

# **Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa**

by

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## DECLARATION

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# ABSTRACT

Natural and semi-natural ecosystems and human communities worldwide are under siege from a growing number of destructive invasive alien species. Alien species are those whose presence in an area is due to intentional or accidental introduction as a result of human activities. *Some* alien species become invasive, and *some* cause tremendous destruction to the ecosystem and their stability, but we do not yet understand fully the many factors that determine the levels of invasiveness in alien species. However, management of alien plants requires a detailed understanding of the factors that make them invasive in their new habitat. The aim of this study was to explore in detail the processes and potential for invasion of *Schinus molle* (Peruvian pepper tree) into semi-arid savanna in South Africa and to examine the potential for this species to invade further in these ecosystems, and in other South African biomes.

In this thesis I explored the patterns and processes of invasion of *S. molle* in semi-arid savanna using small-scale experiments to investigate physical and ecological barriers to invasion that prevent or accelerate the invasion of this species. I examined factors such as pollination; seed production; seed dispersal; seed predation and viability, all known to contribute to invasiveness. I highlighted the critical role of microsite conditions (temperature, humidity, water availability) in facilitating *S. molle* seedling establishment in semi-arid savanna and demonstrated that microsite type characteristics need to be considered for management and monitoring of the species in South Africa. I demonstrated the ability of *S. molle* to out-compete indigenous woody plants for light and other resources and also showed that disturbance of natural ecosystems was not a prerequisite for invasion, although human activities such as tree planting have played a major role in disseminating this species in South Africa.

Predicting the future distribution of invasive species is very important for the management and conservation of natural ecosystems, and for the development of policy. For this reason, I also assessed the present and potential future spatial distribution of *S. molle* in South Africa by using bioclimatic models and a simulation-based spread model. I produced accurate profiles of environmental conditions (both biophysical and those

related to human activities) that characterize the planted and naturalized ranges of this species in South Africa, by linking species determinants, potential habitat suitability and likely spread dynamics under different scenarios of management and climate change. All those components provided insights on the dynamics of invasions by fleshy-fruited woody alien plants in general, and on *S. molle* invasions in South Africa in particular. I developed a conceptual model that described *S. molle* population dynamics leading to an understanding of the processes leading to the invasive spread of this species in South Africa. This work also emphasized the need for policy review concerning the invasive status of *S. molle* in South Africa, and recommendations are made for future research.

# UITTREKSEL

Die natuurlike and half-natuurlike ekosisteme sowel as menslike gemeenskappe wereldwyd word bedreig deur 'n groeiende hoeveelheid indringerplantspesies. Indringerplantspesies (daardie spesies wie se teenwoordigheid toegeskryf kan word aan opsetlike of toevallige inbringings deur menslike toedoen) is 'n bedreiging nie net vanweë die massiewe verwoesting van die ekosisteme en ekosistestabiliteit nie, maar ook omdat ons nog nie ten volle verstaan hoe hulle van skaars in hul natuurlike omgewing tot dominant in hul nuwe habitat gaan nie. Bestuur van indringer plante vereis 'n begrip van biologiese en ekologiese faktore wat lei tot hulle indringing in die nuwe habitat. Die primêre doel van hierdie studie was om in detail uit te vind wat die prosesse en potensiaal is vir die indringing van *S. molle* (die Peruviaanse peper boom) in droë savanna en om indringingspatrone in droë savanna met huidige en potensieële toekomstige patrone in ander Suid-Afrikaanse biome te vergelyk.

In hierdie tesis ondersoek ek die patrone en prosesse wat verband hou met die indringing van *S. molle* in droë savanna deur gebruik te maak van kleinskaalse eksperimente om fisiese en ekologiese hindernisse te ondersoek wat indringing van *S. molle* in Suid-Afrika voorkom of versnel. Dit sluit faktore in wat bekend is om by te dra tot indringing van plant spesies, soos bestuiwing, saadproduksie, saadpredasie en kiemkragtigheid. Ek het die kritieke rol beklemtoon van mikroomgewingskondisies (temperatuur, humiditeit, waterbeskikbaarheid) in die fasilitering van *S. molle* saailingvestigings in droë savanna en het gedemonstreer dat die tipe mikroomgewingskarakteristieke in ag geneem moet word by betuur en monitering van die verspreiding van *S. molle* in Suid-Afrika. Ek het die vermoë van *S. molle* om inheemse plante te uitkompeteer gedemonstreer, en het gewys dat versteuring van natuurlike ekosisteme nie 'n voorvereiste vir *S. molle* indringing was nie, hoewel menslike aktiwiteite soos boomaanplantings 'n groot rol speel deur by te dra tot indringing van hierdie spesie in Suid-Afrika.

Voorspelling van toekomstige verspreiding van indringerspesies is baie belangrik vir die bestuur en bewaring van natuurlike ekosisteme, sowel as vir ontwikkeling van wetgewing. Daarom is die huidige en potensiele toekomstige ruimtelike verspreiding van *S. molle* in Suid-Afrika bereken deur inkorporering van bioklimaatsmodelle en simulering gebaseer op 'n verspreidingsmodel. Ek het derhalwe akkurate profiele van omgewingstoestande (beide fisiese en daardie wat verband hou met menslike aktiwiteite) wat die aangeplante en natuurlike omvang van die spesie in Suid-Afrika kenmerk geproduseer deur spesiedeterminante, potensieële geskiktheid van habitatte en moontlike verspreidingsdinamika onder verskillende bestuurssenarios en kimaatsverandering te koppel. Al hierdie komponente verskaf insig in die dinamika van die indringing van houtagtige plante met vlesige vrugte oor die algemeen en *S. molle* in besonder in Suid-Afrika. Hierdie werk beklemtoon ook die behoefte vir hersiening van beleidsrigtings wat betrekking het op die indringerstatus van *S. molle* in Suid-Afrika en maak aanbevelings vir toekomstige navorsing.



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# THESIS STRUCTURE

The experimental component of this research is presented in seven self-contained scientific articles (chapters 3 to 9), each with its own aims, methods, and conclusions. Some of the chapters have been submitted, accepted or published in various international and local journals. Most chapters are co-authored, and I have indicated the names of co-authors in the overview below. All chapters contribute to the overall understanding of the main objectives, which is to refine predictions about the spatial limits and potential rates of spread for *Schinus molle* and to gain a better understanding of the potential distribution and impact of this species on South Africa ecosystems under scenarios of climate and land use changes.

## Overview

**Chapter 1 - General introduction:** The chapter deals with the general problem of biological invasions world wide and alien plant invasions in South African landscapes in particular. This section also introduces the study species *S. molle* (its distribution, distribution beyond its natural range, potential barriers to increased range and density). This is followed by a literature review (**chapter 2**) that explores the problem of biological invasions in general and plant invasions in South Africa in particular. Special emphasis is given to plant invasions in semi-arid savannas and to the dynamics of fleshy-fruited or woody plants. *These chapters were the entirely the work of D.M. Iponga. S.J. Milton and D.M. Richardson made comments and suggestions to refine it.*

**Chapter 3** – This chapter is based on: D. M. Iponga., S.J. Milton., and D.M. Richardson. 2008. Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Anacardiaceae) in South Africa. *Austral Ecology* 34 (in press) - This chapter deals with the reproductive potential and seedling establishment of *S. molle* in semi-arid savanna. *D.M. Iponga designed the framework with assistance from S.J. Milton. D.M. Iponga carried out all the field work, data collection and data analysis. The verification of all statistical analysis in this thesis was made by the Centre for Statistical*

*Consultation (CSC) of Stellenbosch University. D.M. Iponga wrote the first draft of the paper, and S.J. Milton and D.M. Richardson assisted with its finalization.*

**Chapter 4** – D.M. Iponga., J.P. Cuda., S.J. Milton., and D.M. Richardson. 2008. *Megastigmus* wasp damage to seeds of *Schinus molle*, Peruvian pepper tree, across a rainfall gradient in South Africa: Implications for invasiveness. *African Entomology* **16**: 127-131 - This chapter presents observations of seed predation across a rainfall gradient. *D.M. Iponga developed the framework of the study with the assistance of S.J. Milton. D.M. Iponga wrote the paper and S.J. Milton, D.M. Richardson, and J.P. Cuda contributed to the final version. J.P. Cuda confirmed the identification of the Megastigmus wasp.*

**Chapter 5** – D.M. Iponga. 2008. Seed set of the invasive alien tree *Schinus molle* (Anacardiaceae) in semi-arid savanna, South Africa: the role of pollination and selfing. *MS under review for Journal of Arid Environments* - This chapter deals with pollinator dependence of *S. molle*. *D.M. Iponga developed the experimental design with the support of S.J. Milton. D.M. Iponga carried out field work, data collection and analysis and wrote the paper. D.M. Richardson reviewed the manuscript.*

**Chapter 6** – D.M. Iponga., S.J. Milton and D.M. Richardson. 2008. Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna. *Biological Invasions* **11**: 159-169 – This chapter reports on a small-scale manipulative experiment that explores the effects of different treatments (microsite type, soil type and browsing) on the performance of *S. molle* seedlings. *D.M. Iponga developed the framework and experimental design with the assistance of S.J. Milton. D.M. Iponga carried out all the field work, data collection and analysis and wrote the paper. S.J. Milton and D.M. Richardson made inputs to the manuscript.*

**Chapter 7** – D.M. Iponga., S.J. Milton., and D.M. Richardson. 2008. Performance of seedlings of the invasive alien tree *Schinus molle* under indigenous and alien host trees in semi-arid savanna. *African Journal of Ecology (in press)* – this chapter evaluates the results on the importance of host tree identity for *S. molle* seedling establishment. *D.M. Iponga formulated the basic hypothesis from personal observations in the field and*

*developed the framework of the experimental design with support of S.J. Milton. D.M. Iponga carried out all the field work, data collection, analyses and wrote the draft paper. S.J. Milton and D.M. Richardson contributed to the final version.*

**Chapter 8** – D.M. Iponga., S.J. Milton., D.M. Richardson. 2008. Superiority in competition for light: a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Peruvian pepper tree) in South African savanna. *Journal of Arid Environments* **72**: 612-623 – this chapter compares the competitive ability of *S. molle* and two indigenous tree species (*Acacia tortilis*, *Rhus lancea*) for light when growing together in semi-arid savannas. *S.J. Milton developed the central hypothesis and D.M. Iponga developed the framework and experimental design, carried out field work, data collection and analysis, and wrote the paper. S.J. Milton and D.M. Richardson contributed to the final version of the paper.*

**Chapter 9** – D.M. Iponga, D. M. Richardson, S.J. Milton, R.M. Krug, W. Thuiller and N. Roura-Pascual. Distribution of the invasive alien tree *Schinus molle* in western South Africa: current determinants and projections under scenarios of climate change and management. *MS under review for Journal of applied Ecology* – this chapter presents the results of habitat suitability models based on a large-scale national distribution survey of *S. molle* across a rainfall gradient (summer- to winter-rainfall), under current and predicted future climates and management scenarios developed using bioclimatic and spread modelling for the whole of South Africa. *D.M. Iponga developed the framework and experimental design for the sampling with assistance from S.J. Milton. D.M. Iponga carried out field work and data collection. D.M. Iponga and D.M. Richardson developed the framework for the bioclimatic modelling and management scenarios, with technical assistance from R.M. Krug and N. Roura-Pascual. R.M. Krug and N. Roura-Pascual assisted with technical aspects of the modelling. W. Thuiller provided GIS data and advice on modelling protocols. D.M. Iponga and D.M. Richardson collaborated on writing the paper, with inputs from all above-mentioned collaborators.*

The outcomes of this study (conceptual model for prediction of the distribution and spread of fleshy fruited alien species) and my recommendations (how the climate-based model of *S. molle* invasion potential for South Africa be improved) are presented in the

conclusion (**chapter 10**). *This was the entire work of D.M. Iponga. S.J. Milton and D.M. Richardson made comments and suggestions.*

To structure the thesis in a logical way, I have placed the main objectives in a framework (Figure 1), to which I refer at the beginning of each chapter.

# Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa

**Chapter 1:** General problem of biological invasion in South Africa landscape

**Chapter 2:** Dynamics of alien woody plant invasions: review of processes and ecological impacts

## Main objectives

**Chapter 3:** Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 4:** *Megastigmus* wasp damage to seeds of *Schinus molle* (Peruvian pepper tree) across a rainfall gradient in South Africa: Implication for invasion

**Chapter 5:** Seed set of the invasive alien tree *Schinus molle* (Anacardiaceae) in semi-arid savanna, South Africa: the role of pollination and selfing

**Chapter 6:** Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 7:** Performance of seedlings of the invasive alien tree *Schinus molle* under indigenous and alien host trees in semi-arid savanna

**Chapter 8:** Superiority in competition for light: a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Peruvian pepper tree) in South Africa

**Chapter 9:** Distribution of the invasive alien tree *Schinus molle* in western South Africa: current determinants and projections under scenarios of climate change and management.

