact that the data were constrained to values between 0 and 1. Frequency data were normalised using a logarithm transformation prior to performing ANOVA. Following a significant fire treatment effect, Tukey's difference tests were performed to detect significant pairwise differences between groups. All tests were carried out in Statistica version 7.0 (StatSoft, Inc.).

Results

Plant species richness and identity of alien invaders

A total of 110 vascular plant species were identified in the experimental plots, nine of which were alien species having invaded the experimental plots. The alien species consisted of two woody species (*Lantana camara* and *Jacaranda mimosifolia*) and seven forbs (namely *Aster squamatus*, *Bidens pilosa*, *Conyza bonariensis*, *Desmodium uncinatum*, *Richardia brasiliensis*, *Sida cordifolia*, and *Tagetes minuta*).

Effects of fire frequency on alien plant invasion

The frequency of burning had a profound effect on the proportion of alien species ($F_{4, 12}$ = 7.65, $P < 0.01$). Alien species accounted for a significantly higher proportion of plant species richness in regularly burnt plots than in the unburnt control plots (Fig. 8). In the burnt plots, the proportion of alien species was highest in the annually burnt plots and lowest in plots burnt quadrennially, but did not differ between plots burnt either biennially or triennially.

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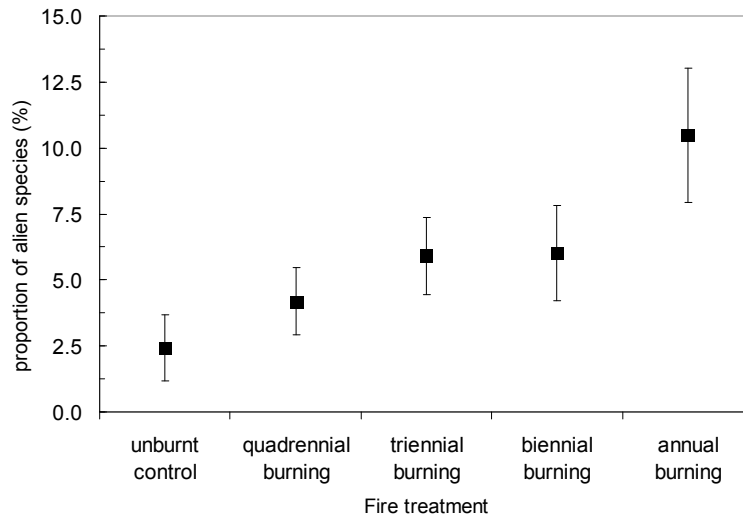
Fig. 8. Effect of fire on alien plant invasion at a humid savanna experimental site (Grasslands Research Station, Zimbabwe). Black squares indicate the mean proportion of alien species, and whiskers represent the 95 % confidence intervals per treatment. Data for the proportion of alien species were normalised using an arcsine transformation during statistical analysis, but are presented here as percentages to make comparisons between treatments easier.

Effects of frequency of burning on the abundance of alien forbs

Fire frequency also had a significant effect on the abundance of common alien forbs. These forbs occurred more frequently in burnt plots than in the unburnt control plots and their abundance increased as the interval (in years) between fires became shorter (Fig. 9). On average, the frequency of occurrence of these forbs in the annually burnt plots was at least twice as high as the frequency in plots protected from fire.
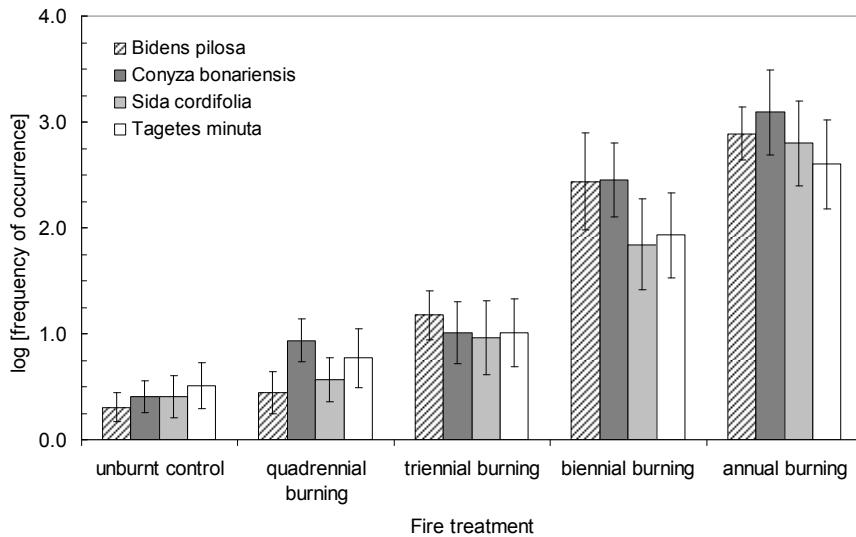
Fig. 9. Response of four common alien forbs to the frequency of burning at a mesic savanna experimental site (Grasslands Research Station, Zimbabwe). Bars represent means and whiskers represent 95 % confidence intervals for: *Bidens pilosa* (hatched); *Conyza bonariensis* (dark grey); *Sida cordifolia* (light grey); and *Tagetes minuta* (white).

Discussion

Data from this long-term fire experiment suggest that frequent burning of mesic savannas enhances the invasion by alien plants. Two lines of evidence were presented in support of this hypothesis. Firstly, the proportion of alien plant species relative to the total species richness was significantly higher in regularly burnt plots than in the unburnt control plots, with plots that were burnt annually containing the highest proportion of alien species followed by those burnt either biennially or triennially. Plots protected from fire had the lowest proportion of alien invaders. Secondly, alien forbs occurred more frequently in regularly burnt plots than in those protected from fire, and their abundance increased as intervals (in years) between fires shortened. All together, these differences in the proportion of alien species and abundance of alien forbs between frequently burnt plots and the unburnt control plots suggest that, in savannas, frequent burning is a key disturbance providing opportunities for alien species to invade.

Previous results published on this fire experiment showed that regular burning had a significant effect on vegetation structure. It reduced tree height growth regardless of the frequency of burning, but failed to eliminate woody plants, or significantly alter tree species diversity at the experimental site (Strang 1974; Furley et al. 2008). These results are in line with results from another long-term fire experiment in the Kruger National Park of South Africa (Govender et al. 2006). In Australian savannas, Lonsdale and Braithwaite (1991) also found that different fire regimes resulted in negligible changes in tree composition, because fires were generally of low intensity there. However, so far, the effect of the frequency of fire on alien plant invasions had not been evaluated. Thus, the present study shed light on the role of fire in facilitating alien plant invasion in savannas.

The fact that, compared to other treatments, the largest differences in the proportion of alien plant species, and the frequency of occurrence of alien forbs, were between the annually burnt plots and the unburnt control plots, raises the question: "Which mechanisms explain the consistent increase in the abundance of alien plant species as fire return intervals were shortened?". Short intervals between fires may create vacant niches, thus favouring alien species which can tolerate a wider range of fire frequency than dominant grasses (Uys et al. 2004). Further, by killing or damaging dominant grass species, frequent fires may prevent their competitive dominance, thereby creating niche opportunities for aliens (Huston 1993; Shea and Chesson 2002; Alpert 2006; Barney and Whitlow 2008; MacDougall et al. 2009). Frequent fires can also create gaps in a plant assemblage suitable for colonisation by alien species, particularly those with a relatively short life cycle (Sousa 1984). Thus, reduced competition from dominant native species may act in concert with increased availability of empty niches to enhance the invadibility of a frequently burnt savanna. This is consistent with ecological theory, which predicts that frequent disturbances favour ruderal annuals and short-lived perennials (Grime 1977; Lavorel et al. 1997).

Conclusion

This study has shown that fire can have profound effects on the invasion of a humid savanna by alien plant species. Data from this rare long-term fire experiment lead to the

conclusion that frequent burning of mesic savannas increases the invasion by alien plants, with short intervals between fires favouring alien forbs with a short life cycle. Reducing the frequency of burning may be necessary to minimise the risk of invasion, since alien species pose a threat to native biodiversity. In the past, research on alien plant invasion in savannas focused mostly on invaders with a long life span, ignoring the less conspicuous forbs. This has tended to limit our understanding of the effects of fire on alien plant invasion in savanna ecosystems.

Acknowledgments

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Chapter 6

Anthropogenic disturbance increases the level of plant invasion in African savannas

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Abstract

Understanding the mechanisms driving plant invasions is a widely recognised priority for the development of successful strategies for controlling invasive species and conserving biodiversity. African savannas are a unique biome, harbouring the largest diversity of mammal herbivores on the planet and supporting more than half of the African human population. Nevertheless, the mechanisms explaining the increasing plant invasion in these ecosystems are practically unknown. Here, a combination of field studies and remote sensing was used to assess the impact of anthropogenic disturbance on plant invasions in savannas with contrasting disturbance regimes in Zimbabwe, namely Kyle Game Reserve (a protected savanna) and Mutirikwi communal area (a human-disturbed savanna). To test whether the proportion of alien species relative to the total plant species richness differed between the human-disturbed and protected savannas, all vascular plant species occurring in randomly selected plots were recorded. Furthermore, the cover of the most widespread invasive species in southern Africa, *Lantana camara* L., was successfully mapped using a novel hybrid neural network plus expert system classifier. This pioneering method can be applied to assess the extent of plant invasions on a large spatial scale through satellite imagery. The results showed that alien taxa represented a significantly higher proportion of the total species richness in the human-disturbed savanna than in the protected savanna. This result was confirmed, when taxonomically closely related species were compared. While alien plant species associated positively with the human-disturbed savanna and negatively with the protected one, their native confamilial species exhibited a positive association with the protected savanna, and a negative association with the human-disturbed savanna. The most abundant alien species, *L. camara,* covered a significantly higher proportion of the human-disturbed savanna than of the protected savanna. These results suggest that anthropogenic disturbance enhances the susceptibility of savannas to invasion, and imply that managing disturbance may be the key to reducing plant invasions and conserving biodiversity in savanna ecosystems.

Key words: agriculture, alien plant, biodiversity, exotic herbivore, *Lantana camara*, livestock, Zimbabwe

Introduction

Invasive alien plant species have profound adverse effects on biodiversity, structure and functioning of ecosystems (Mooney 1999; Chapin et al. 2000; Mack et al. 2000; Cronk and Fuller 2001). Understanding the mechanisms, which explain variations in habitat invasibility within and across ecosystems, is a widely recognised priority for the development of successful strategies for managing invasive species and conserving global biodiversity (Ewel et al. 1999; Huston 2004; Blumenthal 2005).

Many alien species seem to owe their invasive success to changes in disturbance regimes, caused by human activity (Crawley 1987; Hobbs and Huenneke 1992; D'Antonio et al. 1999; Mack et al. 2000). Both empirical and experimental evidence from a wide range of terrestrial biomes suggests that the level of invasion tends to increase with human disturbance (Baker 1986; Duggin and Gentle 1998; Chytrý et al. 2008a). One proposed explanation is that disturbance favours invasion, as it creates gaps and reduces competition from native species (Davis et al. 2000). Disturbance may also assist invasion by causing a reduction in resource uptake by native species, thereby increasing the availability of limited resources, such as nutrients, to invaders (Sher and Hyatt 1999; Davis and Pelsor 2001; Shea and Chesson 2002).

In well-studied regions of Europe and North America, comparisons between the levels of invasion in disturbed and undisturbed habitats generally confirm that disturbed habitats tend to contain a higher proportion of exotic species (Stohlgren et al. 1999; Cadotte et al. 2006; Vilà et al. 2007; Chytrý et al. 2008b). However, generalising and projecting this conclusion onto other regions, with a different climate, land use history, or species pool, is risky (Chytrý et al. 2008b). Indeed, the role of disturbance in plant invasion remains controversial with some studies showing no effect at all (Fornwalt et al. 2003). Current knowledge of the processes determining plant invasion in African savanna ecosystems is notoriously poor (Lonsdale 1999; Pyšek et al. 2008). African savannas form a unique biome, harbouring the largest diversity of mammal herbivores on the planet (Scholes and Archer 1997; Sankaran et al. 2005), yet the mechanisms responsible for the increase in plant invasion experienced in these ecosystems are practically unknown (Lonsdale 1999).

This study tests the hypothesis that the level of invasion (i.e., the proportion of alien taxa and their dominance) in savannas increases with anthropogenic disturbance. We tested this hypothesis at different spatial scales in two adjacent savanna landscapes of southern Zimbabwe with contrasting disturbance regimes. In randomly selected field plots, we recorded all vascular plant species and calculated the proportion of alien species relative to the total plant species richness. Alien plant species numbers were also compared to the numbers of their native confamilial species to determine whether the frequency of their occurrence differed significantly between the human-disturbed and the protected savannas. For both study areas, the cover of *Lantana camara* L., the most widespread invasive shrub species in southern Africa (Henderson 2007), was mapped from satellite imagery, using a novel hybrid neural network plus expert system classifier to test whether alien shrub dominance was significantly higher in human-disturbed than in protected savannas. Mapping the cover of invasive species across landscapes is of great relevance to resource managers, as cover is directly related to ecological impact (Hejda and Pyšek 2008). Thus, accurate estimates of the spatial extent of invasion may help land managers to prioritise resource allocation in their struggle against invasive species.

Methods

Study sites

The study was conducted in the 44 km^2 Kyle Game Reserve and the adjacent 344 km^2 Mutirikwi communal area (Fig. 1). The study sites are located between latitudes 20° 06′ and 20° 20′ south and longitudes 30° 58′ and 31° 08′ east in southern Zimbabwe. Lake Mutirikwi separates the study sites. Annual rainfall is low and erratic, with a mean of 635 mm (Vincent and Thomas 1960). The rainy season is relatively short, extending from November to March, while the dry season (April-October) is prolonged.

Soils are predominantly coarse-textured sandy soils of low nutrient status, derived from granite (Nyamapfene 1991). The vegetation consists of a mosaic of broad-leaved deciduous woodland, bushland, and open savanna grassland (Vincent and Thomas 1960). *Brachystegia spiciformis* Benth. and *Julbernardia globiflora* (Benth.)