**Chapter 10:** General conclusions and recommendations

**Figure 1:** Schematic overview of the thesis chapters.



# CHAPTER ONE

## GENERAL INTRODUCTION

### Introduction

#### *Problem of biological invasions*

Biological invasion is the geographical expansion of a species into a region that it has not previously occupied. It is currently a global phenomenon that threatens terrestrial, marine and freshwater biodiversity (Leslie and Spotila, 2001; Kolar and Lodge, 2001; Jenkins, 2003; Olden *et al.*, 2004). Interactions resulting from biological invasions may lead to the establishment of mutualisms between introduced organisms and organisms already found in the system, i.e. “new mutualisms” (Richardson *et al.*, 2000b). Co-existence of species once separated by geographical barriers may lead to hybridization and increasing replacement of native species by non-native invaders. Invasions have also altered global biodiversity, reducing it at local habitat scale, increasing diversity at regional scale and tending towards homogenization at global scales (Pauchard and Shea, 2006), with widespread ecological and evolutionary implications. Most of the ecosystems worldwide have already been affected to a greater or lesser extent by biological invasions (Parker *et al.*, 1999; Williamson, 1999; Olden and Proff, 2003; Olden *et al.*, 2004). The rate of invasions resulting from anthropogenic activities is increasing as global trade and travel increase (Sala *et al.*, 2000; Brown and Sax, 2004; Mckinney, 2006).

Considered the second largest global threat to biodiversity after direct habitat destruction (Walker and Steffen, 1999; Wilcove *et al.*, 1998; Vitousek *et al.*, 1997), the problem of biological invasion is growing rapidly in severity. Regardless of their often harmful characters, invasions provide unique opportunities to understand some basic ecological processes. The subject of biological invasion is widely addressed in the literature, but some recent reviews indicate that research has focused separately on understanding the factors influencing the invasiveness (the capacity of species to invade an ecosystem) and invasibility (susceptibility of an ecosystem to be invaded) (Lodge,

1993; Richardson *et al.*, 1992; Hector *et al.*, 2001). Some progress has been made in the integration of information from case studies and theory to produce general rules for understanding invasion ecology, but much more work is needed.

It has been suggested that it is unrealistic to expect there to be robust general rules for predicting which organism will invade and which environment will be invaded, given the extreme complexity of the many interactions that affect the outcome of introductions (Gilpin, 1990; Lodge, 1993; Vermeij, 1996; Richardson and Higgins, 1998).

### *Invasive alien plants in South Africa*

The introduction of alien plant species is one of the global-change factors threatening the conservation of native species and integrity of the all ecosystems worldwide (Pimentel *et al.*, 2005), with significant economic repercussions that challenge scientists and land managers today (Pimentel *et al.*, 2005). This process has impacted ecosystems at different levels, such as genetic contamination (i.e., hybridization), altered population dynamics and modified community structure and ecosystem processes (Parker *et al.*, 1999).

South Africa's natural and semi-natural ecosystems have been severely affected by invasive alien plants (Macdonald *et al.*, 1986; Richardson *et al.*, 1997). The influx of alien plant species into South Africa began long ago, especially once the Cape of Good Hope became a major refurbishing stop for European ships. Thousands of species of plants have been introduced and cultivated for various purposes. South Africa became one of the focal points in Africa for the establishment of alien plants from all over the world, especially from Australia and from South and Central America. Since then, the spread of these alien plants has affected most South African ecosystems (Richardson *et al.*, 1997).

One of the reasons for introduction of woody alien plant species was the absence of natural resources such as fast-growing timber trees in the Fynbos and Grassland biomes of South Africa. Most widespread invasive trees and shrubs were introduced intentionally to establish timber plantations (King, 1943; Le Maitre, 1998), woodlots for fuel, or to stabilize drift sand. Other species were introduced to supply shade, or for aesthetic

purposes. In the more arid areas, plants such as *Agave*, *Atriplex*, *Opuntia*, *Prosopis* were introduced to stabilize erosion, control livestock movement or supply shade and drought forage (Milton *et al.*, 1999).

Some of the major woody invaders were introduced to South Africa before 1870 and most have been planted all over the country (Richardson *et al.*, 1992). Invasive alien plants have become a major problem in South Africa, impacting on both human well-being and biodiversity. They cause problems in agricultural lands, river courses and catchments, and in wilderness and conservation areas.

Estimation has been made of the spatial extent of alien plant invasions in South Africa. Versfeld *et al.*, (1998) in their national survey, showed that about 10 million hectares, approximately 6.8% of South Africa, have been invaded to some degree by woody alien plants. Henderson (2001) stressed that alien plant species have already invaded an area equivalent to the size of the KwaZulu-Natal province and they are spreading so quickly that, if left alone, the area invaded could double within fifteen years.

The South African Plant Invader Atlas (Henderson, 1998) provides some quantification of the extent of invasions in forest, fynbos, grassland, Karoo (Nama and Succulent Karoo combined) and savanna biomes. Several studies have produced detailed distribution maps of invasive alien plants at finer scales for some regions and biomes, but detailed studies are still needed in all biomes for all the problematic and emerging alien plants for an accurate prediction of alien plants invasion in South Africa.

The highly diverse Fynbos biome is the most heavily invaded of the biomes. Dense stands of alien *Acacia* and *Pinus* species now occupy mountains and lowland terrestrial areas as well as river courses (Van Wilgen *et al.*, 2001). Grassland and savanna are also extensively invaded, but mostly in the moister regions and particularly along river courses. The semi-arid Nama and succulent Karoo biomes (semi-arid low shrublands) are invaded by mesquite trees (*Prosopis* species), cacti (*Opuntia* species) and saltbushes (*Atriplex* species). However, information on distributions of invasive alien plants in these biomes in South African ecosystems is still poorly quantified (Milton *et al.*, 1999). The forest biome has been heavily invaded but the extent of invasion has yet to be accurately quantified (Richardson *et al.*, 1997).

Riparian areas have been particularly severely invaded, for example by trees such as jacaranda (*Jacaranda mimosifolia*) and syringa (*Melia azedarach*) which have spread into semi-arid savanna by dispersing along perennial rivers. Studies have also documented that woody invaders, notably *Prosopis* species, several cacti (*Opuntia* species) and saltbushes (*Atriplex* species) have invaded large areas of alluvial plains and seasonal and ephemeral watercourses in the Nama Karoo, Succulent Karoo and also thicket biomes (Milton *et al.*, 1999).

The most damaging group of invaders in South Africa are woody plant species, trees and shrubs, that have invaded more than 4.6 million ha (Versfeld *et al.*, 1998), among them species in the genera *Acacia*, *Hakea* and *Pinus*. There are many more and the ecological and economical impacts of these invasions have been fairly well assessed, but the potential for spread of those species is not always fully understood (Van Wilgen *et al.*, 2001).

The problems associated with plant invasions in South Africa are escalating rapidly. Since limited resources are available for fighting alien plant invasions, choices need to be made about where to focus control efforts and research and which species to target for control. Some studies in South Africa and elsewhere have focussed on the history of introduction and the dynamics of invading species at various hierarchical levels (Richardson *et al.*, 1997). Others have sought to identify the main factors determining invasion at local (Milton and Hall, 1981), regional (Anneke and Moran, 1978), nation-wide or indeed larger scales level (Richardson and Bond, 1991; Rejmánek, 2000; Vilà and Pujadas, 2001; Pyšek *et al.*, 2002; Hulme, 2003). Further investigation needs to be done to understand why particular plant species succeeds in invading new habitats while other species fail, the factors controlling the susceptibility of an area to invasion, and the barriers to invasion experienced by some plant species in certain habitats.

Although some invaders are already well established and have caused substantial change of many South Africa biomes, others are at the early stage of invasion. Research and management programmes should target not only well-established invaders, but also give appropriate attention to emerging problems.

South African studies dealing with alien plant invasion have mainly focused on established invasions or priority taxa such as *Acacia*, *Hakea*, *Opuntia*, *Pinus* (Anneke and Moran, 1978; Milton and Hall, 1981; Le Maitre *et al.*, 2000, Richardson, 1998; Le Maitre *et al.*, 2002; Rouget *et al.*, 2002), but little attention has been given to species already identified as emerging invaders or potential invaders but which are in the early stages of the process. Potentially harmful taxa need to be also assessed, before they spread widely and have major ecological or economic impacts.

### *Need for predictive understanding*

The first challenge in the field of invasion ecology is to understand the factors that determine whether or not a species will become an invader. Those factors include both the species and the habitat. There are several reasons why alien plants might fail to become invasive. One of them would be the unsuitability of the climate of the new region, such that an introduced plant species cannot establish in sufficient numbers to overcome local enemies. There are many descriptions of the attributes of ideal invaders. Among them is Baker's (1965) description of "the ideal weed" as one that germinates in a wide range of physical conditions, grows quickly, flowers early, is self-compatible, produces many seeds which disperse widely, reproduces vegetatively and is a good competitor.

However, there are tradeoffs in plant allocation of resources to stress tolerance, reproduction and rapid growth (Grime, 1977), so that, as Baker (1965) points out, no species is likely to possess all these characters. Moreover, some species do not need all these characters to invade successfully, and possession of the characters of an ideal weed does not mean that a species can invade all habitats. Those "ideal weed" attributes may be useful in understanding some patterns concerning alien plant invasion and also could be used as checklist for potential warning signs.

Residence time, i.e. how long an alien plant has been present in the region, is also one of the characteristics which could provide information about invasion potential. Invasion status is, in general, closely related to residence time as shown for several data sets from various parts of the world (Pyšek *et al.*, 2003). This is because invasions are

often triggered by rare events; the longer a plant is present at a given locality, the better its chance of experiencing conditions conducive to invasion (Rejmánek, 2000). Knowledge of the residence status of alien plant species in a region is important since assessment of species invasiveness is sometimes made after too short a residence time.

The risk associated with an alien plant species is a function of its potential to spread and become abundant, together with its potential to alter natural environments, displace indigenous species or reduce the flow of water or other ecosystem services. Some woody plants introduced to South Africa a century ago appear to have naturalised without becoming invasive (see chapter 2 for definitions), despite good climatic matching. One such species is the focus of this thesis, *Schinus molle* L.

The long-lived and drought-tolerant, hardy Peruvian Pepper tree (*Schinus molle*) was first introduced to South Africa in the middle 1800's. It is indigenous to the arid zone of South America (Chile and Peru). For the past 50 years, the tree has been planted at many picnic sites and along South Africa national and provincial roads. Unlike many other alien trees, it has shown little sign of becoming invasive. But this apparent non-invasive behaviour may be an artefact of the observation timescale and initial planting sites. A tree with a life span of 200 years or more cannot be expected to grow fast or recruit abundantly, unless conditions are particularly favourable.

In South Africa, the naturalization of *S. molle* into savannas is usually from trees planted for shade along roadsides or in gardens. *S. molle* has already colonized some disturbed areas in semi-arid and arid regions of South Africa, such as mine dumps and river beds, and the species is now showing clear signs of invasive behaviour in those areas (Figure 1.1).

In North America, where *S. molle* is growing outside its natural range, its seeds are dispersed by animals and by water. At several upland sites in California, *S. molle* seeds were found in crevices on rocks covered with bird droppings, and the rather large, hard-seeded *S. molle* drupes are also regurgitated by mockingbirds, cedar waxwings, and bluebirds (Howard and Minnich, 1989). Coyote scats often consisted almost entirely of undigested *S. molle* seeds with broken exocarps (Howard and Minnich, 1989). We assume that the same process of dispersal might be occurring in South Africa. The

seedling survival rate is not known, but is probably promoted by moist sites (drainage lines) and conditions (big rain events), and reduced by competition from grasses, and the influence of browsing and grazing mammals.

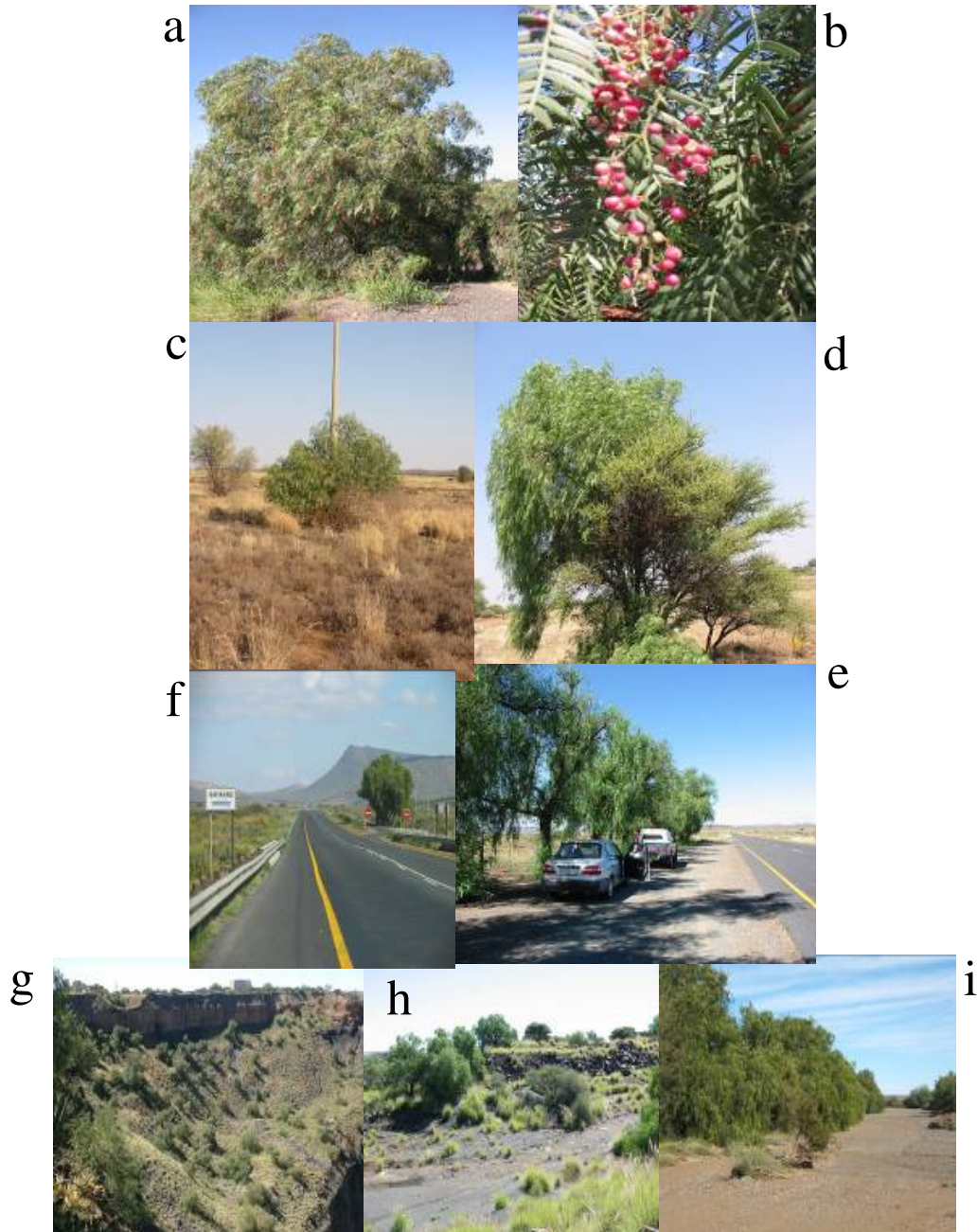
In South Africa, there are no reliable answers to questions such as which ecosystems and habitats are susceptible to *S. molle* invasion, and what the ecological and economic impacts invasion by this species could cause.