Troupin form the dominant canopy species in the broad-leaved woodland, whereas the bushland is dominated by *Dodonaea viscosa* Jacq., *Dichrostachys cinerea* (L.) Wight & Arn., and *L. camara*. Perennial grasses, such as *Hyparrhenia filipendula* (Hochst.) Stapf and *Hyperthelia dissoluta* (Steud.) Clayton, dominate the open grassland areas. The nomenclature for woody species and grasses corresponds with authorities in Palgrave (2002) and Oudtshoorn (2000), respectively.

Although the study sites border onto each other, they have contrasting land management practices and disturbance regimes. The Kyle Game Reserve is a relatively pristine, protected savanna. It was fenced in 1961 to protect biological diversity. Since then, human interference has been minimal. In contrast, the communal area is a fragmented and degraded agricultural landscape with a history of over 150 years of continuous human settlement (Whitlow 1988; Masocha and Kariaga 2001). The estimated total human population in the communal area is 14,923, with an average density of 45 people per km^2 (CSO 2004). Subsistence farming and continuous grazing by introduced domestic herbivores, such as cattle, goats and sheep, form the main disturbances. Cattle density is approximately 11 heads per km^2 (Chenje et al. 1998). Arable farming and vegetable gardening are both practised mainly along the perennial rivers. From here onwards, the Kyle Game Reserve will be referred to as the protected savanna, and the communal area as the human-disturbed savanna.

Floristic inventories

All vascular plants occurring in the 65 (20 m x 20 m) randomly selected plots were identified at species level and recorded during the growing season in March 2008. Thirty five plots were located in the protected savanna while the remainder were situated in the adjacent, human-disturbed savanna landscape. In both landscapes, plots were selected in a stratified random fashion. The strata identified were broad-leaved woodland, bushland, and open grassland.

Plant specimens and records kept at the National Herbarium and Botanical Garden in Harare (Zimbabwe), as well as vegetation checklists and regional floras, were used to determine whether the plant species identified in the field plots were native or alien to southern Africa. Plant species were considered alien, if they were not

indigenous to southern Africa and introduced either deliberately or unintentionally by humans (Chytrý et al. 2008a). The relative richness of aliens was calculated as the number of alien plant species divided by the total number of plant species present in a plot. The proportion of alien species was used as a direct measure of the level of habitat invasion, because it is easy to measure and not affected by other confounding factors, such as propagule pressure (Chytrý et al. 2008a).

In order to compare whether the frequency of occurrence of alien species in the human-disturbed and protected savannas differed from that of native confamilial species, information on phylogeny was extracted from national and regional floras (Chapano 2002; Palgrave 2002; Mapaura and Timberlake 2004; Henderson 2007). The species native to the region represented 'control' species in the comparisons, as recommended by previous studies (Cadotte et al. 2006; Pyšek and Richardson 2007).

Mapping the cover of invasive Lantana camara

In another test to ascertain whether invasive species were more dominant in human-disturbed than in protected savannas, the cover of the most widely distributed invasive species in southern Africa, *Lantana camara* (Henderson 2007), was mapped using supervised classification of satellite imagery. To facilitate image classification, presence/absence, number of stems and cover of *L. camara* were recorded for 187 (30 m x 30 m) field plots. Field data were divided into three *Lantana* cover classes, namely absent (0 % cover), low (1-50 % cover), and high (> 50 % cover). The high cover class corresponded with more than 1,000 stems per 900 m^2 and indicated that *L. camara* was the dominant species in that plot. The data set was split into a training set ($n = 90$) and a testing set ($n = 97$).

To map the cover of *L. camara,* cloud free Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) imagery of October 22, 2006, was obtained. Three spectral bands (1, 2, and 3) in the visible and near-infrared range (0.52 - 0.86 μm), with a 15 m spatial resolution, were corrected for geometric distortions using 15 ground control points (Abrams 2000). The ground control points were evenly spread across the study area at points with features, obvious on both the image and in the field, such as road intersections and river bifurcations. Each ground control point had its field

location measured using the global positioning system. The image was re-sampled to a Universal Transverse Mercator coordinate system (zone 36 South), using the nearest neighbour interpolation technique. A root mean square error of 0.4 of a pixel was achieved. The ASTER image used provided the most recent data set available at the time field work was undertaken.

Neural network classification

A three-layer feed-forward and error-back propagation artificial neural network was used to map *Lantana* cover from the ASTER image (Atkinson and Tatnall 1997; Skidmore et al. 1997). The neural network was presented with three ASTER bands and trained using 30 training samples for each of the three cover classes of *L. camara*. The training phase involved empirically establishing the best combination of optimum learning rate and momentum to yield the lowest root mean square error (RMSE) between the observed and the predicted cover (Skidmore et al. 1997). The optimal results were achieved with a learning rate of 0.2, a training momentum of 0.7, and one hidden layer. The RMSE stabilised after 15,000 epochs. In total, 30 classifications each consisting of 15,000 epochs were performed, and the classification with the lowest RMSE was selected. The neural network yielded a thematic cover map and a rule image with three bands. Each band in the rule image represented the probability that a pixel belonged to one of the three cover classes of *L. camara*. The neural network algorithm was programmed using the Interactive Data Language (IDL; Research Systems Inc.).

Hybrid neural network plus expert system

The image classification by the neural network was based entirely on the spectral signatures of the training samples. Consequently, due to the environmental heterogeneity and the complexity of the vegetation cover, some pixels became misclassified (Lu and Weng 2007). In order to further improve classification, the cover map and the associated rule image produced by the neural network were input into an expert system. These input layers together with two ancillary Geographical Information

System (GIS) layers (i.e., habitat type and terrain position) were used to infer the most probable cover of *L. camara* occurring at each grid location.

Habitat types (see Table 5) were distinguished from an ASTER image (obtained on the 22nd of October 2006) using the support vector machine algorithm (Sanchez-Hernandeza et al. 2007). A digital elevation model (DEM) with a grid resolution of 30 m was used to deduce terrain position. Using the algorithm developed by Skidmore (1990), each grid cell in the DEM into was classified into one of five terrain classes, namely gully, lower midslope, midslope, upper midslope, and ridge. The terrain position raster map was resampled to a 15 m grid size, using nearest neighbour interpolation to match the spatial resolution of the ASTER image.

A spreadsheet containing the rules (Table 5) was accessed by the expert system. The rules represented conditional probabilities that an item of evidence (for example a gully) was present, for instance, when it was known that the cover of *L. camara* at a location was high. Thus, the rules provided the direct link between *a priori* knowledge about the distribution of *L. camara* and the ancillary GIS layers used to predict its cover (Skidmore 1989). Field data in combination with literature on *L. camara* ecology (Gentle and Duggin 1997; Day et al. 2003; Foxcroft and Richardson 2003) were used to derive these rules, from which the expert system inferred the probable *L. camara* cover.

Using Bayes' theorem, the expert system inferred the most probable cover of *L. camara* to occur at each grid cell location, given a certain item of evidence (e.g., a gully) being present at that location, as follows:

$$P(H_a / E_b) = \frac{P(E_b / H_a) P(H_a)}{P(E_b)} \qquad (1)$$

where $P(E_b/H_a)$ is the conditional probability that any grid cell location has an item of evidence (E_b) given H_a (e.g., that the cover of *L. camara* at that grid cell location is high); and $P(H_a)$ is the prior probability of the cover of *L. camara* at grid cell location. The probability of the evidence $P(E_b)$ was calculated as:

$$P(E_b) = \sum_{a=1}^{n} P(E_b / H_a) P(H_a) \qquad (2)$$

where a = 1…*n* represent the cover classes of *L. camara*, and the other notations are as defined above.

Table 5: Rules used to predict the cover of the invasive shrub *Lantana camara* from a GIS database in the Kyle Game Reserve and the adjacent Mutirikwi communal area, Zimbabwe.

Item of evidence (habitat type & terrain position)	*Lantana camara* cover		
	high	low	absent
surface standing water	0.1	0.1	0.9
dense broad-leaved woodland	0.20	0.40	0.5
sparse broad-leaved woodland	0.4	0.6	0.4
bush thicket	0.7	0.6	0.4
sparse bushland	0.2	0.4	0.4
dry open grassland	0.1	0.2	0.7
seasonally-wet grassland	0.1	0.2	0.5
bare soil	0.1	0.2	0.6
cliffs/rock outcrop	0.1	0.2	0.7
gully	0.6	0.6	0.4
lower midslope	0.4	0.4	0.4
midslope	0.2	0.2	0.4
upper midslope	0.1	0.3	0.6
ridge	0.1	0.2	0.8

The inference worked forward from the data (items of evidence) to the hypothesis (the most probable cover of *L. camara*) and the search was terminated only after all the evidence had been evaluated (Skidmore et al. 1996). The cover class, which had the highest posterior probability of occurring at grid cell location, was assigned to that grid cell location. To calculate the proportion of each study site covered by *L. camara* and evaluate classification accuracy, the cover map generated by the hybrid neural network plus expert system was exported to the ENVI 4.3 software package (ITT Visual Information Solutions).

Accuracy assessment

To assess map accuracy, the overall accuracy and Kappa coefficient were calculated from an independent test data set. The overall accuracy is the ratio of the sum of correctly classified pixels in each class to the total number of pixels tested. The Kappa coefficient, which ranges from 0 to 1, measures the level of agreement between the classified map and the ground truth data (Congalton 1991; Skidmore 1999). A Kappa value of one indicates perfect agreement, whereas a value of zero indicates total disagreement between ground truth data and the classification result (Congalton 1991).

Statistical analysis

A two sample *t*-test was used to test whether the mean proportion of alien species differed significantly between the human-disturbed and the protected savannas. The proportion of alien species was transformed using a square-root, in order to comply with the assumption of normality for the *t*-test. The Wilcoxon matched pairs test was used to test for significant differences in the frequency of occurrence of alien species, common to both the human-disturbed and protected savannas. In order to test whether alien plants as well as their native confamilial species were significantly associated with the human-disturbed savanna, the Pearson's chi-square (χ^2) test was used. This test was restricted to species for which the observed frequency of occurrence was five or greater (Crawley 2002). Finally, the *Z*-test was used to determine whether the proportion of the savannas invaded by *L. camara* differed significantly between the human-disturbed and the protected savannas. All statistical analyses were performed using Statistica version 7.0 (StatSoft, Inc.).

Results

Variation in the level of invasion

A total of 355 vascular plant species, belonging to 80 families, were found. Of these, 22 species (6 % of the total species pool) were alien taxa. Alien plant species represented a

significantly higher proportion of the total species richness in the human-disturbed savanna than in the protected savanna ($t = 3.13$, d.f. $= 63$; $P < 0.01$; Fig. 10). Fourteen alien plant species were common to both the human-disturbed and the protected savannas. However, results of the Wilcoxon matched pairs test show that these common alien species occurred more frequently in the human-disturbed savanna than in the protected savanna ($Z = 2.39$; $P < 0.05$).
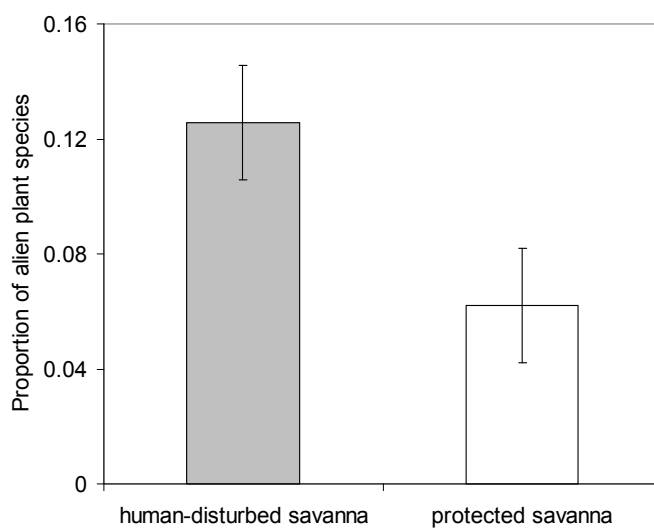
Fig. 10. Proportion of alien plant species (mean ± SE) in the human-disturbed savanna (Mutirikwi communal area) and the adjacent protected savanna (Kyle Game Reserve), Zimbabwe.

Contrasting effects of disturbance on alien and native confamilial species

Table 6 presents the observed frequencies of occurrence of four alien species versus their native confamilial species in the human-disturbed savanna and the protected savanna. Results of χ^2 tests show that, alien species had a significant positive association with the human-disturbed savanna, whereas their association with the protected savanna was negative ($P < 0.05$; Table 6). By contrast, their native confamilial species were positively associated with the protected savanna, whereas their association with the human-disturbed savanna was negative ($P < 0.01$; Table 6).

Table 6: Frequencies of occurrence of alien and native confamilial species in the human-disturbed savanna (Mutirikwi communal area) and the protected savanna (the Kyle Game Reserve), Zimbabwe (* = significant positive association; underlined values represent significant negative association; $P < 0.01$).

Family	species	status	human-disturbed savanna	protected savanna
Asteraceae	*Acanthospermum australe*	alien herb	14*	5
	Bidens pilosa	alien herb	11*	5
	Dicoma kirkii	native herb	5	9*
	Nidorella resedifolia	native herb	5	12*
$\chi^2 = 10.3$; $P < 0.01$				
Rubiaceae	*Richardia scabra*	alien herb	18*	7
	Agathisanthemum bojeri	native herb	5	13*
$\chi^2 = 9.4$; $P < 0.01$				
Verbenaceae	*Lantana camara*	alien shrub	27*	11
	Lippia javanica	native shrub	13	29*
$\chi^2 = 12.8$; $P < 0.01$				

Spatial patterns of Lantana camara invasion

Fig. 11 presents the *L. camara* cover map produced by the hybrid neural network plus expert system classifier. This map has an overall accuracy of 87 % and Kappa of 0.80 and clearly shows that *L. camara* was more widely distributed in the human-disturbed savanna, with denser and more extensive clusters along perennial rivers. From this cover map (Fig. 11), the area invaded by *L. camara* was calculated separately for each study site and cover class to allow Z-tests to be performed.
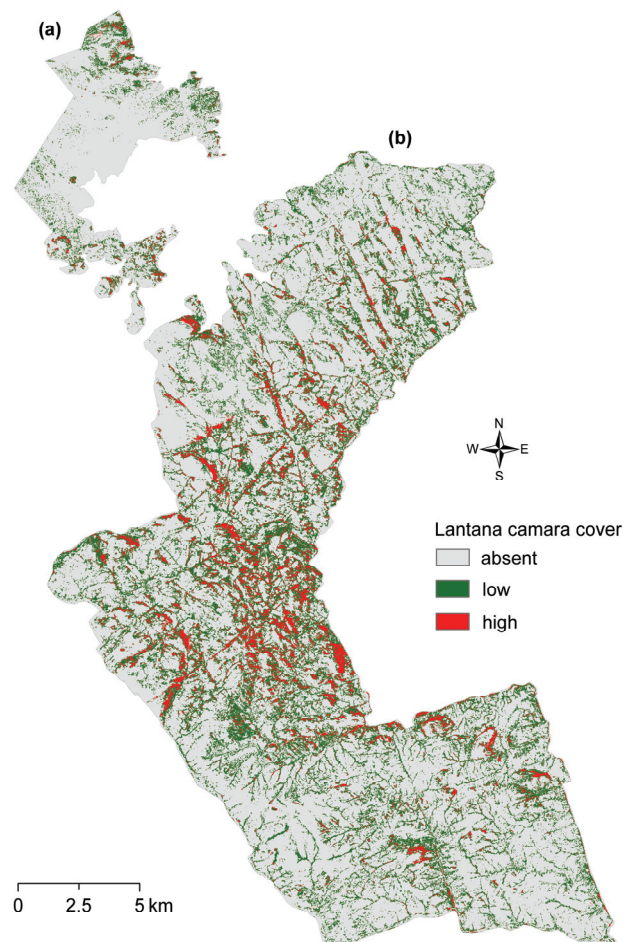
Fig. 11. Distribution and abundance of the invasive alien shrub *Lantana camara* in (a) the Kyle Game Reserve (a protected savanna) and (b) the adjacent Mutirikwi communal area (a human-disturbed savanna), Zimbabwe. Red represents high *L. camara* cover (>50 %), green represents low *L. camara* cover (1-50 %) while areas not yet invaded by *L. camara* are grey.

Results of the Z-test confirmed that the area covered by *L. camara* differed significantly between the two study sites (Table 7). A quarter of the human-disturbed savanna had been invaded by *L. camara*, whereas of the protected savanna 15 % had been invaded; the difference is significant ($P < 0.01$; Table 7). Furthermore, 4 % of the

human-disturbed savanna was now dominated by *L. camara*, versus 1 % of the protected savanna. This difference is also significant ($P < 0.01$; Table 7).

Table 7: Estimates of the proportion of the human-disturbed savanna (Mutirikwi communal area) and the protected savanna (the Kyle Game Reserve) covered by the invasive alien shrub *Lantana camara,* in hectares (ha) and as a percentage of the total area. Note, high cover indicates that *L. camara* is the dominant species, whereas low cover indicates that it is a subordinate species.

Lantana camara	human-disturbed savanna	protected savanna	*Z* statistic
absent	23,839 ha (75 %)	3,685 ha (84 %)	-13.87*
low cover	7,436 ha (21 %)	628 ha (14 %)	11.02*
high cover	1,082 ha (4 %)	37 ha (1 %)	8.04*
total invaded	8,518 ha (25 %)	665 ha (15 %)	13.87*
total area	34,357 ha	4,351 ha	

significance level: * < 0.01

Discussion

The results of this study indicate that anthropogenic disturbance enhances alien plant invasion in these southern African savannas. Five pieces of evidence were presented. First of all, the mean ratio of alien plant species to total plant species richness was twice as high in the human-disturbed savanna (Mutirikwi communal area) as in the adjacent protected savanna (Kyle Game Reserve). Secondly, although most (64 %) of the alien taxa recorded were common to both the human-disturbed and the protected savanna, their frequency of occurrence was significantly higher in the human-disturbed savanna than in the protected savanna. Thirdly, alien plant species were positively associated with the human-disturbed savanna, whereas their association with the protected savanna was negative. By contrast, their native confamilial species showed the opposite pattern, namely a negative association with the human-disturbed savanna and a positive one with the protected savanna. Fourthly, a quarter of the human-disturbed savanna landscape had now been invaded by the invasive shrub *Lantana camara*, compared to 15 % of the protected reserve. Finally, the proportion of the human-disturbed savanna dominated by *L. camara* was four times higher than of the protected savanna. These

results support a global study, which revealed that sites outside nature reserves were twice as likely to be invaded as nature reserves (Lonsdale 1999). Our findings in tropical savannas are consistent with those of Chytrý *et al*. (2008a), who reported that agricultural land use, high population density, and a long history of human settlement increased the level of plant invasion in temperate ecosystems. Similar results were also reported in Mediterranean ecosystems (Vilà et al. 2007).

The fact that some alien plant species were significantly associated with the human-disturbed savanna, while their native confamilial were significantly associated with the protected savanna, clearly suggests that anthropogenic disturbance has opposing effects on alien versus native flora. Multiple human disturbances may constantly reset succession, depleting the seed bank of native species, while at the same time creating the conditions that favour the recruitment of alien species, especially those with a ruderal strategy (D'Antonio and Meyerson 2002; Martin et al. 2009). Invaders may also be better adapted to grazing by introduced mammal herbivores, such as cattle, whereas native plants may not have strong defences against these novel herbivores (Maron and Vila 2001; Chaneton et al. 2002; Holmgren 2002). Introduced herbivores may selectively consume native species, while avoiding alien plant species with stronger anti-herbivore adaptations. Indeed, the most widespread invader, *L. camara*, contains toxic phenolic compounds that render it unpalatable to most domestic herbivores (Sharma et al. 1988). Such preferential consumption of native species may suppress their competitiveness and favour invaders (Parker et al. 2006). Overgrazing by introduced domestic herbivores has been found to promote plant invasions in a wide variety of other terrestrial systems, such as temperate grasslands (Chaneton et al. 2002), temperate woodlands (Cross 1981), Mediterranean shrublands (Holmgren et al. 2000; Holmgren 2002), and dry rainforests (Fensham et al. 1994; Gentle and Duggin 1997). These studies suggest that changing the abiotic environment and introducing one or more alien species may facilitate the establishment and spread of other exotic species, which is consistent with the invasional meltdown hypothesis (Simberloff and Von Holle 1999; Simberloff 2006). Clearly observational studies are insufficient to reveal the causal mechanisms involved, and controlled field experiments comparing the responses of exotic and native congeners should be conducted in both the native and introduced

ranges to be able to assess the relative importance of herbivory, disturbance, and propagule pressure (Hierro et al. 2005).

In this study, for the first time, the cover of the most widespread invasive alien species in southern Africa, *L. camara* (Henderson 2007), was successfully mapped at a landscape scale through supervised classification of satellite imagery. The results indicate that both the protected and human-disturbed savannas had been invaded by *L. camara*, but the extent of the invasion was significantly higher in the human disturbed savanna. A similar pattern was reported in a field study conducted in the Kruger National Park of South Africa and the communal areas upland of the park (Foxcroft and Richardson 2003). The enhanced invasion of the human-disturbed savanna by *L. camara* could be attributed partly to direct human activities, since communal farmers deliberately propagate *L. camara* around their vegetable gardens to keep livestock out. The vegetable gardens are mostly located along rivers and are watered throughout the dry season. Because *L. camara* is known to grow and reproduce throughout the year, if moisture is available, and a mature plant typically produces about 12,000 seeds per m^2 per year (Swarbrick et al. 1995; Day et al. 2003), it is likely that the high propagule pressure, assisted by moisture availability, accelerates invasion along rivers. Other studies have also shown that, because of enhanced seed dispersal and eutrophication, riparian areas tend to be hotspots of invasion (Stohlgren et al. 1998; Alpert et al. 2000; Tickner et al. 2001; Foxcroft et al. 2009).

Invasive plant species are becoming increasingly common in tropical African savannas, reducing native biodiversity and productivity of agro-ecosystems (Le Maitre et al. 2002; Richardson and Van Wilgen 2004; Henderson 2007). Hence, invasive species might also negatively affect the livelihoods of rural people who rely on the income from livestock production, as many invasive species are avoided by domestic livestock (Parker et al. 2006). Given that savannas support more than half of the African human population and most of its large herbivore biomass (Scholes and Archer 1997), further studies are needed to gain a better understanding of the impact of invasive species on rural livelihoods and the functioning of these ecosystems. Such studies should also explore ways in which invasion might interact with other processes such as climate change so that possible adaptation and mitigation measures can be developed.

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Conclusion

Because studies comparing the occurrence of alien taxa in nature reserves and non-reserve sites are scarce in African savannas, this study has shed light on the role of human disturbance in facilitating alien plant invasion in tropical savannas. The results suggest that the susceptibility of savannas to invasion increases with anthropogenic disturbance, and although alien taxa often account for a small proportion of the total plant diversity, the few that become invasive can dominate landscapes. Hence, managing the intensity of disturbance is crucial for the reduction of plant invasions in these savanna ecosystems.

Acknowledgments

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Chapter 7

Integrating conventional classifiers with a GIS expert system improves invasive species mapping

Mhosisi Masocha and Andrew K. Skidmore

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Abstract

Mapping the cover of invasive species using remotely sensed data alone is difficult, because many invaders occur as mid-level canopy species or as subtle understorey species and therefore contribute little to the spectral signatures captured by remote sensing devices. In this study, two common non-parametric classifiers, namely the neural network and the support vector machine, were each combined with identical expert system rules, in order to test whether the new hybrid methods produced significantly more accurate invasive species cover maps than the single classifiers. The neural network, when used on its own, mapped the cover of the invasive species *Lantana camara* in a nature reserve of southern Zimbabwe with an overall accuracy of 79 % and a Kappa of 0.69. However, when the neural network was combined with an expert system, the overall accuracy and Kappa increased to 87 % and 0.80, respectively. Similarly, the support vector machine algorithm achieved an overall accuracy of 71 % with a Kappa of 0.56, whereas the hybrid support vector machine and expert system achieved a higher overall accuracy of 81 % and a Kappa of 0.72. Pair-wise comparisons based on the Kappa *Z*-test confirmed that these increases in mapping accuracy were significant. Overall, the results suggest that integrating conventional classifiers with an expert system results in the mapping of invasive species with a greater statistical confidence. It is hoped that others, who wish to detect and map cryptic invasive species with improved accuracy, may now also consider combining different classifiers with GIS expert systems.

Key words: accuracy, invasion, *Lantana camara*, management, savanna, Zimbabwe

Introduction

Numerous alien plants are invading natural and agro-ecosystems resulting in loss of native biodiversity (Mooney 1999; Mack et al. 2000; Levine et al. 2003). When native biodiversity, the driving force in ecosystem functioning, is lost, this in turn reduces the ability to provide environmental services (Sala et al. 2000; Hooper et al. 2005). In order to control the spread of invasive alien species and conserve biodiversity, natural resource managers require accurate maps about the extent and severity of invasions (Le Maitre et al. 1996; Ewel et al. 1999). Accurate mapping of invasions may also assist resource managers in optimising resource allocation, thereby making the management of invasive species cost-effective and achievable (Anderson et al. 1993; Le Maitre et al. 2002).

Traditionally, quantitative estimates of the cover of invasive species are obtained from ground-based surveys (Mack et al. 2007). However, ground-based surveys tend to be time consuming and inefficient, and in addition some parts of the landscape may be inaccessible (Hierro et al. 2005). Consequently, remote sensing is increasingly being used to detect and map the cover of invasive species, especially those with distinct morphological or phenological features (Anderson et al. 1993; Underwood et al. 2003; Madden 2004; Asner and Vitousek 2005; Ustin et al. 2005; Hamada et al. 2007; Mack et al. 2007; Pellikka et al. 2009). Many invasive species, however, occur as subtle understorey species or as mixed-canopy invaders (Joshi et al. 2006). On its own, remote sensing has little capability to detect these invasive species, because they do not dominate the canopy and therefore contribute little to the spectral signatures captured by remote sensing devices (Asner et al. 2008).

This problem may potentially be overcome by integrating conventional image classification methods, that rely entirely on the spectral signatures of remotely sensed data, with expert systems (Lu and Weng 2007). Expert systems can handle ancillary data from diverse sources as well as capture prior knowledge about the distribution of the target invasive species in the form of rules (Skidmore 1989). Expert systems are computer programmes using symbolic logic to mimic human experts, and are consequently expected to arrive at the same conclusion as human experts (Skidmore et al. 1996). When implemented in a Geographical Information System (GIS) environment,

expert systems can infer the most probable cover of a target invasive species at a specific location.

Previous research has shown that combining conventional image classification methods with expert systems for the purpose of vegetation mapping often yields results that are comparable or superior to, those obtained from single classification methods (Stefanov et al. 2001; Liu et al. 2002; Lu and Weng 2007). For example, Schmidt et al. (2004) combined hyperspectral imagery with topographic data and successfully mapped 19 vegetation types in the salt marshes of the Netherlands, using a hybrid spectral angle mapper and expert system. In another study, Vaiphasa et al. (2006) combined soil pH data with ASTER imagery and discriminated mangrove species in Thailand, using a hybrid maximum likelihood and expert system. Recently, Wang et al. (2009) combined an artificial neural network with an expert system and successfully mapped understorey bamboo species in the Qinling mountains of south-western China. However, to date the integration of conventional image classification methods and expert systems has not been extended to mapping the cover of invasive species.