## **Schinus molle L.**

### *General description*

*Schinus molle*. L. in the family Anacardiaceae is very familiar as a cultivated ornamental in southern and northern California (USA), Mexico, the arid parts of Australia and in many other moderately warm and semiarid regions, where it is known as Pirul, Peruvian mastic and pepper tree. The tree is fast-growing, up to 15-20 m tall; evergreen, with alternate pinnate leaves (Copeland, 1959; Henderson, 2001). The branchlets and leaves are often pendant, and the small yellow flowers are abundant in terminal clusters. The species is dioecious.

The pepper tree does not have the typical reproductive cycle of plants of temperate regions. It produces flowers continually and maintains a continuous seed supply for germination whenever conditions are favourable (Kramer, 1957). Seeds are widely dispersed by birds, mammals, and running water, so that trees occasionally become established in washes, canyons, old fields, and rock outcrops (Howard and Minnich, 1989); once well established seedling mortality is rare. Growth is greatest in the warm season until soil moisture is depleted (Nilsen and Muller, 1980a, b). With continuous seed production and reliable dispersal the major problem to establishment appears to be germination and seedling survival.



**Figure 1.1:** Examples of some features of *Schinus molle* that were investigated during this study: (a) *S. molle* showing large numbers of conspicuous fleshy fruits, (b) close-up of *S. molle* fruits; (c) *S. molle* plant established under a pole – the result of dispersal by birds, (d) *S. molle* growing in association with an indigenous *Acacia tortilis* tree (e & f) *S. molle* planted along roads, (g & h) naturalized *S. molle* in areas disturbed by mining, (i)



self-sown *S. molle* trees along the banks of an ephemeral river. Photo credits: D.M. Iponga (a,b,c,d,g,h); S.J. Milton (e, i); D.M. Richardson (f).

### *Natural distribution*

The Anacardiaceae comprises of 60 to 80 genera and about 600 species, mostly trees and shrubs, among them cashew, pistachio, mango, sumac and poison oak (Cronquist, 1981). The family is distributed through tropical and warm temperature regions, with a few taxa extending into the cool temperate northern hemisphere. The genus *Schinus* has 28 species and its centre of distribution is northern Argentina (Barkley, 1944, 1957). Some studies have suggested that *Schinus* species may be native to Argentina, southern Brazil, Uruguay, Paraguay, Chile, Bolivia, and Peru (Barkley, 1944, 1957). *Schinus molle* is the only species that historically extended its range north into Mexico but its origin remains under discussion (Barkley, 1944, 1957; Bahre, 1979; Corkidi *et al.*, 1991).

*S. molle* grows normally along water courses and elsewhere mostly at high altitudes (Copeland, 1959; Kramer, 1957; Howard and Minnich, 1989). In Peru the species grows up to an elevation of 3300 m, (Corkidi *et al.*, 1991; Bahre, 1979) and it occurs in similar habitats in northern Chile.

### *Distribution beyond natural range*

*Schinus molle* is now well established and assimilated in many plant communities throughout tropical and warm temperature regions. It can be found in western South America and is widely distributed throughout Mexico. The tree was brought to Mexico around 1540 or 1550 by the Spanish, where it was spread by man and birds (Corkidi *et al.*, 1991; Bahre, 1979). The spread of the tree in Mexico is attributed to birds which eat the seeds to which they are attracted by the red colour when ripe (Kramer, 1957). It was then brought to Europe in the early 18th century, probably first to Spain from where it was dispersed by man to other Mediterranean countries.

In the early 18th century the tree subsequently became very widespread in Spain, Italy, and on the French Riviera, due to its value as an amenity and ornamental tree. *S.*

*molle* is now locally naturalized throughout the Mediterranean region, and semi-arid subtropical areas of the Canary Islands, India, Australia, Hawaii, the south-western United States, Mediterranean Europe, North Africa, Southern Asia and southern Africa (Kramer, 1957; Barkley, 1944; Markham, 1864).

In South Africa the tree was introduced around 1835 and was valued by early colonists for its fast growth compared to most indigenous species. *S. molle* has been known to cause hay fever, asthma, and also dermatitis in South Africa (Potts, 1919, 1922). The research that has been done on the *S. molle* is sparse; much of its introduction history is undocumented. Naturalization of *S. molle* in South Africa is now obvious in semi arid savannas. However, little is known about life history and the ecology of the tree.

### *The uses of S. molle*

The main reason for the importation of *S. molle* into different regions is not clearly known. But the use of the tree is less intensive in countries where it is non-native compared to its country of origin (Goldstein and Coleman, 2004). From the intensive use in Peru as a source of medicine, beverages, and possibly dye, it declines to minor usage in Mexico. In California and in Europe the tree is used only as an ornamental, because of its pretty leaves, its wide, shade-giving crown, its yellowish flowers and reddish berries (Howard, 1986), but it is not used for any of the purposes for which it is so highly esteemed in Peru.

In South Africa the use of the tree is not well documented. As mentioned previously, the tree was valued by early colonists for its fast growth compared to most indigenous species, shade and its heat and drought tolerance and it is mostly used as an ornamental tree (Milton *et al.*, 2007; Iponga *et al.*, 2008). However it is also used for medicinal purposes, keeping insects out of clothing, for curing headaches and also as an antibacterial by some communities in Africa (see Watt and Breyer-Brandwijk, 1932), but this use has not been well documented in literature. It was also planted next to the graves of English soldiers during the Anglo-Boer war in the late 1800 s (unpublished records Kimberley War Graves Trust).

## Aims and objectives of the research

The research described in this thesis comprises a detailed study of the processes and potential for *Schinus molle* (pepper tree) invasion in southern Africa, particularly in semi-arid savanna ecosystems. The climatic suitability envelope model of potential spread of *S. molle* developed by Rouget *et al.*, (2004) showed that suitable habitat existed in 57.4% of quarter-degree squares (QDS) in South Africa. Within biomes, suitable habitat occurred in 63.8% of Succulent Karoo QDS, 87.72% of Nama karoo QDS and 50% of savanna QDS (Rouget *et al.*, 2004).

The main hypothesis for this study is that there are physical and ecological barriers to invasion that prevent *S. molle* ever reaching the potential predicted from the broad-scale climatic envelopes. Instead of purely climatic control, the invasive potential of a plant species may be limited by failure to set viable seed, to disperse, to germinate, to establish as a seedling, or to reach reproductive maturity. External factors that may affect one or more of these life history stages are:

- a) Pollinators, seed dispersers, seed predators and pathogens that influence the abundance of viable seed (includes production, viability and dispersal)
- b) Climatic conditions – including temperature maxima and minima and humidity
- c) Water availability (quantity, timing and distribution of rainfall, surface or ground water, soil water-holding capacity)
- d) Competition with indigenous herbaceous or woody plants for water or any other resources
- e) Disturbance regime (frequency of herbivory, fire or frost that cause dieback or top kill of saplings)
- f) Suitable microsites for establishment

The main objectives of this research are to refine predictions about the spatial limits and potential rates of spread for *S. molle* and to gain a better understanding of the potential distribution and impact of this species on South African ecosystems under scenarios of climate and land use changes. The following specific questions were addressed:

1. What are the physical and biological barriers to dispersal, germination and establishment of *S. molle* in semi-arid savanna?
2. At the landscape level in semi-arid savanna, how do conditions, interactions or disturbances influence the survival and growth of *S. molle*?
3. Does *S. molle* show similar demographic trends in all major South African biomes (fynbos, karoo, grasslands, savanna, and forest)?
4. Does *S. molle* have the potential to become a transformer (see chapter 2 for definition) in any South African vegetation types?
5. How can the climate-based model of *S. molle* invasion potential for South Africa be improved so as to predict invasion rates and probabilities at habitat scale?
6. What is the relative importance of understanding interactions at micro-habitat, habitat, landscape, region and biome scales in prediction of the distribution and spread of fleshy fruited alien species?

Finding answers to these questions involved comprehensive analysis of the literature on the natural history and ecology of the selected species and of related or ecologically comparable invasive species; field observations to document its seed production, seed dispersal, germination requirements, and growth rate under gradients of rainfall and disturbance in South Africa, and experiments to ascertain the effects of soil type, herbivory and facilitation by other tree species, on seedling survival. Seed dispersal mechanisms were quantified using a variety of field techniques. Establishment probabilities were compared using transplant experiments and demographic data for a variety of microsites defined in terms of availability of moisture, shade and soil nutrients, and potential competition from woody and herbaceous plants.

The research contributes to an improved understanding of *S. molle* life history, ecology and dispersal mechanisms with a view of understanding the relative sensitivity of the population to reductions in each life stage, understanding the vulnerability of each life stage to biological control, and prioritizing stages for control of the species during its lifecycle, and will develop a lifecycle model (matrix model of population growth) for *S. molle* from seed bank to reproductive stage. The knowledge gained should improve our ability to make reliable predictions about the invasiveness of *S. molle* at landscape,

regional, nation-wide or indeed larger scales and the control these species in South Africa. This would inform policies for regulation and control of this species. A more general outcome of the work will be an improved understanding of the factors that make some species highly invasive when moved to new habitats.

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# Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa

**Chapter 1:** General problem of biological invasion in South Africa landscape

**Chapter 2:** Dynamics of alien woody plant invasions: review of processes and ecological impacts

## Main objectives

**Chapter 3:** Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 4:** *Megastigmus* wasp damage to seeds of *Schinus molle* (Peruvian pepper tree) across a rainfall gradient in South Africa: Implication for invasion

**Chapter 5:** Seed set of the invasive alien tree *Schinus molle* (Anacardiaceae) in semi-arid savanna, South Africa: the role of pollination and selfing

**Chapter 6:** Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 7:** Performance of seedlings of the invasive alien tree *Schinus molle* under indigenous and alien host trees in semi-arid savanna

**Chapter 8:** Superiority in competition for light: a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Peruvian pepper tree) in South Africa

**Chapter 9:** Distribution of the invasive alien tree *Schinus molle* in western South Africa: current determinants and projections under scenarios of climate change and management.

**Chapter 10:** General conclusions and recommendations

## CHAPTER TWO

### DYNAMICS OF WOODY PLANT INVASIONS: A REVIEW OF PROCESSES AND ECOLOGICAL IMPACTS

#### Introduction

Invasions of non-native species (i.e. those moved to regions beyond their natural dispersal range) pose a major threat to the conservation of native species and integrity of ecosystems worldwide. It has become a major environment problem and a focus of ecological research (Vitousek *et al.*, 1997; Dukes and Mooney, 1999; Higgins *et al.*, 1999). Invasion ecology has emerged as an important interdisciplinary field of science, although the desire to turn this discipline into a predictive science remains a challenge. This is not to say that invasion ecology should be treated uniquely on a case-by-case basis, but rather that invasions integrate large-scale ecology and evolutionary biology in a human-dominated world and that predictions are inherently extremely complex.

Invasion ecology has organized itself around three main topics: a) invasiveness (the delineation of features of an organism that enable it to invade); b) vulnerability to invasion or “invasibility” (the properties of a community or ecosystem that render it susceptible to invasion by alien plants); and c) impacts. Each of these topics addresses a basic question in community ecology but also has practical applications for understanding invasion patterns, and for controlling invasive species (Alpert *et al.*, 2000).

However, the overriding frustration in invasion ecology has been that very general answers to explain questions related to patterns across a wide range of systems have been elusive. Some authors argue that there are no generalizations to be made other than trivial correlations that have very limited value for management (Rejmánek, 2005). The most important factor preventing the formulation of generalization at a scale useful to managers might be the influence of the environment.

This introductory chapter first explains concepts and definitions related to the different terminologies used in field of invasion ecology. Those concepts will contribute

to understanding various descriptions, processes and / or phases that may be identified in the invasion of new regions by introduced taxa. The chapter goes on to focus on understanding the processes of alien plant invasion, processes that will contribute to the understanding of the patterns of alien plant invasion in semi-arid and arid savannas and woodlands. I also describe what is known about driving forces behind alien plant invasions, processes which have a direct influence on the rate and likelihood of invasion.