This study tests the hypothesis that integrating conventional image classification methods with an expert system significantly improves invasive species mapping. To test this hypothesis, the cover of the invasive *Lantana camara* was mapped in a nature reserve situated in southern Zimbabwe, using two common non-parametric classifiers, namely the neural network and the support vector machine (Lu and Weng 2007). These classifiers were then each combined with identical expert system rules, in order to test whether the new hybrid methods produced significantly more accurate cover maps than the single classifiers. Unlike probabilistic classifiers such as the maximum likelihood, the neural network and support vector machine classifiers do not make any explicit assumptions about the distribution of training data (Atkinson and Tatnall 1997; Skidmore et al. 1997; Karimi et al. 2006), hence one does not need to collect training data from all classes occurring in a study area during classification (Sanchez-Hernandeza et al. 2007). This saves time and reduces research costs. Moreover, these non-parametric classifiers are often able to classify a data set with higher accuracy than statistical classifiers can, because of their ability to detect subtle and non-linear patterns in a data set (Foody and Mathur 2004; Lu and Weng 2007).

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Lantana camara is a good model species for comparing the relative performance of individual versus hybrid methods, because it exhibits a complex growth pattern (Day et al. 2003), making it difficult to detect and map its cover from remotely sensed data alone. In open and disturbed sites, for instance, this invasive species may typically form dense monotypic stands easily detectable via remote sensing. However, under the shade and canopy of tall trees, it can either grow as a climber or as a mid-level canopy species, or even as an understorey invader (Foxcroft and Richardson 2003). Remote sensing alone has limited capability to detect and map invasive species hidden beneath the canopy (Joshi et al. 2006; Asner et al. 2008).

Methods

Study species

Lantana camara L. (Verbeneceae) is native to the tropical and sub-tropical regions of South and Central America (Swarbrick et al. 1995). It is a perennial polycarpic shrub, growing to 4 m tall and flowering throughout the year, if sufficient moisture and high temperature conditions prevail (Day et al. 2003). A single plant is capable of producing up to 12,000 seeds per m^2 per year (Swarbrick et al. 1995). The seeds are dispersed mostly by birds which feed on the ripe fruit.

Lantana camara is invasive or naturalised in 60 countries and island groups worldwide (Cronk and Fuller 2001). It was introduced into southern Africa around 1858 as an ornamental shrub, but is now one of the most widespread terrestrial invaders in the region (Foxcroft and Richardson 2003; Henderson 2007). *Lantana camara* invasion poses a threat to both natural and agro-ecosystems, because the species suppresses the growth of other plants through shading and nutrient sequestration (Gentle and Duggin 1998). It is also unpalatable to livestock and native vertebrate herbivores and often results in death if ingested (Day et al. 2003). Furthermore, it can harbour insects such as tsetse flies and mosquitoes, which spread diseases to domestic stock and humans (Holm et al. 1997; Syed and Guerin 2004).

Due to its widespread geographical distribution and the environmental and economic damages associated with its rapid spread, many countries including

Zimbabwe (Chenje et al. 1998), Australia (ARMC-ANZ 2001) and South Africa (Cilliers and Neser 1999) have declared *L. camara* a weed of national significance. However, the lack of accurate spatial information concerning the extent and severity of its invasion hampers management and control.

Study area

The study was conducted in the 44 km^2 Kyle Game Reserve (20° 13′ S and 31° 03′ E), established in 1961 and fenced off with the management objective to conserve biological diversity. It is situated about 30 km southeast of Masvingo town in southern Zimbabwe and encompasses an undulating plain with isolated hills stretching northwards from Lake Mutirikwi to the Beza mountain range (1,080 to 1,485 m). The climate is semi-arid with a relatively short growing season (November to March) and a long dry season (April to October). Annual rainfall averages 635 mm, but is variable within and between seasons (Vincent and Thomas 1960). The mean daily maximum temperature ranges from 21° C in June to 29° C in October while the mean daily minimum temperature ranges from 5° C in July to 17° C in January.

Soils are predominantly coarse-textured sandy soils of low nutrient status derived from granite (Nyamapfene 1991). The vegetation consists of a small area of evergreen forest found at the Beza spring and a complex mosaic of broad-leaved deciduous woodland, bushland, and open savanna grassland. The deciduous woodland is dominated by *Brachystegia spiciformis* and *Julbernardia globiflora*, whereas the open grassland is dominated by perennial grasses such as *Hyparrhenia filipendula* (Vincent and Thomas 1960). Woody species such as *Schotia brachypetala* and *Diospyros mespiliformis*, which occur frequently at termite mounds, are scattered throughout the open grassland matrix. Bushlands are characterised by closely spaced shrubs and small trees, consisting of various species such as *Dichrostachys cinerea* and *Lantana camara*. The botanical nomenclature for woody species and grasses follows the taxonomy described by Palgrave (2002) and Oudtshoorn (2006), respectively.

Data sets

The GIS data sources used in this study were: an ASTER image from 22 July 2006; a digital elevation model; and geo-referenced point data representing the percentage cover of *L. camara* measured in the field. The ASTER image (path 169, row 74) contained 15 spectral bands, but only three bands (1, 2, and 3N) in the visible and near-infrared range, with a spatial resolution of 15 m, were used (Abrams 2000). The spatial resolution of the remaining bands was considered too coarse to enable accurate detection and mapping of *L. camara*, and hence these were excluded. The selected bands were corrected for geometric distortions using 15 ground control points (GCPs). An affine transformation was applied and a root mean square error of 0.42 pixels (i.e., approximately 6 m) was achieved. The GCPs were located evenly across the image at obvious features on both the image and field such as road intersections and river bifurcations. Each GCP had its field location measured using global positioning system. After geometric rectification, the image was re-sampled to a Universal Transverse Mercator coordinate system (zone 36 South) using the nearest neighbour interpolation technique. The ASTER image used provided the most recent data set available at the time field work was undertaken.

Habitat types

The support vector machine algorithm (Vapnik 1999) was used to classify the ASTER image into nine habitat types (Sanchez-Hernandeza et al. 2007). The habitats distinguished were: surface standing water; dense broad-leaved woodland; sparse broad-leaved woodland; bush thicket; sparse bushland; dry open grassland; seasonally-wet grassland; bare soil; and rock outcrop. The classifier was trained using 20 training cases per habitat. The testing data set, which was used to evaluate classification results, consisted of 15 training cases per habitat. The classification yielded a habitat map with an overall accuracy of 82 % and a Kappa of 0.72. The habitats differed in the level of invasion by *L. camara*. Table 8 captures the variation in the level of invasion of these nine habitats in the form of conditional probabilities that a specific habitat occurs if, for example, the cover of *L. camara* is high or low.

Table 8: Rules used by the expert system to predict the cover of *Lantana camara* from a raster GIS database in the Kyle Game Reserve of Zimbabwe.

GIS layers	Item of evidence	*Lantana camara* cover		
		high	low	absent
Habitat type	surface standing water	0.1	0.1	0.8
	dense broad-leaved woodland	0.2	0.4	0.5
	sparse broad-leaved woodland	0.4	0.6	0.4
	bush thicket	0.7	0.6	0.4
	sparse bushland	0.2	0.4	0.4
	dry open grassland	0.1	0.2	0.7
	seasonally-wet grassland	0.1	0.2	0.5
	bare soil	0.1	0.2	0.6
	rock outcrop	0.1	0.2	0.7
	gully	0.6	0.6	0.4
Terrain position	lower midslope	0.4	0.4	0.4
	midslope	0.2	0.2	0.4
	upper midslope	0.1	0.3	0.6
	ridge	0.1	0.2	0.8

Terrain position

Using the algorithm developed by Skidmore (1990), five terrain position classes, namely gully, lower midslope, midslope, upper midslope, and ridge, were derived from a digital elevation model with a grid resolution of 30 m. The output terrain position raster map was re-sampled to a 15 m grid size, using nearest neighbour interpolation to match the spatial resolution of the ASTER bands. Terrain position influences the availability of soil moisture, which is critical for *L. camara* establishment and growth (Gentle and Duggin 1997; Fowler 2002). For instance, gullies receive more run-off from the upper slopes and hence tend to be more infested with *L. camara* than ridges, which are often drier (Foxcroft and Richardson 2003).

Field plots

Presence/absence, number of stems and cover of *L. camara* were recorded for 187 (30 m x 30 m) field plots during the growing season in December 2006. The field plots were selected in a stratified random manner, strata being based upon habitat type and terrain position. To minimise the problem of spatial autocorrelation, the plots were placed at least 800 m apart. Moran's I index was used to check for spatial autocorrelation and field data were found to be uncorrelated (Moran's $I = 0.01$; $Z = 1.02$; $P > 0.1$).

In order to facilitate image classification, the field data were divided into three *Lantana* cover classes, namely: absence (0 % cover), low (1 to 50 % cover), and high (> 50 % cover). The high cover class corresponded with more than 1,000 stems per 900 m^2 and indicated that *L. camara* was the dominant species in that plot. The data set was split into a training set ($n = 90$) and a testing set ($n = 97$). Field data in combination with documented literature on *L. camara* distribution and growth (Gentle and Duggin 1997; Day et al. 2003; Foxcroft and Richardson 2003) were used to derive the rules the GIS expert system needed to infer *L. camara* cover throughout the study area.

Image classification

Neural network

A three-layer feed-forward and error-back propagation artificial neural network (Skidmore et al. 1997) was used to map the cover of *L. camara*. The algorithm minimised the root mean square error (RMSE) between the observed and the predicted cover (Atkinson and Tatnall 1997). The neural network (with 30 training samples for each of the three cover classes of *L. camara* and three ASTER bands) was trained, and the best combination of optimum learning rate and momentum to yield the lowest RMSE was established empirically, following Skidmore et al. (1997). Optimal results were achieved with a learning rate of 0.2, a training momentum of 0.7, and one hidden layer. The RMSE stabilised after 15,000 epochs. A total of 30 classifications, each consisting of 15,000 epochs, was performed and the classification with the lowest RMSE was selected. The neural network yielded a thematic cover map and a rule image

with three bands, where each band in the rule image represented the probability that a pixel belonged to one of the three cover classes of *L. camara.* The classified map and the associated rule image were input into a GIS expert system to improve classification. The neural network algorithm was programmed using the Interactive Data Language (IDL; Research Systems Inc.).

Support vector machine classifier

The support vector machine algorithm was also used to classify the ASTER image into three cover classes of *L. camara*. The algorithm fits an optimal separating hyperplane between classes of interest, focusing only on training samples that lie at the edge of the class distributions, known as the support vectors; those samples that lie in the centre of the class distribution do not play any part in the classification and are therefore redundant (Foody and Mathur 2006). The classifier was trained with 30 training cases per cover class. It yielded a cover map and a rule image with three bands, where each band represented the probability that a pixel belonged to one of the three cover classes of *L. camara*. Both the classified map and the rule image were input into the GIS expert system to improve the classification. Image pre-processing and classification were performed using the ENVI 4.3 software package (ITT Visual Information Solutions).

GIS expert system

Thirdly, an expert system was used to predict the cover of *L. camara* from a raster GIS database. The raster layers accessed by the expert system were habitat types and terrain position classes. The rules for all the items of evidence, *viz.* habitat types and terrain position classes, were stored in a spreadsheet (Table 8), which was accessed by the expert system. The rules represented conditional probabilities that an item of evidence (for example a rock outcrop) was present, for instance, when it was known that *L. camara* was absent. Thus, the rules provided the link between the abundance of *L. camara* and the GIS data layers used to predict its cover (Skidmore et al. 1991).

       The expert system algorithm was programmed using the Interactive Data Language (IDL; Research Systems Inc.). It was described in detail by Skidmore (1989)

and is therefore not repeated here. The algorithm worked forward from the data (item of evidence) to the hypothesis (the most probable cover of *L. camara*) and terminated the search only after all the evidence had been evaluated. The cover class, which had the highest posterior probability of occurring at a grid cell location, was assigned to that grid cell location (Skidmore et al. 1991; Beven 2008).

Hybrid classifiers

To construct hybrid classifiers, the thematic cover map and the associated probability rule image, produced by the neural network and support vector machine, were presented to the expert system separately. These input layers together with ancillary GIS data layers were used by the expert system to infer the most probable cover of *L. camara* occurring at each grid cell location. The expectation was, that the expert system would correct misclassifications generated by the individual classifiers due to spectral confusion between *L. camara* and other plants. In total, five methods were used to map the cover of *L. camara*, *viz.* neural network, support vector machine, expert system, hybrid neural network plus expert system, as well as hybrid support vector machine plus expert system.

Assessing the accuracy and performance of classification methods

To evaluate the accuracy of cover maps produced by each of the five methods used, the overall accuracy and Kappa statistics were calculated from an independent testing data set (Congalton 1991; Skidmore 1999). Error matrices of the ground truth data versus the classification results were generated to allow calculation of additional measures of map accuracy, such as user accuracy. Pair-wise comparisons based on the Kappa Z-test were performed to test for significant differences in the accuracies of the maps generated by the three individual methods and the two hybrid methods (Congalton 1991; Skidmore 1999; Foody 2004).

Results

Maps of the distribution and cover of *L. camara* in the Kyle Game Reserve produced by the three individual classifiers and the two hybrid methods (i.e., neural network; support vector machine; expert system; hybrid neural network plus expert system; and hybrid support vector machine plus expert system) are presented in Fig. 12 (a, b, c, d, and e respectively). Table 9 presents the error matrices of the classification generated by each method. The error matrices have a label sequence (from 'a' to 'e') corresponding with the one used in Fig. 12.

Table 9: Error matrices for the classification produced by three individual classifiers and two hybrid methods, used to map the cover of the invasive *Lantana camara* in the Kyle Game Reserve, Zimbabwe. The main diagonal presented boldface in each matrix shows the number of correctly allocated pixels. The overall accuracy (OA), Kappa coefficient, omission error (OE), producer accuracy (PA), commission error (CE), and user accuracy (UA) are also shown.