The main aim of this chapter is to explore why some plant species establish as invaders while others do not, and why some habitats, regions or biomes seem more prone than others to invasions from some plant species. Understanding what makes aliens more successful than indigenous plants in disturbed and anthropogenic habitats, and the processes contributing to a particular mix of species are among the challenges that this chapter is trying to explore. The discussion in this review will cover the problem of terminology in invasion ecology, the process of invasion and factors contributing towards invasion success. Given that the subject of this thesis, *Schinus molle*, is a fleshy-fruited tree, the focus will be on dispersal of woody fleshy-fruited alien plants, the mechanisms for invasions by this guild of species, and their potential impacts on ecosystem processes.

## **Concepts and terminology**

Invasion ecology is a fast-developing branch of ecology (Williamson and Fitter, 1996). Recent developments in this field have brought the need to standardize terminology (Richardson *et al.*, 2000a; Pyšek *et al.*, 2004). The past few decades have seen a rapid increase in the number of studies devoted to plant invasions. On the other hand, the accumulating body of knowledge has unfortunately also spawned increasing confusion in terminology with lack of clarity and consistency in the use of some terms, especially in recent invasion ecology literature (Richardson *et al.*, 2000a; Pyšek *et al.*, 2004). For the purpose of this study, terms that are commonly (but often not accurately) used in the literature, are defined.

However, this is not to say that the terminology given in this chapter will fit in every case in the field of invasion ecology. The interpretation of invasive species distributions will probably still remain context-dependent and the choice of terminology

will determine the perceived range, spatial distribution, rate of spread and environmental drivers. For this reason, the terminology of invasive species should be clearly defined before trying to explain various and complex invasion patterns.

Every species of plant, animal, fungi, bacteria and other organism has a home in some part of the world, where it has evolved and existed over long time periods due to the influence of different natural forces like climate, moisture, fire, soils and species interactions (natural range) (Richardson *et al.*, 2000a; Pyšek *et al.*, 2004). A native (indigenous) plant species is the one that occurs in a particular region, ecosystem, and habitat without direct or indirect human actions. Organisms that occur artificially in locations beyond their known historical natural ranges are considered as non-native (alien, foreign, introduced, or non-indigenous) (Richardson *et al.*, 2000a; Pyšek *et al.*, 2004). Non-native can also refer to species brought in from other continents, regions, ecosystems and even other habitats (Weber, 1997). From a biological-invasion perspective, the biogeographical approach (alien species encroach the areas where they are not native) should be preferred (Rejmánek, 2000). Some recent checklists and catalogues in the field of invasion ecology now follow this approach (Pyšek *et al.*, 2002).

The definition of native and non-native species should be based on the involvement of people moving the species from one region to another and political boundaries should not be considered to define alien species, because they do not correspond to biological and ecological barriers (Richardson *et al.*, 2000a). A naturalized species is defined as one that has the ability to establish a self-perpetuating population outside its natural range without the input of resources or direct intervention by humans. Naturalized plant species often recruit offspring freely, but mainly near adult plants, and do not necessarily invade natural ecosystems (Richardson, 2001; Richardson *et al.*, 2000a).

Richardson *et al.*, (2000a) stated that naturalization starts when environmental barriers do not prevent individuals from surviving and when various barriers to regular reproduction are overcome. Pyšek *et al.*, (2004) stated that naturalized plants are alien plants that sustain self-replacing populations for at least 10 years without direct intervention by people (or in spite of human intervention) by recruitment from seed or ramets (tillers, tubers, bulbs, fragments, etc.) capable of independent growth. Table 2

gives the combined suggestions for definitions and standardization of invasion ecology terminologies proposed by Richardson *et al.*, (2000a) and Pyšek *et al.*, (2004) and which will be the standard in this thesis.

**Table 2:** Suggested standardized terminology and definitions in invasion ecology (based on definitions proposed by Richardson *et al.*, 2000a and Pyšek *et al.*, 2004).

Terminology	Synonyms	Proposed definitions	Interpretations
Native plants	Indigenous plants	Taxa that have originated in a given area without human involvement or that have arrived there without intentional or unintentional intervention of humans from an area in which they are native	Excluding products of hybridization involving alien taxa since human involvement in this case includes the introduction of an alien parent
Alien plants	Alien plants; non-native plants; non-indigenous plants	Plant taxa in a given area whose presence there is due to intentional or accidental introduction as a result of human involvement, or which has arrived there without the help of human from an area in which they are not native.	Human involvement here does not include habitat changes, global warming, atmospheric nitrogen fertilization, acid rain, etc. Native species that change their geographical range due to these processes should not be considered aliens unless there is clear evidence of significant leaps in distribution attributable to human-aided dispersal of propagules.



<b>Terminology</b>	<b>Synonyms</b>	<b>Proposed definitions</b>	<b>Interpretations</b>
Casual alien plants	Waifs, transients, occasional escape, ephemeral taxa, persisting after cultivation	Alien plants that may flourish and even reproduce occasionally in an area, but which do not form self-replacing populations, and which rely on repeated introductions for their persistence	
Naturalized plants	Established plants	Alien plants that reproduce consistently and sustain populations over many life cycles without direct intervention by humans; they often recruit offspring freely, usually close to adult plants.	Naturalized plants do not necessarily invade natural, semi-natural or human made ecosystems.

<b>Terminology</b>	<b>Synonyms</b>	<b>Proposed definitions</b>	<b>Interpretations</b>
Invasive plants	Established plants	Invasive plants are a subset of naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants, and thus have the potential to spread over a large area.	Approximate scale: > 100 m in < 50 years for taxa spreading by seeds and other propagules; 6 m in 3 years for taxa spreading by roots, rhizomes, stolons, or creeping stems.
Weeds	Pests, harmful species, problem plants, noxious plants	Plants (not necessarily alien) that grow in sites where they are not wanted and which usually have detectable economic or environmental effects.	The term is anthropocentric and a plant is considered a weed if it interferes with human objectives. The term environmental weed or species of environmental concern are used for alien plant taxa that invade natural vegetation, usually adversely affecting native biodiversity and/or ecosystem functioning.

<b>Terminology</b>	<b>Synonyms</b>	<b>Proposed definitions</b>	<b>Interpretations</b>
Transformers	Edificators (environmental forming plants)	A subset of invasive plants (not necessarily alien) that change the character, condition, form or nature of the ecosystems over a substantial area, relative to the extent of that ecosystem.	The term is an ecological one; a plant can be a transformer without receiving human attention by way of economic concern or control efforts. Several categories of transformers may be distinguished: excessive users of resources (water, light, oxygen), donors of limiting resources (nitrogen), fire promoters / suppressors, sand stabilizers, erosion promoters.

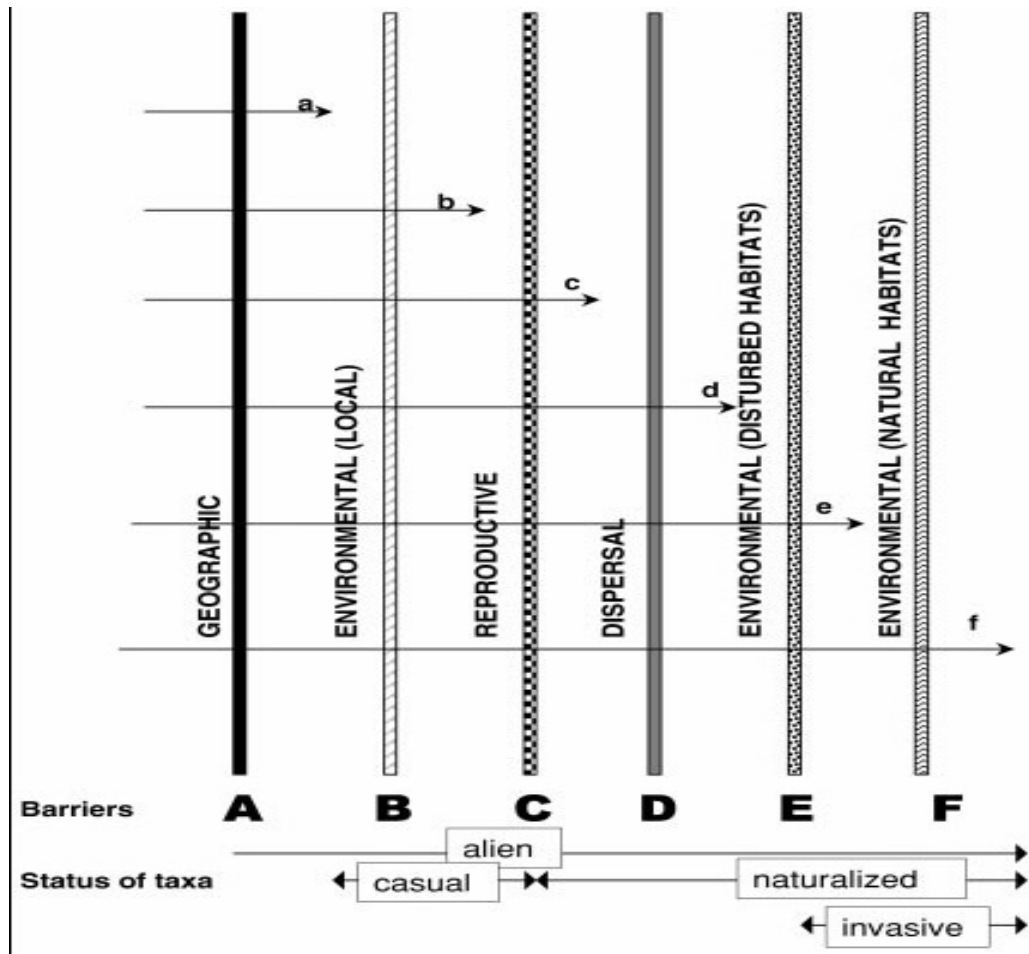
<b>Terminology</b>	<b>Synonyms</b>	<b>Proposed definitions</b>	<b>Interpretations</b>
Invasibility		The properties of a community or ecosystem that render it susceptible (or resistant) to invasion by alien plants.	
Invasiveness		The delimitation of features of an organism (e.g. life history traits) that enable it to invade (i.e. to overcome various barriers to invasion).	

An invasive alien plant has come from a donor biota with the direct aid of humans, and establishes itself and expands its range in new habitat (Mack, 2000; Richardson *et al.*, 2000a). Invasion will be considered as a process that enables a taxon to overcome various abiotic and biotic barriers; it is the geographical expansion of a species into an area not previously occupied by that species and its measurement should be based on population growth and spread in the new region (Ehrlich, 1986).

## **Invasion processes and barriers to invasion**

The processes of invasion and invaders have been studied for many decades and a few attempts to generalize the processes have been made (Elton, 1958, Ehrlich, 1986, Lodge, 1993). However, because of the strong particularity of individual cases, doubts have been raised about the existence of general patterns relating to invasion processes (Ehrlich, 1986). Now it is important to redefine the approach of looking at the invasion processes and to identify crucial questions which will lead to some outcome on a broad comparative context.

Plant movements in the landscape depend on dispersal and the ability to find suitable habitat for recruitment (Milton *et al.*, 2007). In order to extend their population ranges, plants must overcome numerous barriers, including: geographic barriers, which must be overcome by dispersal; habitat barriers, that require pre-adaptation and ecological interactions with other species in the habitat, or genetic adjustment to the condition of the new environment; biotic barriers, that integrate the forces of predation, herbivory, competition, and; interference, or the new mutualistic relationships that must be developed (Richardson and Bond, 1991; Richardson *et al.*, 2000b; Richardson, 2001). In general, plant invasions in natural and semi-natural ecosystems involve the fundamental phases of introduction, naturalization and spread, on the basis of relevant barriers that should be overcome in the new habitat (Figure 2).



**Figure 2:** A schematic representation of major barriers limiting the invasion of introduced plants (Richardson *et al.*, 2000a). Each horizontal line represents a population migration. The likelihood that any emigrant population will survive in transit and enter a new range is low.

In invasions, introduction is, by definition, mediated by humans, providing alien plant species assistance in overcoming geographical barriers. The arrival phase is the consequence of introduction; this phase can be studied by assessing routes of transport of an invader; such analyses need to consider the frequency of introduction, number and places to which it was introduced, and number of genotypes introduced and also potential dispersers. The phase of naturalization as defined in Table 2 is a result of the new

population being able to sustain itself through reproduction and recruitment leading to population persistence in the recipient region, at least over several life cycles.

However, in practice it might be difficult to determine whether a naturalized species has become an invader. Some species may establish so frequently that they appear to maintain local populations, when in fact, the populations are continually being recharged by dispersal from elsewhere (Mack, 2000). Such species are better termed “casuals” (Richardson *et al.*, 2000a). In many cases, such frequent introduction pressure means that populations are sufficiently large that the probability of extinction due to environmental stochasticity is low (Panetta and Randall, 1994). Naturalization often results in such cases, where established new self perpetuating populations, undergoes widespread dispersal and becomes incorporated into the resident flora (Richardson *et al.*, 2000a).

The final stage of invasion is the integration and spread of alien plants in the new habitat, a phase in which population growth and spread to new areas within the recipient region occurs. The interaction with the local biota and disturbance regime, and displacement of native elements can also occur (Richardson and Bond, 1991). However, understanding those invasion processes might enhance the ability to make reliable prediction on the spread of alien plants and also better understanding of the field of invasion ecology.

## **Dispersal of alien trees and shrubs**

### *Dispersal processes*

Seed dispersal of plants is a crucial process which determines the structure and dynamics of the plant population in the community. Seed dispersal can be seen primarily as a spatial demographic process and can be defined as the movement of seeds away from their parent plants (Nathan and Muller-Landau, 2000). Dispersal of seeds usually declines with increasing distance from the seed source (Willson, 1993; Higgins and Richardson, 1999). Fleshy-fruited trees produce seed crops that are dispersed by animals. Dispersal can limit recruitment of plant species if the probability of seeds being dispersed is lower than the probability of dispersed seeds becoming established plants (Herrera, 1995).

However, dispersal potential and different modes of dispersal vary greatly. Some processes such as wind, water and vertebrates can potentially carry seeds far from the parent plant. But ants, for example, typically generate shorter seed-dispersal distances (Willson, 1993). There is also a great variation in the dispersal potential within each general mode of dispersal. Birds are mainly short-range dispersers since they retain seeds in their guts for relatively short periods (usually less than 1.5 hours), often regurgitate seeds, and generally move relatively short distances during digestion (Godoy and Jordano, 2001). Horvitz and Le Corff (1993) found that bird-dispersed species went further than ant-dispersed species. Nevertheless, bird dispersal can direct plants to ideal germination sites (Milton *et al.*, 2007). The ability of propagules of alien plant species to disperse and invade natural or semi-natural habitats in a new region will be greatly enhanced by adaptations for transport by animals (birds, mammals) or any moving organisms or objects.

Dispersal patterns of alien plants that lead to species naturalization and invasion depend not only on the mode of dispersal of seeds, but also seed size, seed caching, seed predation, seed bank dynamics, and germination processes (Rejmánek and Richardson, 1996). Given that the focal species for this thesis, *Schinus molle*, is fleshy fruited, further discussion will focus mainly on the ecology of bird dispersed fleshy-fruited plants, fruit display, fruit quality, fruit removal rates, bird behaviour and microsite patterns that may influence the distribution of fleshy-fruited alien plant species in the landscape.

### *Dispersal of fleshy-fruited woody species*

The importance of understanding of seed dispersal patterns in the battle against invasive plants is widely recognized (Lonsdale *et al.*, 1988; Buckley *et al.*, 2006). However, the effectiveness of fleshy-fruited plant dispersal does not only rely on the quantity of dispersed viable seeds, but also relies on features of the habitat receiving the seeds. These include the distance from seed sources, and biotic and abiotic features of the microsites receiving the seed (Schupp, 1993; Herrera, 1998).



### *Fruit display type*

In several studies, invasive plants have been shown to produce more fruits than their native congeners, contributing to their enhanced dispersal when compared to native species (Sallabanks and Courtney, 1992; Vila and D'Antonio, 1998). In South Africa, invasive plants also tend to have larger and more conspicuous fruit displays than native species (Knight, 1986). The characteristics of the fruits themselves such as fruit size can also play a significant role in determining which animals disperse them (Jordano, 1995; Corlett, 1996). In general, large frugivores can handle a wider range of fruit sizes than small frugivores (Noma and Yumoto, 1997). Smaller fruits predominate among both indigenous and invasive plants, and are accessible to a larger variety of fruit-eating birds (Kitamura *et al.*, 2002). Plants with large fruits have fewer bird dispersers in both native and invasive assemblages, which may limit the potential for range expansion (Rey *et al.*, 1997).

### *Fruit quality*

The nutritional quality of fruit pulp depends on the digestive abilities of frugivores, and may play an important role in fruit choice (Martínez del Río and Restrepo, 1993). Snow (1965) suggested that adaptive strategies of fruit production, presentation, and nutritional reward are intended to attract the greatest number and variety of potential dispersers. Fruits coming from different tree species may differ in energy and nutritional quality. However, the nutritional quality of invasive plant fruits is currently poorly documented, especially in comparison with co-occurring native plants (Vila and D'Antonio, 1998). The quantity of seed produced might be related to the quality of those seeds. Some fleshy-fruited plant species might be investing little energy and quality in individual seeds and fruits, but producing more seeds to attract a variety of opportunistic birds willing to use a superabundant, but nutritionally limited (per fruit basis) source of food. In other words, low investment fleshy-fruity plants should produce superabundant small fruits in peaked displays (Howe and Smallwood, 1982). In regard to this, alien plant species with abundant seed production might have a greater probability of increasing their range than species that produce few seeds, because most relationships between

frugivorous birds and invasive plants involve generalized dispersal systems (Richardson *et al.*, 2000b).

### *Fruit removal rates*

Frugivorous birds directly affect seed dispersal of fleshy-fruited plants through the number of seeds they remove (quantity component) and to where, and in what condition, those seeds are deposited (quality component) (Loiselle and Blake, 1999). High temporal and spatial variation of removal rates can be observed among individual plants in the same year and site (Alcántara *et al.*, 1997) or between years and sites (Parciak, 2002) with rates varying by several orders of magnitude. Phenological patterns of fruits are also highly important for plant population dynamics, since dispersal success depends on matching of fruit maturation and bird abundance (Herrera, 1995). The abundance of frugivorous birds varies at any site over time because many such species are migrants; this may have positive or negative impacts on fruits removal and dispersal.

The relative size and chemistry of the edible seed-covering, as well as environmental variables may influence the rate of seed removal and also dispersal (Mark and Olesen, 1996). In particular, knowledge is lacking about the ecological importance of removal rate, i.e. percent of total seeds removed from an individual plant (Willson and Whelan, 1993) and seed-dispersal distance (Portnoy and Willson, 1993). Considering long-term population dynamics, possible effects are hard to judge, as both habitat mosaics and dispersal processes are likely to change.

### *Bird behaviour*

In savannas, for example, where rainfall is unpredictable, many bird species show nomadic and erratic movement patterns (Gosper *et al.*, 2005), which may affect seed dispersal. However, plants with similar fruits might be used by similar frugivores, and subsequently might have similar distributions of dispersed seeds (Gosper *et al.*, 2005). But despite widespread similarities in fruit traits across many bird-dispersed plant taxa, generalizations about fruit choices remain difficult to make. Hence, knowledge of how

frugivorous birds increase propagation of alien plants in the ecosystem is required as a basis for understanding invasion potential of fleshy-fruited alien trees and shrubs, in order to manage and control them (Buckley *et al.*, 2006). Nevertheless, few studies on alien plant dynamics have explicitly included quantitative assessment of the role of frugivore mediated dispersal patterns (Gosper *et al.*, 2005).

### *Seed deposition in different microsites*

Dispersers may disseminate different numbers of seeds in a variety of microhabitats, and thus either shape the spatial distribution of the seedlings or limit recruitment by depositing large numbers of seeds in places that are unsuitable for recruitment. However, large plants clearly disseminate more seeds than small ones and fleshy-fruited seeds are mostly dispersed to microhabitats below suitable bird perches (Dean *et al.*, 1999; Wenny, 2000). The number of fleshy-fruited colonizers is particularly high under and near existing forest or scrub edges where perching by birds is common (Kollmann, 2000). It has been argued that directed dispersal agents take seeds to non-random places that are well suited for establishment and growth (Vander wall and Balda, 1977). A good example comes from the Australian saltbush, where closely related shrubs (*Sclerolaena diacantha* and *Dissocarpus bilflorus*) occupy ant mounds. Davidson and Morton (1981) showed that both ant-dispersed and non ant-dispersed plants grow well on mounds, but that ant-dispersed species have demonstrated poor growth off mounds. For instance, in the arid savanna of southern Africa, large solitary *Acacia* trees act as recruitment foci for bird-dispersed, fleshy-fruited plant species because plant and seed deposition is generally higher under trees than in the open grassland habitat (Dean *et al.*, 1999). This pattern is typical for bird-mediated seed dispersal and may be generally more common than expected (Dean and Milton, 2000; Kollmann, 2000).

However, from a long-term perspective, the ratio of open habitats to *Acacia* microsites and the spatial distribution of trees is unstable as a result of extrinsic factors such as precipitation (supports increase in woody plant cover), fire (reduces woody plant cover) or herbivory (may support either increase or reduction) (Jeltsch *et al.*, 2000).

Although these patterns have not been tested fully for fleshy-fruited alien plants, the same pattern of distribution could be observed in semi-arid and arid savannas.

## **Towards a predictive understanding of invasion success**

According to Williamson's "tens rule", (Williamson and Fitter, 1996), only 10% of introduced plant species will become naturalized while 10% of naturalized species become invasive. Many authors consider that an integration of information on environment type, disturbances and plant attributes is needed for understanding of the ecology of plant invasion (Hobbs and Humphries, 1995; Huston, 2004). For alien plants that clearly attain higher population sizes in the introduced than in the native range, understanding the demographic forces that lead to this difference is a necessary step towards understanding the mechanisms by which some species become invasive.

### *Species attributes*

Regardless of extensive research, identifying particular traits that are consistently associated with the tendency of plant species to be invasive have shown to be a battle for invasion ecologists (Reichard and Hamilton, 1997). However, knowing the history of past invasion of the species may help to speculate on the invasiveness (Reichard and Hamilton, 1997). For example, the success of species abundance in their native habitats may point to their superior ability to find a suitable habitat when introduced (Lodge, 1993). Species that occur more widely in introduced range and produce more propagules should have a better chance of being collected and transported, while scarce species are less likely to invade new habitats, although exceptions to this rule have been reported (Richardson *et al.*, 1994; Rejmánek and Richardson, 1996).

Certain life-history traits may be associated with invasiveness (small seeds, short juvenile periods and short intervals between large seed crops), fastest-growing species, some of those species are often used for commercial forestry (Rejmánek and Richardson, 1996). For example, in the genus *Pinus*, and indeed all woody plants, these traits seem important for allowing the species to disperse passively over long distances and win in

competition against other plants (Higgins and Richardson, 1998). Rejmánek and Richardson (1996) found that small seed mass (<50 mg), short juvenile period (<10 yrs), and short intervals between large seed crops (1 to 4 yrs) consistently separated invasive from non-invasive pines. Small seeds are correlated with increased seed output and are easily dispersed by wind, and persist longer in soil than do large seeds (Thompson *et al.*, 1993).

In contrast, large fruits are more attractive to vertebrate dispersers (Richardson *et al.*, 2000b). A key challenge to understand the relationship between fruit and frugivore is to relate fruit morphology and accessibility to removal by birds (Galetti *et al.*, 2003). In addition, ingestion of fruits by birds can sometimes enhance or inhibit the proportion of seeds that germinate (Barnea *et al.*, 1991). The outcome of passage of fruits through a digestive tract may be influenced by the animal species that consumes the seeds, the size and weight of the ingested fruits, and the time these are retained in the animal digestive system (Their retention time from ingestion to excretion) (Traveset, 1998; Renne *et al.*, 2000). However, the role of those traits in the invasion process are habitat specific (Pyšek and Richardson, 2007). Traits that confer an advantage at a given stage in the process and in a particular habitat may be neutral or even detrimental at another phase and for different habitats (Pyšek and Richardson, 2007).

### *Population size*

Populations with a small range are more likely to go extinct than larger ones as consequences of environmental stochasticity (Menges, 1998). Persistence and the opportunity for range expansion for an alien plant population in a new habitat are dependent on the maintenance of at least a minimum population size (Shaffer, 1981). The more plants are distributed across the habitats, the more likely some will survive combinations of stochastic events (e.g. frost, drought, predation, weather), simply as a result of growing in effective sites. For example, a metapopulation of alien plants would be more likely to persist under environmental uncertainty than a single population because its members are collectively sampling a potentially large array of microsites across a large spatial scale (Simberloff, 1988).

### *Propagule pressure*

Propagule pressure, the composite measure of the number of individuals released into a region to which they are not native (Carlton, 1996), is also a crucial determinant of the rate of geographical spread of alien plant populations (Rouget and Richardson, 2003). Propagule pressure incorporates estimates of the absolute number of individuals involved in any one release event (event size) and the number of discrete release events (event frequency). As the number of releases and/or the number of individuals released increases, propagule pressure increases (Lockwood *et al.*, 2005). Some evidence suggests that propagule pressure is the cause of many invasions by non-native species in their new habitat (Richardson *et al.*, 1994, Turnbull *et al.*, 2000).

The number of seeds produced by a plant is the biological propagule pressure that is independent from the effect of multiple introductions by people. For example, in the case of *Chromolaena odorata* which produces masses of seeds, this biological character may well be more important in terms of possible invasiveness of the species, than its distribution by people (de Rouw, 1991). The lack of invasiveness of *Pinus sylvestris* in South Africa might be, at least partly, due to the low propagule pressure (Richardson *et al.*, 1994). Studies showed that the chance of becoming established or naturalized, and invasiveness, increased markedly with an increase in the number of propagules introduced and the frequency of introduction, and with multiple introductions. That will include also the introduction at different times and from different source populations and also the number of genotypes introduced (Lockwood *et al.*, 2005). Moreover, more propagules reduce the likelihood of extinction and increase the chance of long-distance dispersal.

### *Residence time*

Residence time, the period since introduction of an alien species, is an important factor in determining the invasion potential of an alien plant species (Scott and Panetta, 1993; Hobbs and Humphries, 1995; Wilson *et al.*, 2007). Populations of introduced species often remain small and localized for long periods before they exhibit very rapid expansion. Until now little evidence is available to support hypothetical explanations for

these observed time-lags or lag phases. The reasons for these time-lags could be genotypic adaptations, cyclical disturbance, allee effects, or a combination of environmental conditions (Hobbs and Humphries, 1995).

The time between the introduction of a species and its first record of spread can vary dramatically. A species may suddenly become highly invasive even after it has already been present for a long time in a particular region. Kowarik (1995) reported that in Germany the average duration of the time-lag between the introduction and the initiation of an invasion was 131 years and 170 years for shrubs and trees respectively. For example, Binggeli *et al.*, (1998) showed that duration of known time lags between introduction and the first spread of *Schinus terebinthifolius* was 50 years, and it was noted as a problem or pest only 75 years after arriving in Florida.