9a. Neural network

Lantana camara cover	high	low	absent	CE	UA
high	**29**	1	0	3 %	97 %
low	1	**19**	7	30 %	70 %
absent	0	11	**29**	28 %	73 %
OE	3 %	39 %	19 %	OA	79 %
PA	97 %	61 %	81 %	Kappa	0.689

9b. Support vector machine

Lantana camara cover	high	low	absent	CE	UA
high	**26**	1	0	4 %	96 %
low	4	**13**	6	43	57 %
absent	0	17	**30**	36	64 %
OE	13 %	58 %	17 %	OA	71 %
PA	87 %	42 %	83 %	Kappa	0.562

9c. GIS expert system

Lantana camara cover	high	low	absent	CE	UA
high	**8**	1	0	11 %	89 %
low	11	**23**	3	38 %	62 %
absent	11	7	**33**	35 %	65 %
OE	73 %	26 %	8	OA	66 %
PA	27 %	74 %	92 %	Kappa	0.480

9d. Hybrid neural network and expert system

Lantana camara cover	high	low	absent	CE	UA
high	**28**	1	0	3 %	97 %
low	2	**22**	2	15 %	85 %
absent	0	8	**34**	19 %	81 %
OE	7 %	29	6	OA	87 %
PA	93 %	71 %	94 %	Kappa	0.797

9e. Hybrid support vector machine and expert system

Lantana camara cover	high	low	absent	CE	UA
high	**28**	1	0	3 %	97 %
low	1	**17**	2	15 %	85 %
absent	1	13	**34**	29 %	71 %
OE	7 %	45 %	6 %	OA	81 %
PA	93 %	55 %	94 %	Kappa	0.718

The results show that, among the three individual classifiers, the highest mapping accuracy was achieved by the neural network with an overall mapping accuracy of 79 % and a Kappa of 0.689 (Table 9a), followed by the support vector machine, which achieved an overall mapping accuracy of 71 % and a Kappa of 0.562 (Table 9b). These methods mapped the high cover class with much higher producer and user accuracies than the expert system. However, the expert system predicted the non-*Lantana* and low cover classes better than the neural network and the support vector machine (Table 9c).

Comparisons of the performance of individual versus hybrid classifiers

The hybrid neural network achieved an overall accuracy of 87 % and a Kappa of 0.797 (Table 9d). The Kappa Z-test was used to test the research hypothesis that combining the neural network with the expert system improves invasive species cover mapping. This may be stated formally as H_o: $\kappa_1 = \kappa_2$ versus the alternative hypothesis H_a: $\kappa_2 > \kappa_1$, where κ_1 is the Kappa statistic representing the accuracy achieved by the neural network, while κ_2 is a measure of the map accuracy achieved by the hybrid neural network plus expert system. The null hypothesis was rejected at $P < 0.05$; so it was concluded that combining the neural network with the expert system resulted in a significant increase in mapping accuracy.

The hybrid support vector machine plus expert system achieved an overall mapping accuracy of 81 % and a Kappa of 0.718 (Table 9e). The Kappa Z-test was used to test the research hypothesis that the hybrid support vector machine plus expert system yields a more accurate invasive species cover map, compared to the one produced by the support vector machine alone. Formally, this may be stated as H_o: $\kappa_1 = \kappa_2$ versus the alternative hypothesis H_a: $\kappa_2 > \kappa_1$, where κ_1 is the Kappa coefficient representing the map accuracy achieved by the support vector machine alone, while κ_2 is a measure of the map accuracy achieved by the hybrid support vector machine plus expert system. The null hypothesis was rejected at $P < 0.05$. The conclusion from this test is that integrating the support vector classifier with the expert system significantly increased mapping accuracy.

Patterns and extent of invasion

All the maps generated by the five methods (Fig. 12) indicate a clear gradient of invasion, with the north-eastern and southern sections of the game reserve under sparse broad-leaved woodland being invaded more heavily than the central section dominated by grasses. Estimates of the extent of invasion derived from the cover map generated by the hybrid neural network and expert system, which achieved the highest mapping accuracy, showed that *L. camara* had invaded 665 hectares (ha) of land, representing

15 % of the total area of the game reserve and was the dominant species in about 37 ha of the game reserve.
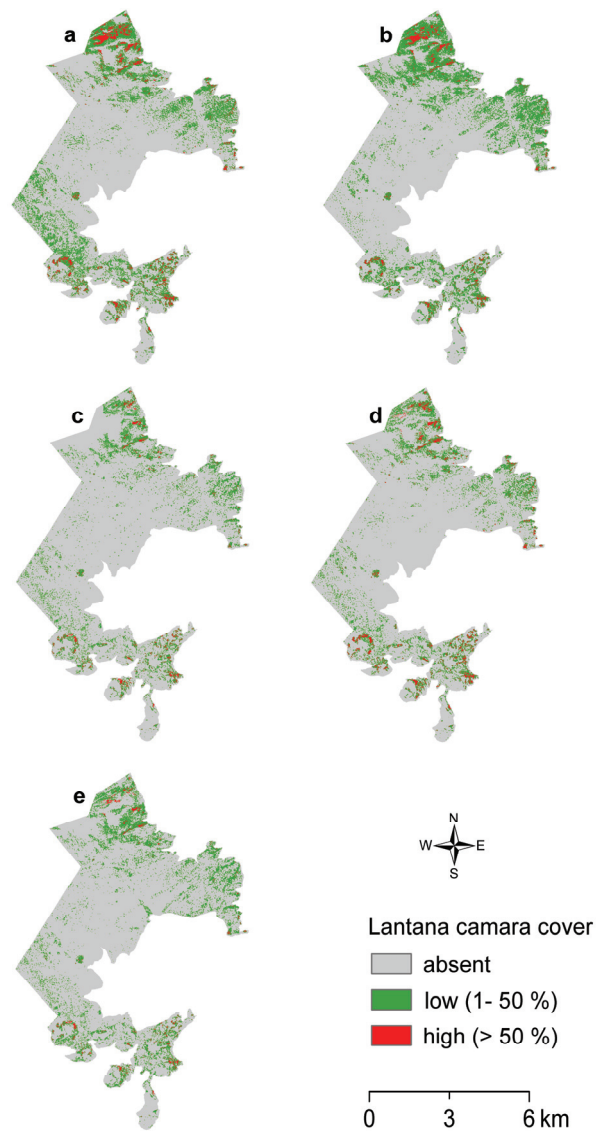

Fig. 12. Distribution and cover of the invasive alien shrub *Lantana camara* predicted by (**a**) neural network; (**b**) support vector machine; (**c**) GIS expert system; (**d**) hybrid neural network and expert system; and (**e**) hybrid support vector machine and expert system classification methods in the Kyle Game Reserve of Zimbabwe.

Discussion

The results of this study suggest that combining conventional image classification methods with an expert system improves invasive species cover mapping. When the neural network was combined with the expert system in order to map the cover of the invasive *Lantana camara* in a nature reserve of southern Zimbabwe the overall accuracy increased by 8 %. Similarly, when the support vector machine classifier was integrated with the expert system the overall mapping accuracy increased by 10 %. The Kappa *Z*-tests confirmed that these increases in mapping accuracy were significant. While the neural network and the support vector machine alone were able to map the high cover class more accurately than the expert system could, the expert system predicted the low cover and non-*Lantana* classes more accurately. Consequently, integrating the individual methods with the expert system produced an overall more accurate invasive species cover map. The best classification result was achieved by the hybrid neural network plus expert system method (overall accuracy of 87 % and a Kappa of 0.797). This exceeds the overall mapping accuracy of 85 % recommended in the literature (Mather 1999) and indicates that the performance of this hybrid method was excellent and its results are of practical use.

The results reported here corroborate the work of other researchers, who also combined conventional classification methods (e.g., the maximum likelihood and spectral angle mapper) with an expert system to map vegetation and land cover and reported an improvement in mapping accuracy (Stefanov et al. 2001; Schmidt et al. 2004; Vaiphasa et al. 2006; Nangendo et al. 2007; Wang et al. 2009). However, this is the first time the neural network and support vector machine classifiers have been integrated with a GIS expert system in order to successfully map the cover of an invasive alien species. This approach made it possible to accurately estimate, for the first time, the extent and severity of *L. camara* invasion at a landscape scale. In other words, this study demonstrates that combining the spectral signatures of remotely sensed data with ancillary spatial data and knowledge about the distribution of the target invasive species, enhances the capability of remote sensing to detect and map invasive alien species.

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Apart from demonstrating the superiority of hybrid methods over individual classification methods, the present study indicates that 15 % of the total area of the reserve has been invaded by *L. camara*, making this alien species the most widespread terrestrial invader in the Kyle Game Reserve. In the Kruger National Park (South Africa), Foxcroft and Richardson (2003) also reported that *L. camara* is the most widely distributed invasive alien species, although quantitative estimates of the extent of the invasion were not provided. The high cover class mapped in this study corresponds with approximately 3,000 stems per ha. Similar densities (i.e., about 5,000 individuals per ha) were also reported in the Forty Mile Scrub National Park of Australia (Fensham et al. 1994). Such high densities suggest that *L. camara* could start to dominate native flora, resulting in a biologically impoverished environment, and thus making its control crucial (Richardson et al. 2000; Foxcroft and Richardson 2003).

Furthermore, this study revealed a gradient of *L. camara* invasion, with the sparse broad-leaved woodland tending to be more susceptible, and the open grassland more resistant to its invasion. The higher susceptibility of the sparse woodland to invasion may be attributed to the interaction effects of physical disturbance of the soil by feral pigs, which creates bare patches suitable for *L. camara* recruitment and enhanced seed dispersal by birds. *Lantana camara* seeds are mostly dispersed by birds such as the dark-capped bulbul (*Pycononotus tricolor*), which often perch, nest, and roost in tall trees, thereby increasing seed supply beneath canopies (Milton et al. 2007). Indeed, high propagule pressure has been frequently invoked to explain the invasion success of numerous alien species, because it increases the probability that the arrival of propagules coincides with suitable environmental conditions (Rouget and Richardson 2003; Lockwood et al. 2005; Von Holle and Simberloff 2005; Thomsen et al. 2006; Melbourne et al. 2007).

At the same time, bottom-up (direct) interactions, such as competition for water and nutrients, with fast growing grass species might limit *L. camara* invading the open grassland areas. Research has shown that most savanna grasses have dense fibrous root systems and easily out-compete seedlings of woody plants, where they exploit the same resource base (Scholes and Archer 1997; Van der Waal et al. 2009). In addition, high grass biomass may increase fuel loads, thereby resulting in more intense fires (Scholes and Archer 1997; Van Langevelde et al. 2003), which may potentially cause

high seedling mortality among *L. camara* recruits. Further studies would be needed to disentangle the mechanisms of invasion.

Management implications

Since the cover of invasive plant species is directly related to their dominance and ecological impact (Hejda and Pyšek 2008), the quantitative estimates of the extent of invasion and cover of *L. camara* provided here have implications for its management and control. The clear gradient of invasion revealed here leads to two recommendations. Firstly, a management approach in stages, involving the targeting of areas of light infestation first before moving to areas of dense infestation, may be necessary. Secondly, an integrated management programme, to be sustained long-term (given the high risk of re-invasion), may be the best strategy for tackling the spread of *L. camara*. This may include a careful blend of mechanical control methods, such as the uprooting of light infestations and controlled burning, followed by the re-vegetation of cleared areas with native species, in order to provide shade to suppress the recruitment of *L. camara* (ARMC-ANZ 2001).

Conclusion

This study explicitly revealed areas of a nature reserve in southern Zimbabwe which are more susceptible to invasion by *Lantana camara*. Importantly, the study demonstrated the superiority of hybrid classification methods over single classifiers when mapping invasive species from remotely sensed data. The best classification result was obtained when the neural network was combined with a GIS expert system. The conclusion from this study is, that integrating conventional image classification methods with a GIS expert system results in the mapping of invasive species with a greater statistical confidence. It is hoped that others, who wish to detect and map cryptic invasive species with improved accuracy, may now also consider combining different classifiers with GIS expert systems.

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Acknowledgments

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Chapter 8

General discussion

Introduction

The main aim of this thesis was to investigate and gain an understanding of how rainfall, soil nutrient availability, fire, and grazing influence the invasibility of African savanna systems by alien plants. Rainfall, nutrient availability, grazing, and fire are the four principal factors determining vegetation structure, composition, and distribution in African savannas (Scholes and Archer 1997; Sankaran et al. 2005) but whether these factors play a similar role in the invasion and rates of spread of alien plants in these ecosystems is unclear. Davis et al. (2000) predicted that the susceptibility of an ecosystem to invasion by alien species (invasibility) increases with resource availability. Fig. 13 shows that resource availability and consequently invasibility can increase due to a pulse in resource supply or a decline in resource uptake by resident species caused by disturbance, or both (Hobbs 1989; Sher and Hyatt 1999; Davis et al. 2000).

This thesis brings together several chapters on how rainfall, which replenishes soil moisture, and termites which modulate nutrient availability to plants, as well as major disturbances (fire and grazing), determine the invasibility of African savanna ecosystems. In this final chapter, the main results from the previous chapters are brought together in order to gain a better understanding of the major factors controlling the invasibility of African savannas. In addition, the mechanisms of invasion are highlighted and the applicability of our results to other terrestrial ecosystems is discussed. Finally, the practical relevance of this thesis for managing invasive species is emphasised and two suggestions are made for future research.
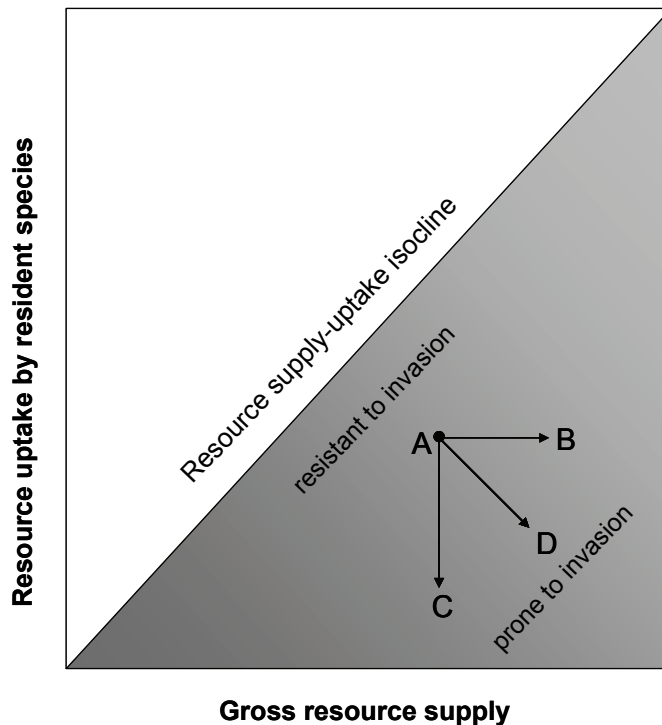
Fig. 13. The theory of fluctuating resource availability predicts that a plant assemblage's susceptibility to invasion by alien species (invasibility) increases with resource availability. Resource availability is the difference between gross resource supply and resource uptake. It can increase due to a pulse in resource supply (A → B), a decline in resource uptake (A → C) or both (A → D). In the plot shown, resource availability, and hence invasibility, increases as the trajectory moves further right and/or below the resource supply-uptake isocline. At the resource supply-uptake isocline resource uptake by resident species equals gross resource supply hence invasion is inhibited. After Davis et al. (2000).