Because the duration of the phase between the introduction of a species and its spread is so variable it is not possible to be certain that a species, although present for several decades, is “safe”, i.e. will not spread. For any particular region it is essential to understand the long-term disturbance regime as well as the specific ecology (including reproductive biology and regeneration requirements) of the introduced species before any predictions can be made. Otherwise close monitoring of natural and semi/natural vegetation, particularly after exceptional disturbance events, is necessary for the early detection of new invasions (Smith *et al.*, 1994).

### *Habitat attributes*

Several hypotheses have been postulated to explain differences in invasibility between habitats by alien plants. Those hypotheses include evolutionary history of the habitats, community structure, propagule pressure, and disturbance. Interaction among these factors is likely to be important in determining habitat invasibility (Higgins and Richardson, 1998; Blumenthal, 2006). One aspect of evolutionary history thought to affect the invasibility of habitats is past intensities of competition and of human disturbance. In some habitats having intense competition over evolutionary time, invasibility might be low because natives have been well adapted for high competitive ability thereby preventing establishment of potential invasives (Blumenthal, 2006).

Alternatively, the theory of fluctuating resource availability argues that the susceptibility to invasion of a community increases whenever the amount of unused resources such as light, water, and soil nutrients in that community is enhanced through disturbance (Davis *et al.*, 2000). High resource availability benefits fast-growing native or alien species (Davis *et al.*, 2000). Elton (1958) first proposed that community resistance to invasions increases in proportion to the number of species in the community - its species richness. This followed his hypothesis that communities are more “stable” if they are species-rich. This idea has been supported by theoretical arguments that less diverse communities have weaker interspecific interactions and more ‘empty niches’ (Post and Pimm, 1983; Crawley, 1987; Drake, 1990). The idea behind the empty niche is that a community with many species is unlikely to have any vacant niches and that the community can probably successfully “defend” itself from invasion by alien plants (Brown and Peet, 2003). However, recently, some ecologists have begun to question this perspective (Stohlgren *et al.*, 1999; Levine and D’Antonio, 1999; Levine, 2000).

Other attributes of habitats that may affect invasibility may include species diversity and vacant niches (Rejmánek, 1996; Rejmánek and Richardson, 1996; Davis *et al.*, 2000; Keane and Crawley, 2002), as well as positive and negative interactions with indigenous, or introduced, species in the adopted environment.

### *Positive and negative interactions in new environment*

One of the most widely cited hypotheses attributes success of plant invasion to the fact that many alien plants, when introduced, are liberated from their specialist herbivores and pathogens (Elton, 1958). Some alien plants are thought to obtain advantage when introduced to a new habitat, because their populations are no longer suppressed by their specialist natural enemies and so gain competitive advantage over native plants that may suffer from native predators (Blumenthal, 2006). The fundamental assumption is that release from strong suppression by native enemies in their native range enables plants to attain greater reproductive output (Milton and Hall, 1981), and survival (Annecke and Moran, 1978) and thus higher densities in their introduced range (Mitchell and Power, 2003; Dewal *et al.*, 2004).



Positive interactions may also facilitate the spread of alien plant in their new habitat. These include soil mycorrhizae, pollinators and dispersal agents (Richardson *et al.*, 2000b). Arbuscular mycorrhizal fungi can aid or disrupt the establishment of a new species by ameliorating or intensifying the abiotic stresses encountered in the new range. Mycorrhizal fungi can alter interactions among plants through direct effects, e.g., by providing more resources to one species than to another (Hetrick *et al.*, 1989), and potentially through indirect effects, e.g., by the transfer of resources and fixed carbon between individuals (Moora and Zobel, 1996; Walter *et al.*, 1996; Simard *et al.*, 1997; Robinson and Fitter, 1999). Some comparative biogeographical studies have demonstrated more positive net effects of soil biota on invasive species in their new regions than in their native regions (Richardson *et al.*, 2000b; Reinhart and Callaway, 2004). Although arbuscular mycorrhizae have been largely ignored as a mediator of plant invasion (Richardson *et al.*, 2000b), they have been shown to increase the growth of an invasive plant species over natives and accelerate the process of invasion in a grassland ecosystem (Marler *et al.*, 1999).

Lack of pollinators has long been recognized as an important factor limiting plant reproductive success and range expansion (Bierzychudek, 1981; Brown and Mitchell, 2001). Because pollinators depend on floral resources such as nectar and pollen, flower availability and plant species composition may be important determinants of the large temporal and spatial variability exhibited by plant–pollinator interactions (Aizen, 2001). Most successful plant and pollinator invaders are expected to be rather generalized in terms of the plant pollination mutualism (Johnson and Steiner, 2000). The larger the flower display, the better competitor for pollinators the plant should be, and the more fruit it is likely to set. Large fruit displays in turn may successfully compete for seed dispersers. Fleshy-fruited alien plant species are known for greater fruit production when introduced to new habitats and these large fruit displays are attractive to bird dispersers (Kitamura *et al.*, 2002).

Another positive facilitation effect is the interaction between the introduced *S. molle* and native trees observed in semi-arid savanna of South Africa (Milton *et al.*, 2007), where the establishment of the fleshy-fruited *S. molle* occurs predominantly under tree canopies, resulting in the formation of a clump around a single indigenous tree. This is

probably because by perching and nesting in trees, frugivorous birds direct seeds of *S. molle* to subcanopy sites (Milton *et al.*, 2007). Some studies have demonstrated that subcanopy microsite is favourable for seed germination and seedling establishment (Belsky *et al.*, 1993). This process is known as nucleation (Pausas *et al.*, 2006) whereby the clumps tend to grow around a single founder tree. However, when reaching maturity *S. molle* tends to compete indigenous trees for light when growing in association one to another.

### *Potential distribution under climate-change scenarios*

It is a widely stated view that climate change is likely to change the capacity of alien species to invade new areas, while simultaneously decreasing the resistance to invasion of the natural communities by disturbing the dynamic equilibrium of those ecosystems (Dukes and Mooney, 1999; Thuiller *et al.*, 2007). It has also been suggested that climate change could potentially favour invasive non-native species by either creating more favourable environmental conditions for them, e.g., increasing fire frequency (D'Antonio and Vitousek, 1992), or by stressing native species to the point of being unable to compete against new invasives (Midgley *et al.*, 2003). Recent projections forecast that range expansion of alien species may be widespread under climate change scenarios and may affect various floras (Peterson *et al.*, 2002). In this section, I discuss some aspects of global change and specially climate change impact on potential alien plants species distribution.

For alien plants that clearly attain higher population densities in the introduced than in the native range, understanding the demographic forces that lead to this difference is a necessary step towards understanding the mechanisms by which some species become invasive. Ideally, detailed surveys should be carried out to establish accurate records of species presence. However, in reality wide scale, detailed surveys are often lacking and searching widely dispersed species can also be time consuming and costly, which can delay the onset of monitoring or conservation effort.

This problem can be overcome by using distribution modelling techniques such as the species-climate envelope modelling approach (also known as ecological-niche

models), whereby present distributions of species are combined with environmental variables to project future distributions of species under predicted future climates (Heikkinen *et al.*, 2006). The bioclimatic modelling is a simple, but useful technique which generates maps of potential species distribution using climatic characteristics where the species occurs (Thuiller, 2003; Busby, 1991). On the other hand, habitat suitability or niche-based models can be made available using information on species locational records and environmental factors to generate statistical functions that allow predictions of potentially suitable habitat distribution (Guisan and Zimmerman, 2000). This allows areas with a high predicted probability of species occurrence to be prioritized for survey.

Many authors have concluded that an integration of information on environment type, disturbances, climatic information and plant attributes, including whether a species is known to be invasive elsewhere, is needed for understanding the ecology of plant invasions (Hobbs and Humphries, 1995; Thuiller *et al.*, 2006). Although range of expansion of species is often determined by biotic and abiotic factors, land use and climate are among the most important driving factor of species distribution at very broad continental and global scales (Sala *et al.*, 2000; Midgley *et al.*, 2003, Thuiller *et al.*, 2004).

## **Ecological impacts of alien plant invasion**

The negative effects of invasive plants on ecosystem structure and function have been broadly recognized. While most alien species have relatively few effects, many others have caused catastrophic ecological impacts (Vitousek *et al.*, 1997; Parker *et al.*, 1999). One of the few accepted generalizations is that the greatest impacts often occur when a non-indigenous species performs an entirely novel function in the new habitat (Ruesink *et al.*, 1995). An increasing number of studies on alien plant species have shown how even a single species can exert profound effects on ecosystems (Dunbar and Facelli, 1999). These effects can be diverse, including negative effect on species richness, altering population and community structure, fire regimes (D'Antonio and Vitousek, 1992), hydrological cycles (Dye *et al.*, 1995), and nutrient cycles (Maron and Connors, 1996).

The most detailed work on assessing the impact of plant invasions in South Africa has focused on tree invasions in the fynbos biome. Several studies have documented the reduction in stream flow caused by invasive trees (mainly *Pinus* species; Dye, 1996; Le Maitre *et al.*, 1996; Prinsloo and Scott, 1999), and the effects of changed nutrient regimes associated with invasions of nitrogen-fixing Australian acacias (Musil and Midgley, 1990; Witkowski, 1991; Musil, 1993). However, no overall framework has been developed to understand the ecosystem processes most vulnerable to alien plant invasion. Certainly, for invasive alien woody fleshy-fruited alien species, it is difficult to predict the type and magnitude of impacts in different ecosystems.

### *Impact on population and community structure*

There is no doubt that alien plant invasions have a considerable impact on the composition and diversity of native plants (D' Antonio and Vitousek, 1992). However, most studies are observational comparisons of native diversity and composition in invaded and uninvaded locations. For example, Martin (1999) found a lower richness of seedlings and saplings in areas invaded by Norway maples than in nearby uninvaded forest locations, while Pyšek and Pyšek (1995) found reduced species diversity in areas invaded by *Heracleum mantegazzianum* as compared with uninvaded areas in the Czech Republic. Alien plant invasions are also the largest threat to endangered plant species in the Cape Floristic Region of South Africa (Hall, 1987). Widespread tree and shrub invasions in South African fynbos that previously had a low tree cover have radically altered habitats for animals. This is shown, for example, by the major changes in distributions of many bird species, including species that invaded the southwestern parts of South Africa from adjacent biomes in response to increased tree cover (e.g., Macdonald, 1986).

Although these kinds of studies provide a good indication about how alien plants impact on species composition, they are of less help in understanding the mechanisms that generate such impacts. Plant invasions can also alter community structure at higher trophic levels. For example, alien plants can modify the activity of pollinators by producing different types or amounts of nectar compared to native species. Along a

European river-bank, the Himalayan *Impatiens glandulifera* produces more nectar than the native *Stachys palustris*, and receives more visitations by European bumble-bees (Chittka and Schüken, 2001).

### *Impacts on ecosystem processes*

Various ecosystem processes are impacted by alien plant invasion, notably water use, herbivory, fire regimes, and nutrient cycling (Richardson *et al.*, 1997; Van Wilgen *et al.*, 1998). The development of an understanding on ecosystem processes that are impacted by invasive alien plants, and their consequences, would be extremely useful for the quantification of impact of alien woody plants on these important ecological processes. Unfortunately, no standard system exists for the objective quantification of the many and varied environmental impacts of invasive alien plants worldwide (Parker *et al.*, 1999). In the case of *Schinus molle*, which establishes mainly along rivers and mountain slopes where it forms dense stands of vegetation and is able to out-compete native species for resources (Howard and Minnich, 1989), the most likely impacts would be to hydrology.

In the invasion ecology literature, relatively few studies have directly measured the hydrologic impacts of invasive species, because experiments involving hydrological impact are quite costly. However, the potential impacts of alien plants on water resources have long been recognized (Wicht, 1945) and in South Africa the total incremental water used of invading alien plants is estimated at 3300 million m<sup>3</sup>; of water per year (Van Wilgen *et al.*, 1992; Le Maitre *et al.*, 2000). Forests are known to use more water than lower-growing shrubland vegetation due to greater aerodynamic roughness which can enhance water losses through interception of water from air humidity before other vegetation and also evapotranspiration (Calder *et al.*, 1997). For example, where grasslands or shrublands are invaded by alien trees, the overall water use by the vegetation increases, leaving less water for the streams and native riparian vegetation (Bosch and Hewlett, 1982; Dye *et al.*, 1995).

Some studies in South Africa have shown severe reduction of water supply following the increased abundance of invasive alien trees and shrubs in water catchments. The greatest impacts occur when seasonally-dormant vegetation is replaced by evergreen

plants with high biomass and leaf area (Dye *et al.*, 1995). For example, most of the invasions in South Africa ecosystems are found along the banks and in the beds of the rivers; there are few, if any, river systems that have not been extensively invaded. Invading trees such as syringa (*Melia azedarach*) and jacaranda (*Jacaranda mimosifolia*) have spread into semi-arid savanna by invading along perennial rivers where the freely available water, allows them to survive the seasonal drought (Le Maitre *et al.*, 2002). The Western Cape is the most heavily invaded province at about a third of the total area, followed by Mpumalanga, KwaZulu-Natal and Northern Province (Le Maitre *et al.*, 2000; Van Wilgen *et al.*, 2001); woody invaders, notably mesquite trees (*Prosopis* species), have invaded at least 18 000 km<sup>2</sup> of the low-lying alluvial plains and the seasonal and ephemeral watercourses. Several cacti (*Opuntia* species) and saltbushes (*Atriplex* spp.) have invaded large areas of the Nama-karoo and Succulent-karoo (winter rainfall) biomes (Milton *et al.*, 1999) and the thicket biome in the Eastern Cape (Richardson *et al.*, 1997). The focus of this thesis, *Schinus molle*, is showing the same pattern of invasion in the arid zone of South Africa.

## Conclusion

There is clear evidence that biological invasions are one of most damaging phenomena that humans have ever generated on ecosystems. Despite intensive research into causes and consequences of biological invasion, we are still far from understanding the full complexity of the phenomenon. This is partly because so many different aspects need to be considered when trying to develop a general theory. This review has shown that no single trait can predict invasion success; those that seem to be correlated with invasiveness are to a large extent habitat specific. Even if the mechanisms to understand and predict processes that lead to invasion are still under investigation, many scientists agree that alien plant species will continue to have negative impact on ecosystems and their processes (D'Antonio and Vitousek, 1992).

The review has highlighted that successful invasion appears to depend on a number of factors that facilitate the surmounting of invasion barriers. Those factors include habitat features, recent disturbances, and distance from putative source populations, life

history traits and seed biology that may interact to facilitate invasions. It is also important to understand the links between traits of alien plants and features of the environment in mediating invasiveness. The crucial roles played by pollination and dispersal during the invasion of alien plants, which have been extensively debated in the literature were also one of the decisive stages of alien plant invasions. Dispersal and establishment of recruits are key steps in the invasion process of alien plants, because the spread of invasive species is influenced by dispersal mode, landscape structure, and the number of foci of introduction of the invasive species (Moody and Mack, 1988). Most plants, however, need animal pollinators and seed dispersers. Introduced alien plants species with highly specialized pollination and seed dispersal systems are at a disadvantage, since the required partners are much less likely to be present outside their natural ranges.

Faced with this situation of complexity in the field of invasion ecology and since no generalizations, beyond rather trivial ones, can be made on invasion, there is need for prioritizing research and some areas need obviously more attention than others, for example, the role of propagule pressure to explain alien plant invasion. The relative roles of density dependence and evolutionary change in generating the lag times characteristic of the population growth of many invasive species also clearly require more research. It seems prudent to concentrate efforts on systems that may serve as models for a more general understanding of biological invasion. For example, suitable areas are systems that are threatened but not yet heavily invaded by alien species, since these are most likely to reveal the early dynamic stage of invasion.

However, because the prediction of species invasive ability is still problematic, especially when considering climate-change scenarios, there is an urgent need for the development of a general framework of early warning systems to determine the likelihood of a given species becoming invasive. This might only be possible through increasing research on early stages of invasion by an alien plant species in their new habitat and the use of distribution modelling techniques such as the climate-envelope modelling approach, whereby present distributions of species are combined with environmental variables to project future distribution of species under climate change scenarios.

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# Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa

**Chapter 1:** General problem of biological invasion in South Africa landscape

**Chapter 2:** Dynamics of alien woody plant invasions: review of processes and ecological impacts

## Main objectives

**Chapter 3:** Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 4:** *Megastigmus* wasp damage to seeds of *Schinus molle* (Peruvian pepper tree) across a rainfall gradient in South Africa: Implication for invasion

**Chapter 5:** Seed set of the invasive alien tree *Schinus molle* (Anacardiaceae) in semi-arid savanna, South Africa: the role of pollination and selfing

**Chapter 6:** Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 7:** Performance of seedlings of the invasive alien tree *Schinus molle* under indigenous and alien host trees in semi-arid savanna

**Chapter 8:** Superiority in competition for light: a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Peruvian pepper tree) in South Africa

**Chapter 9:** Distribution of the invasive alien tree *Schinus molle* in western South Africa: current determinants and projections under scenarios of climate change and management.

**Chapter 10:** General conclusions and recommendations

## CHAPTER THREE

### REPRODUCTIVE POTENTIAL AND SEEDLING ESTABLISHMENT OF THE INVASIVE ALIEN TREE *SCHINUS MOLLE* (ANACARDIACEAE) IN SOUTH AFRICA

#### **Abstract**

*Schinus molle* (Peruvian pepper tree) was introduced to South Africa more than 150 years ago and was widely planted, mainly along roads. Only in the last two decades has the species become naturalized and invasive in some parts of its new range, notably in semi-arid savannas. Research is being undertaken to predict its potential for further invasion in South Africa. We studied production, dispersal and predation of seeds, seed banks, and seedling establishment in relation to land uses at three sites, namely ungrazed savanna once used as a military training ground; a savanna grazed by native game; and an ungrazed mine dump.

I found that seed production and seed-rain density of *S. molle* varied greatly between study sites, but was high at all sites (384,864 - 1,233,690 seeds/tree/year; 3,877 – 9,477 seeds/m<sup>2</sup>/yr). I found seeds dispersed to distances of up to 320 metres from female trees, and most seeds were deposited within 50 m of putative source trees. Annual seed rain density below canopies of *Acacia tortillis*, the dominant native tree at all sites was significantly lower in grazed savanna. The quality of seed rain was much reduced by endophagous predators. Seed survival in the soil was low, with no survival recorded beyond 1 year. Propagule pressure to drive the rate of recruitment: densities of seedlings and sapling densities were higher in ungrazed savanna and the ungrazed mine dump than in grazed savanna, as reflected by large numbers of young individuals, but adult: seedling ratios did not differ between savanna sites. Frequent and abundant seed production, together with effective dispersal of viable *S. molle* seed by birds to suitable establishment

sites below trees of other species to overcome predation effects, facilitating invasion. Disturbance enhances invasion, probably by reducing competition from native plants.

**Keywords:** Biological invasions, land use, invasion, naturalization, seed dispersal, seed predation, seed production, tree invasions.

## Introduction

Invasive species are a serious threat to biodiversity and the functioning of many ecosystems (Vitousek *et al.*, 1996). Considerable research effort is being devoted to improving our understanding of the properties that make some alien species more successful invaders than others, the factors that promote invasibility of different ecosystems, and how these aspects interact (Richardson and Pyšek, 2006). The invasiveness of a plant species at any locality is determined by a complex interplay of many factors, including the traits of the species (Richardson and Rejmánek, 2004; Pyšek and Richardson, 2007), propagule pressure (effectively the number of seeds available over time; Foxcroft *et al.*, 2004), residence time, the extent of human dissemination, and the locality of initial plantings relative to the most favourable sites for the species in the entire region (Thuiller *et al.*, 2006; Wilson *et al.*, 2007). Disturbance is a crucial driver of invasions in most situations (Huston, 2004). Despite considerable progress towards generalizations in plant invasion ecology (see Richardson and Pyšek, 2006 for a recent review), each invasion is influenced by a different combination of factors.

*Schinus molle* (Anacardiaceae) was introduced to South Africa in the 1800s and now occupies a very large range as a planted tree, but is currently only invasive in a small part of its planted range (Iponga *et al.*, 2008b). The species is already classified as a major weed in South Africa (Nel *et al.*, 2004), but is predicted to be able to occupy a much larger area (Rouget *et al.*, 2004). It is important to know what factors are crucial for its further invasion in semi-arid savanna in South Africa.

Given that the invasive potential of a plant species may be limited by failure to set viable seed, to disperse, germinate, establish as a seedling, and maintain a persistent seed bank or to reach reproductive maturity, it is instructive to discriminate among these

processes in understanding invasive potential. Previous studies have shown that *S. molle* establishes more successfully below tree canopies than in open areas (Iponga *et al.*, 2008b). The extent to which reduced seed viability through seed predation in the species in South Africa (Iponga *et al.*, 2008a) influences rates of invasion by *S. molle* is unknown. Information on seed rain, post-dispersal seed viability, dispersal distances and seedling establishment rates is needed to facilitate modelling of the potential rate of spread which in turn can be used in developing a comprehensive strategy for the management of this invasive species.

This study explores the interactions among seed production, dispersal, predation and land use in the establishment of an alien tree species, to gain a better understanding of factors that could drive future invasions. Specific questions addressed were: (1) could seed production, or seed predation, be limiting *S. molle* invasion in semi-arid savanna? (2) How far are viable *S. molle* seeds being dispersed and are they moved to subcanopy sites beneath indigenous trees? (3) Does *S. molle* maintain a soil-stored seed bank? (4) Does land use influence *S. molle* seedling establishment? (5) What is the implication of its seed abundance patterns in the landscape for *S. molle* invasion?

## **Materials and methods**

### *Study site*

Field experiments were conducted at three sites near Kimberley (28° 47' 24.6"S; 24° 46' 58.3"E, 1198 m above sea level) in the Northern Cape province of South Africa. The vegetation in the area is classified as Kimberley Thornveld, a type of semi-arid savanna (Mucina *et al.*, 2006). The area has warm, relatively moist summers, and cool, dry winters. Mean annual precipitation is 431 mm ( $\pm$ SD 127 mm), with most rain falling in mid to late summer (January to March). The mean maximum and minimum temperatures are respectively 37.4° C and 19.5° C in January, and 22° C and 12° C in July.

Study sites were selected in three land use types according to different land use histories within the Kimberley area: (1) ungrazed savanna; (2) grazed savanna; (3) ungrazed mine dump. Because the study was carried out on only one example of each



land use type, comparisons of land use effects on seed production, dispersal and population structure are pseudo-replicated and differences among them cannot necessarily be attributed to particular management factors.

The “ungrazed savanna” site comprises 200 ha of savanna in a semi-natural state and has been used as a military base since 1967. Although it currently has a low level of disturbance, the area, once known as Alexanderfontein, was used for livestock farming in the 1880s. Following the discovery of diamonds in 1899 the land was disturbed by clearing and diamond digging until exploitation stopped 40 years later. Most of the vegetation has recovered in the 68 years since mining activities ceased. No grazing takes place, but grass fires occur periodically, damaging understorey shrubs (Milton *et al.*, 2007). The most common native tree is *Acacia tortilis* (Fabaceae: Mimosoideae), and associated with it are native bird-dispersed plants including the tree *Rhus lancea* (Anacardiaceae) and various sub-canopy shrubs, lianas and herbs (Milton *et al.*, 2007; Iponga *et al.*, 2008b). Seeds of alien fleshy-fruited species planted in the military base have been dispersed by birds to the surrounding savanna where some, including *Brachychiton populneus*, *Celtis* sp., *Melia azedarach*, *Morus alba*, *Punica granatum* and *Schinus molle* (Anacardiaceae) have established beneath *A. tortilis* canopies (Milton *et al.*, 2007; Iponga *et al.*, 2008b).

The “grazed savanna” site is on the game farm Rooifontein which is approximately 3,500 ha in area and belongs to De Beers Mining Company. The dominant native tree species is *A. tortilis*, and associated with it are the fleshy-fruited indigenous species *Rhus lancea* and *Ziziphus mucronata*, and the alien *Schinus molle*. The open areas between the trees are dominated by grasses (*Schmidtia pappophoroides* and *Eragrostis lehmanniana*) and dwarf Asteraceous shrubs such as *Pentzia incana*. Indigenous antelope, zebra and ostrich are stocked at a total density of 17.4 ha/LSU (Large Stock Unit, equivalent to one 450 kg head of cattle), whilst the recommended rate is 18.6 ha/LSU. The area burned during the study period and could be described as moderately disturbed.

The “ungrazed mine dump” is approximately 300 ha in area and comprises a mountain of overburden and tailings some 15 m high that were accumulated from the

start of diamond mining in 1885 until the mining activities ceased in November 1990. There has been no grazing, and no fires were recorded during the study. Nevertheless, the area is highly disturbed, and the vegetation on the dump is numerically dominated by alien plants. Native *Acacia tortilis*, the alien *S. molle* and *Prosopis glandulosa* hybrids (Fabaceae: Mimosoideae) are the most common trees on the dump. The dominant grass is the invasive alien perennial *Pennisetum setaceum* from North Africa. Associated with *Acacia* and *Prosopis* are bird-dispersed plants including native *Rhus lancea* (Anacardiaceae) and the alien *Opuntia ficus-indica* (Cactaceae).

### *Study species*

The genus *Schinus* L. is native to South America and includes approximately 29 species (Barkley, 1957). *Schinus* species have been introduced to many parts of the world as ornamental plants (Morton, 1978) and *S. molle* L. (the Peruvian pepper tree) was introduced to South Africa in the mid 1800s. This long-lived and drought-tolerant hardy evergreen tree is native to the arid zone of South America. It is dioecious, and produces flowers and fruits throughout the year. Female trees produce large crops of small bright pink berries arranged in bunches on pendulous stems, and the seeds are dispersed by birds, mammals, and water (Howard and Minnich, 1989; Corkidi *et al.*, 1991). Saplings are hardy and survive wherever they are planted in mediterranean-climate and subtropical regions (Nilsen and Muller, 1980; Howard and Minnich, 1989; Silva *et al.*, 2005) and the species is invasive in Mexico (Corkidi *et al.*, 1991). Over the past 50 years the tree has been grown for shade in gardens and at picnic sites along national and provincial roads in South Africa. Self-established young plants are most often found below perch sites such as other trees and are thus located very near dominant native trees. The outcome of interactions between the invader and its “nurse plant” are thus crucial for determining whether the invader can maintain its position and also for determining the impact of the invader (Milton *et al.*, 2007). For example, the fact that *S. molle* can out-compete native trees that facilitate its establishment (Iponga *et al.*, 2008c), means that invasion by this species will have a marked influence on vegetation structure.