Do native termites facilitate alien plant invasions of African savannas?

Primary productivity in African savannas is limited by low soil nutrient availability, particularly nitrogen and phosphorus (Huston 1993; Vitousek et al. 1997; Sankaran et al. 2005). This has been confirmed by many fertilisation experiments (O' Connor 1985). However, mound-building termites such as *Macrotermes natalensis,* which are widely distributed in African savannas (Uys 2002), can substantially increase soil nutrient

concentrations at their mounds. This creates 'islands of fertility' (Lee and Wood 1971; Lobry de Bruyn and Conacher 1990). Nutrient enrichment of mound soils occurs because termites incorporate large amounts of organic matter into their mounds. Mound soils are also rich in nutrients because termites use soil from deeper layers in the construction with a higher proportion of clay minerals and a higher cation exchange capacity than the coarser textured soils at the surface (Wood 1988; López-Hernández et al. 2005). Termites also deposit fresh soil around their mounds, which suppresses the growth of resident flora and creates small gaps (microsites) suitable for colonisation by alien plants (Rogers et al. 1999).

These changes in the patterns of nutrient and microsite availability in the landscape caused by termites can have a profound effect on vegetation structure and composition in savannas (Wild 1952; Lee and Wood 1971; Moe et al. 2009). Field studies have revealed that throughout the savannas in Africa, many plant species cluster around termite mounds (Barot et al. 1999; Loveridge and Moe 2004; Grant and Scholes 2006). It was therefore hypothesised that, termites, by amassing nutrients at their mounds and disturbing the soil, create spatial environmental heterogeneities, which may facilitate the invasion of nutrient-limited savannas by alien plants. This hypothesis was tested in a semi-arid savanna in Zimbabwe (southern Africa) by sampling and comparing vegetation as well as nutrient concentrations in plots located at mounds and in off-mound areas (Chapter 2). A greenhouse experiment was also performed to test whether two common invasive alien shrubs (*Lantana camara* and *Duranta erecta*) grow better in nutrient-richer mound soils than in soils from the off-mound areas. Furthermore, seeds and seedlings of *D. erecta* were introduced to experimental plots located both at termite mounds and away from mounds in the Kyle Game Reserve (southern Zimbabwe) to test the hypothesis that seed germination and survival of the invasive alien shrubs is enhanced by increased microsite availability around termite mounds (Chapter 3).

Mound soils had significantly higher concentrations of macronutrients and exchangeable bases than soils from the surrounding off-mound areas did. Consequently, the vegetation at mounds differed significantly in species composition, richness, and abundance from the vegetation at off-mound areas. Alien plant species richness increased threefold on termite mounds compared to the surrounding non-mound areas.

On average, the cover of alien plants in plots located at termite mounds was at least twice the cover at nearby off-mound plots of a similar size. Both *L. camara* and *D. erecta* aggregated around termite mounds with no individuals occurring farther than 25 m from the centre of the nearest termite mound. These invasive alien shrubs accumulated twice the amount of dry matter and grew at least twice as fast in mound soils than in soils from off-mound areas (Fig. 14a, b).
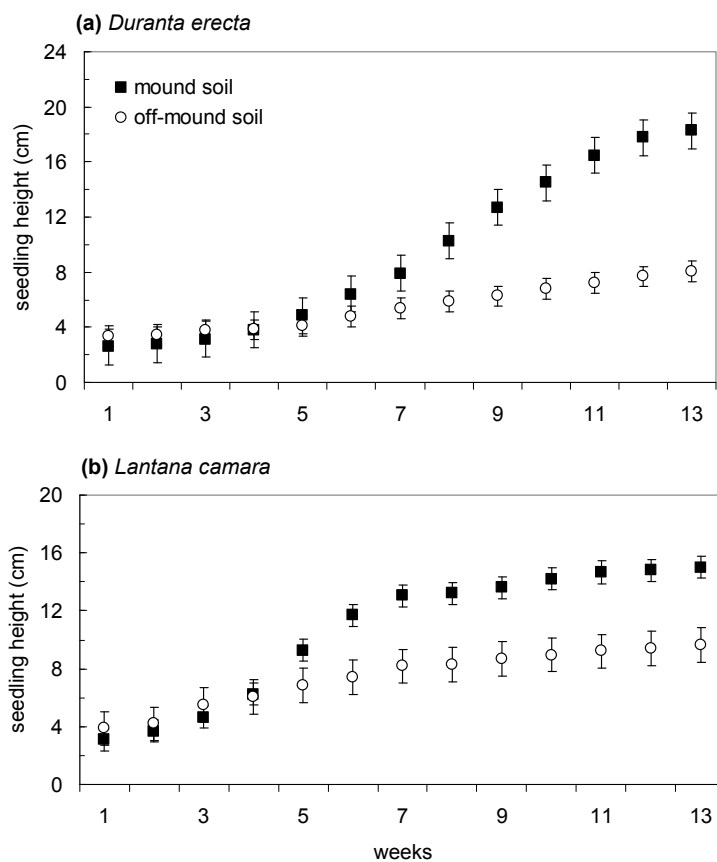

Fig. 14. Effect of mound soil on the growth of two invasive alien shrubs *Duranta erecta* (**a**) and *Lantana camara* (**b**). Black squares represent mean height of seedlings grown in mound soils and open circles represent mean height of seedlings grown in non-mound (control) soils. The whiskers represent 95 % confidence levels (*n* = 10 replicates per species).

Field experiments revealed that the germination rate of the invasive shrub *D. erecta* in mound soils was twice as high as in soils in the surrounding areas undisturbed by termites. In addition, seedling survival of *D. erecta* was consistently higher on termite mounds than away from mounds. These results combined support our hypothesis and provide the first quantitative evidence that termites enhance the invasion of African savannas by alien plant species.

It is suggested here that the interaction effect of elevated nutrient levels and increased microsite availability explains the enhanced performance of alien plant species at termite mounds and the higher diversity of alien taxa recorded there. Termites may further promote alien plant invasion into savannas by exposing bare mineral soil of higher nutrient status to the surface, which is favourable for the germination of seeds of numerous alien species (Eriksson and Ehrlen 1992). Hence, it is concluded that termites enhance alien plant species invasions into savannas by creating new habitats that differ fundamentally from the surrounding habitats in abiotic conditions such as fertility and microsite availability. Because nutrient limitation is widespread in tropical savannas (Huston and Wolverton 2009) and mound-building termites are ubiquitous in these systems (Lobry de Bruyn and Conacher 1990; Uys 2002), nutrient enrichment of savanna soils by these insects may be an important mechanism of invasion operating across tropical savanna systems. The mechanism through which termites engineer the environment, modulate the availability of nutrients and microsites and thus facilitate invasions of alien plants into tropical savanna systems is illustrated in Fig. 15.

In other terrestrial systems, it has also been reported that ecosystem engineers, i.e., organisms that modulate the availability of resources to other organisms by causing physical state changes in the abiotic environment (Jones et al. 1994, 1997) promote alien plant invasions (Crooks 2002; Badano et al. 2007; Hastings et al. 2007). For example, Wagner and Jones (2006) reported that seed-harvesting ants (*Pogonomyrmex rugosus*) increased soil nutrient concentrations, which then favoured the invasion of an alien grass *Schismus barbatus* into arid grassland systems of North America. Likewise, Farji-Brener and Ghermandi (2008) reported that the nests of leaf-cutting ants (*Acromyrmex lobicornis*) were richer in nutrients and invaded to a larger extent by two alien herbs (*Carduus nutans* and *Onopordum acanthium*) than the surrounding off-nest areas.
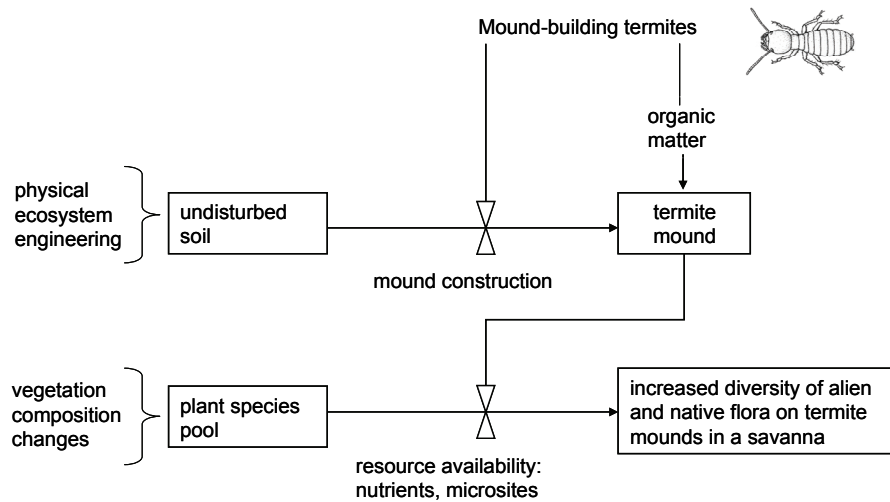
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Fig. 15. A conceptual model of physical ecosystem engineering depicting how termites promote the invasion of savannas by alien plants through creating patches with increased nutrient and microsite availability. Boxes represent state variable, arrows indicate state changes and control pathways are shown with solid lines. The symbol ⋈ represents points of modulation. Modified from Jones et al. (1994).

The link between rates of spread of invasive aliens and rainfall variability

African savannas are heterogeneous and hence soil nutrient availability is not the only key factor determining their invasibility. It has been suggested that rainfall can have an overriding effect on primary production in these ecosystems (Sankaran et al. 2008). Fluctuations in plant species abundance driven by variations in rainfall patterns are the norm in Africa savannas (O' Connor 1985). In semi-arid savannas, temporal variation in moisture availability can exert a stronger influence on plant species' composition, abundance, and distribution than edaphic factors such as fertility (Scholes and Archer 1997; Sankaran et al. 2005). Therefore, in a semi-arid savanna in Zimbabwe under nature conservation (Kyle Game Reserve; *c.a.* 600 mm mean annual rainfall), the link was tested between the rates of spread of an alien invasive shrub *L. camara* and rainfall

variation (Chapter 4). To gain a better understanding of the effect of rainfall on the rates of spread and the dynamics of invasion, historical aerial photographs and field measurements were used to compare the rate of spread of this invasive alien shrub with that of the native shrubs over a long period with variable rainfall in a protected semi-arid savanna in southern Africa.

It was found that during years of above-average rainfall, the mean annual rate of spread of the invasive alien shrub *L. camara* was at least twice that of native shrub encroachers, whereas in other years natives spread at the same rate as the invasive alien shrub. This is a novel finding suggesting that rainfall pulses trigger accelerated spread of invasive alien shrubs in water-limited savannas. Most studies investigating shrub encroachment in African savannas invoked overgrazing by livestock to explain this phenomenon (Van Vegten 1984; Jeltsch et al. 1997; Roques et al. 2001; Wigley et al. 2009). As this study was conducted in a protected nature reserve from which livestock had been excluded for more than 50 years, the results reported here imply that rainfall is the primary factor controlling the rate of spread of invasive alien shrubs in semi-arid savannas and overgrazing by cattle may play a secondary role.

Role of fire in promoting the invasion of savanna systems

Not all savannas in Africa are water-limited. In mesic savannas receiving more than 650 mm of annual rainfall where water is not a limiting resource (Sankaran et al. 2005), disturbances such as fire can have pronounced effects on vegetation structure (Sankaran et al. 2008). In these systems, fire is commonly used to suppress tree growth and promote tree-grass coexistence, which is important for savanna functioning as these two plant life forms provide different ecosystem services (Barnes 1965; Campbell et al. 1997; Bond and Keeley 2005). However, the impacts of fire on ecosystem processes are not understood well enough to recommend appropriate fire regimes for managing savannas without risking promoting invasion by invasive aliens (D'Antonio 2000; Govender et al. 2006). Therefore, at a mesic savanna site in central Zimbabwe (Grasslands Research Station; *c.a.* 850 mm annual rainfall), where fire is frequently used to suppress bush encroachment, vegetation data were used from a long-term fire experiment, beginning in 1953, to test two hypotheses namely, (1) frequent burning of

mesic savannas may reduce the competitiveness of resident species and thereby promote the invasion by alien plants; (2) because alien plants may vary, both within and between species, in which degree they respond to fire, short intervals between fires may favour alien forbs with short life spans and/or a ruderal strategy (Chapter 5). The fire treatments consisted of late season fires, lit at 1-, 2-, 3-, and 4-year intervals, and burnt plots were compared with unburnt control plots.

More than fifty years of experimental burning of a mesic savanna enhanced the invasion by alien plant species. The proportion of alien species relative to the total vascular plant species richness was significantly higher in regularly burnt plots than in the unburnt control plots. It increased as the intervals between fires shortened. Alien forbs occurred more frequently in regularly burnt plots than in the unburnt control plots and their abundance also increased as the intervals between fires (in years) became shorter. These results support both hypotheses and are consistent with well-known effects of fire on savanna vegetation. Previous results published on this fire experiment revealed that regular burning significantly reduced tree height, but did not alter tree species diversity (Strang 1974; Furley et al. 2008). The effect of the frequency of burning on alien plant invasion had not been assessed. Hence, this study shed light on the role of fire in promoting invasion of mesic savannas by alien plant species. Field experiments performed at several other savanna sites in southern Africa have also revealed that fire reduces the cover of competitive dominants, resulting in substantial increases in the abundance of forbs (O' Connor 1985; Fynn et al. 2009). However, to our knowledge this is the first experimental evidence that frequent burning promotes invasion of a mesic savanna by alien plants.

Impact of anthropogenic disturbance on savanna invasibility

It would be negligent not to assess the impact of anthropogenic disturbance on alien plant invasions into African savannas. After all, alien organisms are introduced into novel environments by humans in the first place (Lodge 1993). The introduction of cattle from Europe into Africa and the Americas is a classic example. These exotic herbivores may reduce the competitiveness of native flora, thereby paving the way for other alien species to invade (Holmgren 2002), a phenomenon that is often referred to as

invasional meltdown (Simberloff and Von Holle 1999; Nunez et al. 2008). Whether the introduction of alien plants or their propagules by humans into savannas is deliberate or accidental is not the issue here.

Humans also engage in a wide range of activities, including agriculture, which substantially alter savanna vegetation structure and cover and may lead to invasion by alien plants, especially those adapted to anthropogenic disturbance. It was therefore hypothesised that the interaction of human disturbance and cattle grazing might facilitate alien plant invasion into disturbed savannas. We tested this hypothesis along a gradient of human-and-livestock disturbance in two savanna landscapes in southern Zimbabwe (Chapter 6). The study sites were adjacent to each other, but differed as one is a communal area sustaining a high human population density and the other is a protected nature reserve with a low human population density. In addition, the communal area is grazed by cattle all year round, whereas cattle are excluded from the nature reserve.

Alien taxa represented a significantly higher proportion of the total vascular species richness in the human-disturbed savanna (Mutirikwi communal area) than in the protected savanna (Kyle Game Reserve). A quarter of the human-and-livestock disturbed savanna (8,518 ha) had been invaded by the unpalatable invasive alien shrub *L. camara*, compared to 15 % of the protected reserve (665 ha). These results indicate that intensive (communal) land management practices increase alien plant invasion and are comparable to those reported for South African savannas. Although estimates of the areal extent and intensity of invasion were not provided, Shackleton (2000) also reported that in a South African savanna, *L. camara* was more common in the communal areas than in the adjacent protected nature reserves. Van Gils et al. (2006) similarly observed that unpalatable invasive alien species were more common in the communal areas of South Africa than in the nature reserves.

It has been suggested that selective grazing of palatable resident species results in increased dominance of unpalatable invasive aliens (Augustine and McNaughton 1998). Hence, the enhanced invasion success of *L. camara* in savannas continuously grazed by cattle may be attributed in part to its toxicity to cattle (Day et al. 2003; Sharma et al. 2005). In the African savannas with heavy grazing by cattle, unpalatable invasive aliens like *L. camara* may gain a competitive advantage over palatable natives

whose growth is hindered by these introduced domestic herbivores. The association between cattle grazing and invasive aliens has also been reported in Australian savannas (Fensham et al. 1994; Gentle and Duggin 1997; Duggin and Gentle 1998), tropical rainforests and savannas in India (Kohli et al. 2006), temperate grasslands (Chaneton et al. 2002), and Mediterranean shrublands (Holmgren et al. 2000; Holmgren 2002). Thus, the preponderance of the evidence suggests that worldwide ecosystems with disturbance regimes altered by human activity are more prone to alien species invasion than those less altered.

Anthropogenic disturbance promotes alien plant invasion through a variety of mechanisms (Hobbs 1989). For example, since an alien plant invader cannot occupy space that is already taken by resident species (Sousa 1984), neither can it establish successfully if resident species utilise available resources completely; resource pre-emption is one of the key mechanisms limiting the invasion of intact plant assemblages (Alpert et al. 2000; Davis et al. 2000; Von Holle et al. 2003; Pyšek and Richardson 2008). Disturbances can break this biotic resistance to invasion by damaging or causing mortality of resident species, thereby creating vacant niches and preventing competitive exclusion (Levine et al. 2004; Catford et al. 2009). In other words, disturbance can directly or indirectly create niche opportunities for alien species to invade (D'Antonio et al. 1999; Hobbs 2000; Shea and Chesson 2002; MacDougall et al. 2009). Other mechanisms through which disturbance promotes alien plant invasions can be found in Hobbs and Huenneke (1992), Huston (2004), Lake and Leishman (2004) as well as Eschtruth and Battles (2009), and will not be repeated here.

Which are the main factors controlling savanna invasibility?

Three key factors namely, propagule pressure, abiotic characteristics of the environment, and biotic characteristics of the environment likely interact to determine the outcome of invasion and hence the invasibility of an African savanna (Fig. 16). Propagule pressure, which is the combined measure of the number of propagules per introduction event and the number of introduction events (Lonsdale 1999), can have an overriding effect on savanna invasibility since invasion cannot occur without propagules of alien taxa. High propagule pressure may enable alien species to establish successfully through seed

saturation (Crawley et al. 1999). However, because alien plant invasions were studied *post-hoc* in this thesis and data on the number of propagules of alien taxa introduced into African savannas per introduction event as well as the number of introduction events are scarce (Barney and Whitlow 2008), the role of propagule pressure in enhancing invasibility was not explicitly studied. Nevertheless, the findings presented in Chapter 6 in conjunction with available literature (Rouget and Richardson 2003; Lockwood et al. 2005; Von Holle and Simberloff 2005; Edward et al. 2009) imply that high propagule pressure in interaction with frequent disturbances tend to make African savannas more prone to invasion by alien plants.

The abiotic or physical characteristics of the environment, particularly the availability of the most limiting resources, also influence the invasibility of African savannas, because if abiotic conditions are inhospitable, invasion will fail regardless of the number propagules of an alien species reaching a site (Catford et al. 2009). On the other hand, if environmental conditions are benign, very little propagule pressure may be necessary for successful invasion (Theoharides and Dukes 2007). Because African savannas are heterogeneous, resource availability tends to vary over time and space. This variation inevitably has an effect on invasibility, because an alien invader needs access to resources to establish successfully. For example, the spatial variation in soil moisture, which is a key resource limiting plant growth in African savannas, may explain why in a semi-arid savanna in southern Zimbabwe, stands of an invasive alien shrub *L. camara* were denser and more linear along perennial rivers than in non-riparian areas (Chapter 6), a pattern observed in South African savannas as well (Foxcroft et al. 2009). This suggests that in African savannas, riparian habitats tend to be more invadable than non-riparian habitats. That riparian habitats tend to harbour more alien taxa than non-riparian areas is also the case in other systems (Stohlgren et al. 1998; Tickner et al. 2001; Truscott et al. 2008).
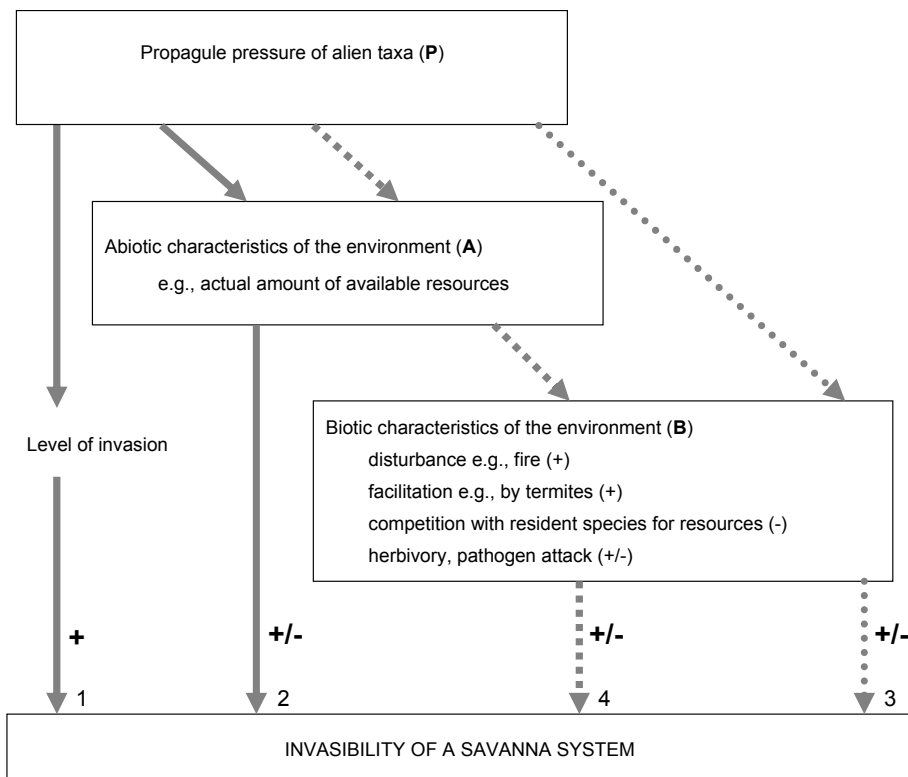
Fig. 16. Key factors determining the susceptibility of savanna systems to invasion by alien plant species (invasibility). These principal determinants are: propagule pressure (**P**), abiotic characteristics of the environment (**A**), and biotic characteristics of the environment (**B**). A plus symbol (**+**) indicates that the factor or the underlying mechanism(s) of invasion associated with that factor has a positive effect on invasibility whereas a plus or minus symbol (**+/-**) indicates the effect could either be positive or negative depending on the outcome of interactions between the factors or causative mechanisms involved. Potential invasion pathways represented by labelled arrows increase in complexity from **1** to **4**. For pathway **1**, the level of invasion is controlled by propagule pressure only; for pathway **2**, the main effects of propagule pressure and abiotic conditions (e.g., actual amount of available resources like soil nutrients) and their two-way interaction (i.e., **P+A+P*A**) determine invasibility; for pathway **3**, invasibility is a function of **P+B+P*B**; whereas for pathway **4** all three factors including their two-way and three-way interactions determine invasibility. The notation follows the figure and ***** indicates interaction of factors. Note more invaded does not necessarily mean more invadable, hence the term level of invasion is used here to simply denote the number of alien plant species a habitat or ecosystem harbours (Pyšek and Richardson 2008). Modified from Catford et al. (2009).

Likewise, the spatial variation in soil nutrient availability, another key factor limiting primary productivity in African savannas, influences invasibility. It was shown in Chapter 2 that termites create spatial heterogeneity in nutrient concentrations thus causing the invasibility of savannas to vary spatially. Disturbances such as overgrazing by cattle, which severely damage or cause mortality of plants thereby reducing resource uptake by native species, also increase the amount of resources available and consequently the proneness of a savanna to invasion by alien plants. It was revealed that savannas which are burned frequently or grazed heavily by cattle tend to be more invaded by alien plants, especially those ruderal alien forbs capable of coping with these disturbances (Chapters 5, 6). Temporal variation in resource supply, for example soil moisture, driven by rainfall variability, also causes the invasibility of savannas to vary temporally, as was shown in Chapter 4.

Biotic interactions, for example competition between native and alien species for environmental resources, although not explicitly studied in this thesis, also have a profound effect on savanna invasibility. For example, pathogen attack and/or herbivory of alien invaders by generalist resident herbivores may make a savanna less susceptible to invasion (Fig. 16). However, if alien taxa (for example *L. camara*) have more potent chemical defences against the generalist herbivores than their native competitors, then herbivory may suppress the competitiveness of native flora and enhance invasibility as suggested in Chapter 6. Evidently the invasibility of a savanna tends to vary over time and space in conjunction with fluctuations in resource availability and disturbance regimes which alter biotic interactions (Crawley 1987; Richardson and Cowling 1992; Davis et al. 2000).

Practical relevance of this thesis

Land managers in Africa are concerned with the threats to ecosystems posed by invasive alien species and would like to remove or control invasive aliens in order to conserve native biodiversity and ensure that ecosystems continue to provide goods and services (Cronk and Fuller 2001; Le Maitre et al. 2002). However, they lack accurate information on how the spatial extent and intensity of invasions vary within and across entire landscapes. This makes it difficult for them to plan how to allocate resources

towards controlling the spread of invasive plants. Ground measurements and remote sensing are the two main sources of spatial data on the level of infestation of a landscape by invasive plants but both present major problems which limit their usefulness.

Firstly, ground measurements are labour-intensive and expensive. Secondly, some areas are not easily accessible, making acquisition of reliable data on the occurrence and cover of invasive plants difficult (Blumenthal et al. 2007). Remote sensing, which gives a synoptic view of the landscape (Skidmore 2001), is a more efficient method for mapping invasive species (Everitt et al. 1995; Underwood et al. 2003; Asner and Vitousek 2005; Barnett et al. 2007). However, it only works well if the invaders have phenological or morphological features that are distinct from those of the native plants (Mack et al. 2007). Unfortunately, many invasive species do not have distinct morphological and phenological characteristics and mapping their cover from remotely sensed data is not a straightforward task. Invasive plants are also often hidden beneath the canopy and contribute little to the spectral signatures captured by remote sensing devices, making them difficult to detect using remote sensing alone (Joshi et al. 2006). The capability of remote sensing to detect invasive plants is further limited by the fact that most alien invaders do not form homogenous stands larger than the spatial resolution of readily available remotely sensed data (Fig. 17).

These problems can be overcome by integrating standard image classifiers with a geographical information system (GIS) expert system. It was demonstrated in Chapter 7 that the resultant hybrid expert system classifier can map invasive plants more accurately than either the standard classifiers or the GIS expert system. The hybrid GIS expert system classifier is superior to traditional methods because it combines remotely sensed data as well as other ancillary data with prior knowledge about the distribution of the target invasive species in a single bayesian prediction framework (Skidmore 1989; Schmidt et al. 2004). This is achieved through the use of expert rules that provide the link between the data and consequent hypothesis to be tested (Skidmore et al. 1996).
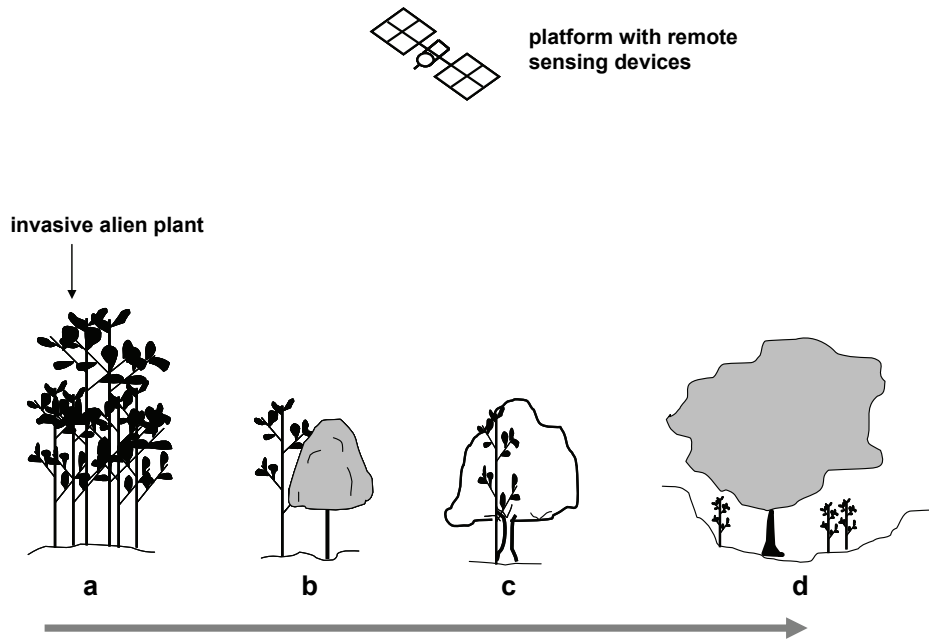
Fig. 17. Limitations of remote sensing in detecting invasive alien plants in heterogeneous environments. The bold arrow indicates that as the morphology or growth habit of the invasive alien plant changes, it becomes more difficult to detect the invader through direct remote sensing. At location **a**, the invasive plant forms homogenous stands easily detectable with remote sensing but from locations **b** to **d**, the invasive plant contributes less to the spectral signatures captured by a remote sensing device than the resident species. This makes it difficult to detect its presence using direct remotely sensing alone.

With regard to invasive species mapping, the main question to be answered by the hybrid GIS expert system classifier is: "What is the probability of finding an invasive species *X* given that a certain piece of evidence (e.g., a termite mound) is available at a given location?". The hybrid GIS expert system classifier was used to map the cover of an invasive shrub *L. camara* across two landscapes, enabling us to test whether the level of invasion differed significantly between an anthropogenically altered savanna and a protected one (Chapter 6). This was the first time that this widespread alien invader of southern Africa savannas (Henderson 2007) was successfully mapped from satellite imagery at a landscape scale.

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Remote sensing has the potential to broaden our understanding of alien plant invasions in poorly studied ecosystems like African savannas. This can be justified on four grounds. Firstly, field data are scarce in Africa. Hence, remotely sensed data such as historical archives of aerial photographs and satellite images may be the only data source available for studying dynamics of invasion (Foxcroft et al. 2004). Secondly, remote sensing can reveal spatiotemporal patterns of invasion, enabling ecologists to infer mechanisms of invasion and understand the factors controlling the rates of spread of invasive aliens (see Chapter 4 in this thesis). Thirdly, as satellite images are now more freely available, other researchers may use the hybrid expert system classifier presented in this thesis to map invasive alien species in other systems at spatial or temporal scales of their choice. The beauty of this hybrid expert system classifier lies in its simplicity and robustness, making it implementable in any standard GIS software. The proposed mapping method offers a final important benefit. It is suitable for detecting nascent invasions as it performs better than standard methods, especially when the target alien species to be mapped is sparsely distributed or does not form extensive monotypic stands. Because early detection of an invasion is the key to successful invasive species management (Mack et al. 2007), other researchers are encouraged to make use of this method in order to generate accurate maps about the extent and intensity of alien species invasions, helping land managers prioritise resource allocation, which will lead to more efficient invasive species management.

General conclusion

The main aim of this thesis was to investigate and understand how rainfall, soil nutrient availability, fire, and grazing influence the invasibility of African savannas by alien plants. The general conclusion of this thesis is that the invasibility of African savannas tends to increase when the availability of limiting resources (water and nutrients) coincides with disturbances like cattle grazing and fire, which open up intact plant assemblages to colonisation by alien plant species. This is consistent with ecological theory (Davis et al. 2000) and implies that human alteration of disturbance regimes as well as the introduction of novel disturbances, for example, cattle grazing, offer increased opportunities for alien plant invasions of savannas (Hobbs 2000). Therefore,

reducing the level of anthropogenic disturbance may be the key to controlling the spread of invasive alien species across savanna landscapes. The most important contribution of this study to invasion ecology is that it showed for the first time that native termites, which are widely distributed in tropical savannas, facilitate alien plant invasions of these ecosystems by creating patches in the landscape with increased nutrient and microsite availability suitable for colonisation by numerous alien species.

Suggestions for future research

Two suggestions can be made for future research. Firstly, the interactions between the major factors controlling savanna invasibility namely propagule pressure, resource availability (i.e., water, nutrients), grazing, and fire were not explicitly investigated here. Hence, to gain a better understanding of the relative importance of these factors factorial experiments performed under field conditions at multiple sites are crucial. The results from such experiments may go a long way in elucidating the mechanisms causing alien plant invasions into savanna ecosystems and so contribute towards invasive species management.

Secondly, climate change is predicted to significantly alter carbon dioxide (CO_2) levels and precipitation patterns over extensive savanna regions (Christensen et al. 2007). An apparent drying trend over southern Africa has already been detected (Sheffield and Wood 2008). At the same time, a three- to fourfold increase in nitrogen deposition is occurring in many parts of southern Africa (Scholes et al. 2003; Dentener et al. 2006). The likely impacts of these changes in the biogeochemical cycles on native and alien flora are not known (Dukes 2000). Therefore, fully-crossed factorial greenhouse and field experiments, in which rainfall, CO_2 and nitrogen are manipulated to mimic their projected levels, need be performed in order to be able to predict the spread of native and alien flora. Insights from these experiments may contribute towards our understanding of the dynamics of invasion and help to shape the way we manage invasive species in savannas in the future.

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Summary

Numerous alien plant species are invading African savannas causing loss of biodiversity and altering ecosystem functioning. The ecological factors and underlying mechanisms causing these invasions are poorly understood. This hinders invasive species management and biodiversity conservation. In this thesis, a range of approaches (i.e., field measurements, a greenhouse experiment, field experiments, a long-term burning experiment, remote sensing, and Geographical Information System (GIS) techniques) was used to understand how the availability of two key resources limiting primary productivity in African savannas (water and nutrients) and how major disturbances (i.e., fire, grazing) determine the invasion of these systems by alien plant species.

In a nutrient-limited Zimbabwean savanna, native termites facilitated alien plant invasion by boosting nutrient concentrations in top soils around their mounds and creating a patchy distribution of microsites in the landscape. Alien plant species richness increased threefold on termite mounds compared to surrounding off-mound areas. In addition, two invasive alien shrubs, *Lantana camara* and *Duranta erecta*, clustered around termite mounds without any occurring beyond the periphery of the nearest termite mound. These invasive shrubs grew more rapidly and doubled dry matter production in termite mound soils compared to the surrounding non-mound soils. Field experiments revealed that the germination rate of the invasive alien shrub *D. erecta* in mound soils was twice as high as in soils in the surrounding areas undisturbed by termites. In addition, seedling survival of *D. erecta* was consistently higher on termite mounds than away from mounds. These findings combined provide the first quantitative evidence that termites, which are widely distributed in tropical savannas, facilitate plant invasion by creating patches in the landscape with increased nutrient and microsite availability suitable for colonisation by alien species.

Rainfall had a profound effect on the rate of spread of an invasive alien species. In a semi-arid savanna in southern Zimbabwe, during years of above-average rainfall, the mean annual rate of spread of the invasive *L. camara* was at least twice that of native shrub encroachers, whereas in other years natives spread at the same rate as the alien shrub. This is the first time that, over a relatively long period, the spatio-temporal patterns of spread of invasive and native encroaching shrub species have been

quantified in savanna systems and the link with rainfall variation tested. These results suggest that in semi-arid savannas, pulses in rainfall may accelerate the spread of invasive alien species.

Data from a long-term fire experiment performed at a humid savanna site in central Zimbabwe, in which plots were burnt at 1-, 2-, 3-, and 4-year intervals for more than 50 years and compared with unburnt controls, revealed that frequent burning of savannas promotes invasion. Alien species accounted for a significantly higher proportion of plant species richness in regularly burnt plots than in the unburnt control plots. The proportion of alien plant species was highest in the annually burnt plots, followed by plots burnt biennially, triennially, and quadrennially. Plots protected from fire contained the lowest proportion of alien invaders. Also, alien forbs occurred more frequently in regularly burnt plots than in the unburnt control plots and their abundance increased as the intervals between fires in years became shorter. These results suggest that frequent burning of mesic savannas enhances invasion by alien plants, with short intervals between fires favouring alien forbs. Previous results published on this fire experiment showed that regular burning had a significant effect on vegetation structure but the effect of fire frequency on alien plant invasion had not been evaluated. Hence, this thesis sheds light on the role of fire in promoting alien plant invasion in savannas.

When the susceptibility to invasion by alien plants of a southern African savanna degraded by human activity and continuous grazing by cattle was compared with that of an adjacent protected savanna, it was found that alien taxa represented a significantly higher proportion of the total species richness in the human-disturbed savanna than in the protected one. While alien plant species associated positively with the human-disturbed savanna and negatively with the protected one, their native confamilial species exhibited a positive association with the protected savanna, and a negative association with the human-disturbed savanna. The most abundant and widely distributed invasive species, *L. camara,* covered a significantly higher proportion of the human-disturbed savanna than of the protected savanna. These results clearly suggest that anthropogenic disturbance increases the invasibility of African savannas.

The findings of this study lead to the general conclusion that the susceptibility of African savanna systems to invasion by alien species increases when the availability of key limiting resources (water and nutrients) coincides with disturbances, like cattle

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grazing and fire, which open up an intact plant assemblage for colonisation by alien invaders. This is consistent with ecological theory and implies that manipulating resource availability and reducing the level of disturbance may be the keys to controlling the spread of alien species across savanna landscapes.

Finally, to improve invasive species mapping, conventional image classifiers were combined with a simple GIS expert system to yield a hybrid classifier. It was demonstrated for the first time that this hybrid classifier can map the cover of invasive plant species from satellite imagery across the entire landscape with greater statistical accuracy than either the standard image classifiers or the GIS expert system alone. Hence, it has the potential to address the data needs of natural resource managers, who require accurate information about the occurrence and abundance of invasive species in order to make invasive species management more cost effective.

Curriculum vitae

Mhosisi Masocha was born on the 9th of May 1975 in Masvingo rural district, Zimbabwe. He did his Ordinary level education at Rukovo secondary school (1988-1991) and Advanced level education at Hama high school (1993-1994). From June 1995 to February 1997, he worked for the Ministry of Education as a secondary school teacher. In March 1997, he enrolled with the University of Zimbabwe to read for an honours degree in Geography and Environmental Science, which he completed in 2000. In January 2001, he joined the University of Zimbabwe as a research assistant in the Department of Geography and Environmental Science. In 2002, while working as a research assistant, he started reading for a master of research degree at the University of Zimbabwe. He completed the master's degree in 2004 and was appointed a teaching assistant. In July 2005, the University of Zimbabwe appointed him a full-time lecturer in the Department of Geography and Environmental Science. In August 2005, he was awarded a fellowship by the Netherlands Organisation for International Cooperation in Higher Education (NUFFIC) to support his PhD studies with the International Institute for Geo-information Science and Earth Observation (ITC) and Wageningen University in the Netherlands. He commenced his PhD research in January 2006, culminating in the writing of this doctoral thesis. He is still with the University of Zimbabwe, teaching Spatial Ecology, Environmental Management, Remote Sensing, and Geographical Information Systems (GIS). His main research interests include: invasive species, spatial patterns in ecological data; and vegetation mapping and monitoring.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

The C.T. De Wit Graduate School PE&RC

PRODUCTION ECOLOGY

& RESOURCE CONSERVATION

Review of Literature (5 ECTS)
- The invasion of the shrub Lantana camara in African savannas: Distribution and mechanisms (2006)

Writing of Project Proposal (7 ECTS)
- The invasion of the shrub Lantana camara in African savannas: Distribution and mechanisms (2006)

Laboratory Training and Working Visits (1.4 ECTS)
- Design and execution of a greenhouse experiment; University of Zimbabwe (2006)

Post-Graduate Courses (6.4 ECTS)
- Basic and advanced statistics; Wageningen University (2007)
- Spatial and temporal statistics; ITC (2007)
- Interactive Data Language (IDL) Basic Programming; ITC (2007)

Competence Strengthening / Skills Courses (2.4 ECTS)
- Scientific Writing; ITC (2007)
- Scientific presentations; ITC (2007)

Discussion Groups / Local Seminars and Other Scientific Meetings (6.5 ECTS)
- PhD discussion group; ITC (2006-2008)
- PhD and research seminars; ITC (2005-2008)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (2.6 ECTS)
- PE&RC Weekend; Wageningen University (2007)
- Research Day of Department of Natural Resources; ITC (2006-2009)

International Symposia, Workshops and Conferences (3 ECTS)
- Sixth Annual Science Networking Meeting; Skukuza, Kruger National Park, South Africa (2008)

Supervision of MSc Student
- A spatio-temporal analysis of Lantana camara across contrasting land tenure regimes in Zimbabwe (24 days)