## Field sampling

### *Seed production*

Seed production per tree was quantified at three different sites. Seed traps, comprising shallow perforated trays covered with wire netting to exclude rodents and birds, and nailed to the ground, were set up beneath tree canopies to estimate the density of seed arriving on that surface. At each site 10 individual female *S. molle* trees were randomly selected and three traps with a total area of 0.14 m<sup>2</sup> were placed under each tree from October 2005 until November 2006. Seed traps were emptied monthly, seed was cleaned and sorted, and the numbers of seeds arriving in each trap were counted. Total seed production per tree (SP) was estimated as seed fall (SF) in the total trap area per tree, divided by the total trap area (TA) and multiplied by the canopy area (CA) of each tree.

$$SP = (SF/TA) \cdot CA$$

The canopy area was calculated using the following formula for an ellipse (Bronstein and Semendjajew 1991):  $Cover = (Pi/4) \cdot canopy1 \cdot canopy2$  (1), where *canopy1* and *canopy2* are two perpendicular diameters of the tree as seen from above.

Using a dissecting microscope, we separated intact seeds from insect-damaged and rotten seeds and stored them in paper bags for germination tests. I also collected *S. molle* seeds on the ground, below non parent trees (*A. tortilis*) and counted the number of damaged and intact seeds. All seeds were sorted the same way as those in the traps. The numbers of bird droppings in the traps were also recorded monthly.

### *Seed dispersal*

It was assumed that *S. molle* seed found in seed traps under trees other than conspecifics had been dispersed to such sites by birds or bats. To estimate dispersal distances, ten individual *Acacia tortilis* trees were randomly selected at distances of 10 to 320 m from seed-producing female *S. molle* trees at each of the three sites. Three traps with a total area of 0.14 m<sup>2</sup> were also placed under each tree in October 2005. Traps were also emptied monthly for 13 months. To examine the effect of distance on dispersal of *S.*

*molle* seeds, I measured the distance between non *S. molle* trees where the traps were located and the nearest *S. molle* fruiting tree in the woodland.

### *Seed predation*

To estimate seed predation of *S. molle*, the number of seeds eaten or damaged by insects in the traps were counted and separated from intact seed using a dissecting microscope. Seeds with insect exit holes were considered to be insect damaged, and soft black seeds were considered to be rotten; both categories were classified as damaged seeds.

### *Seedling establishment*

A demographic survey was conducted in the three study sites between April and May 2006, at the end of the rainy season. The density of *S. molle* plants was measured by counting the number mature (flowering or fruiting) *S. molle* trees that I could find in the study areas. Seedling ( $\leq 0.4$  m of height) and sapling ( $> 0.4$  m of height) searches were performed to a maximum distance of 5 m from the stem to the edge of the selected mature *S. molle* tree. Since *S. molle* seedlings establish beneath canopies of other tree species (Milton *et al.*, 2007; Iponga *et al.*, 2008b), the adult: seedling ratios presented here should be considered to under-estimate the total recruitment potential of the species. In each study site I recorded: (1) the number of mature ( $\geq 1$  m) *S. molle* trees; (2) the number of seedling and sapling beneath conspecifics; (3) canopy radius and basal stem diameter of each plant individual; and (4) the geographic coordinates.

### *Seed bank*

Seed banks were sampled using soil cores of 48 mm in diameter. The soil was sampled at two depths: 0-5 cm and 5-15 cm. Soil core samples (15 samples) were taken randomly from below each of 20 female trees and combined, by depth into a single bulk sample per tree with a surface area equivalent of 0.1 m<sup>2</sup> for each depth. The soil samples (20 for each depth) were spread in 5 cm deep labelled seedling trays in a nursery and watered for 14

months. Seedlings that emerged from the trays were counted, removed and transplanted into individual pots to be grown for identification.

### *Buried seed decay rates*

240 intact seeds were collected from each of ten trees (2400 seeds), mixed and 20 placed in each of 120 bags 50 mm X 50 mm with a mesh size of 0.3 mm. In March 2006, 60 bags were buried at a depth of 50 mm and 60 bags at 100 mm depth. Twelve bags were buried beneath each of the ten trees (2 groups of 6 bags) at 50 mm depth; each bag was attached with a piece of fishing line with the other end tied to a metal stake so as to relocate the bags. As sun angle might have influenced seed survival in the soil, six bags were buried to the east and six to the west of each tree. Two bags were harvested from each tree (one bag from each depth group) every second month; harvesting was random with respect to direction from the tree trunk. A total of 20 bags was harvested every second month. After harvesting the bags, all seeds were removed and checked for damage under the dissecting microscope.

### **Statistical analysis**

Homogeneity of variance and normality were examined for all variables (mean number of bird droppings, seed production per tree, seed arriving on the ground per square metre and intact seed per square metre as well as damaged seed per square metre) (Levene's test, with  $p < 0.05$  used as the minimum level accepted for significant result). When homogeneity and normality of variance were not found, bootstrapping analysis was used to test the non-normal data. The mean number of seeds produced per tree canopy, the mean number of seeds per square metre arriving on the ground, the mean number of intact and damaged seeds per square metre arriving on the ground, and the mean number of bird droppings in the traps were compared between sites for traps beneath *S. molle* female trees and *A. tortilis* trees using one-way analysis of variance (ANOVA,  $p < 0.05$ ), followed by bootstrapping analysis to understand whether seed rain differed among sites. Multiple comparison tests were then employed (a Scheffé post-hoc test, with  $p < 0.05$

used as the minimum level accepted for significant result) to compare the differences of means between sites (Statistica 6.1, StatSoft, Inc. 2003).

I combined monthly seed fall data to estimate annual *S. molle* seed fall beneath *S. molle* and *A. tortilis* for each of the three sites. The proportional contribution of seed predation was then compared for seeds trapped beneath *A. tortilis* and *S. molle* for all the sites using a contingency table and the Chi-squared statistic. The total seed production per *S. molle* tree and seed dispersal to subcanopy sites below *A. tortilis* was estimated as seed fall in the total trap area per tree, divided by the total trap area and multiplied by the canopy area of each tree. Regression analyses were used to describe the relationship between seed density found beneath non-*S. molle* trees (*A. tortilis*) (seed dispersal) and the minimum distances between *S. molle* seed production sources (female *S. molle* trees) and *A. tortilis* trees to determine whether seed dispersed away from female trees decreased or increased with distances in the woodland.

To test the null hypothesis that all sites (grazed and ungrazed savanna, and mine dump) had the same *S. molle* density and population structure, I used Chi-square goodness of fit test to test for differences between the number of young and mature *S. molle* trees in the three sites. Plant basal areas were grouped in different interval classes per sites with a step size of 0.2. I used linear regression between *S. molle* stem basal area and the proportion of the population within a given basal area size class to determine which sites showed greater *S. molle* recruitment. The same regression was also done with total canopy cover of trees, assuming that stem basal area and total canopy cover increased with tree age. To determine whether there was a difference in relationship between canopy radius and stem basal area of *S. molle* populations sampled in different sites, I also used regression analysis.

Seed bank dynamics were analysed using three-way factorial analysis of variance (ANOVA) to test the main factors (depth and direction) and their interactions on the number of intact seed disinterred over time after testing for normality and homogeneity of the data. ANOVA models significant at 0.05 were followed and significantly different treatment means were separated using a Scheffé post-hoc test in Statistica (Statistica 6.1, StatSoft, Inc. 2003).

## Results

### *Seed production by Schinus molle*

Seed production varied greatly between sites. Overall annual seed production per tree was highly variable, but significantly greater at the mine dump than in grazed and ungrazed savanna (Table 3.1). The proportion of damaged seed below *S. molle* trees did not differ significantly between sites (Table 3.1).

The estimated total number seeds falling per square metre below *S. molle* ranged from 2 000 – 10 000 for trees with canopy areas between 25 and 300 m<sup>2</sup> (Figure 3.1a). Stem basal area proved to be a poor estimator of canopy area and thus of seed production per tree in ungrazed savanna ( $r^2 = 0.05$ ;  $n = 10$ ;  $p = 0.533$ ); grazed savanna ( $r^2 = 0.09$ ;  $n = 10$ ;  $p = 0.384$ ) and mine dump sites ( $r^2 = 0.01$ ;  $n = 10$ ;  $p = 0.699$ ).

### *Seed dispersed beneath Acacia tortilis*

Given that the red fruits of *S. molle* have thin fleshy coverings, it was assumed that all *S. molle* seeds found in trays beneath trees had been moved to these perch sites by birds or bats. *S. molle* seed density beneath *A. tortilis* was not significantly correlated with canopy area of the perch tree (Figure 3.1b). The annual seed rain density below *A. tortilis* was significantly lower in grazed savanna, with ungrazed mine dump and ungrazed savanna area having higher densities of dispersed *S. molle* seed (Table 3.2). No difference among sites was found in the quantity or proportion of damaged seed dispersed (Table 3.2). The density of bird droppings deposited annually below *A. tortilis* trees did not differ between sites (Table 3.2), but was three times greater below *A. tortilis* than below *S. molle* canopies (Tables 3.1 and 3.2;  $t = 12.978$ ,  $p < 0.0001$ ).

The comparison of intact and damaged *S. molle* seed rain per square metre below *S. molle* and *A. tortilis* revealed that the proportion of damaged seeds was almost double below conspecific trees (53.5%) compared to *A. tortilis* trees (22%), and the difference was significant (Table 3.3). The results obtained from seed dispersal distance showed that seed density under acacia trees decreased with distance from the closest *S. molle* female

tree in the woodland in all the three sites. However, a significant relationship was only found for ungrazed savanna and ungrazed mine dump (Figure 3.2).



**Table 3.1:** Annual rain of total, damaged and intact *Schinus molle* seeds below conspecific female trees at three sites near Kimberley. Also shown are means for tree canopy area, and total number of seeds below a tree canopy. The annual density of bird droppings is an indication of tree use by birds. Statistical differences determined by one-way ANOVA, and Scheffé post-hoc multi-comparison test. Letters indicate significant differences between columns and significant p-values indicated in bold. D.f. = 2 (3 habitats); n = 10 (trees per habitat).

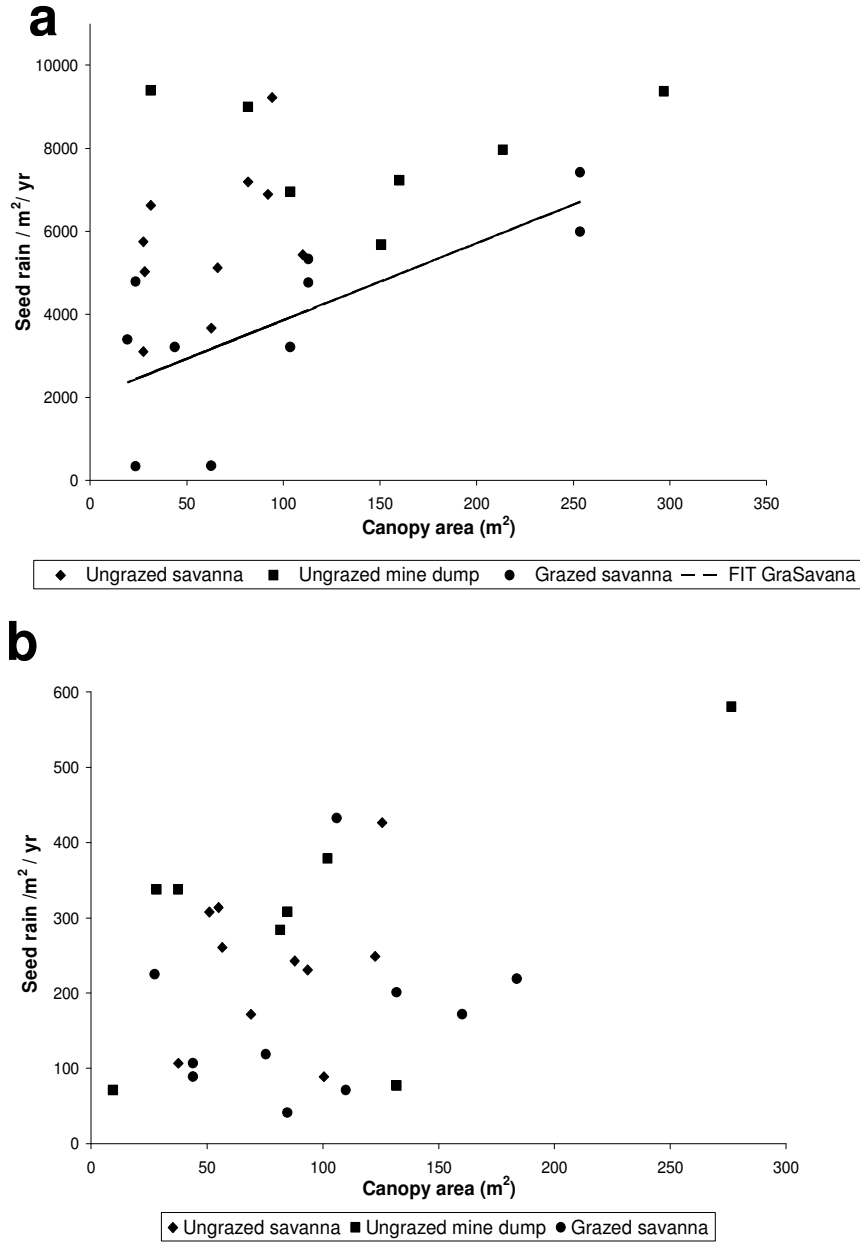
	Ungrazed savanna (mean $\pm$ Std.Err)	Grazed savanna (mean $\pm$ Std.Err)	Ungrazed mine dump (mean $\pm$ Std.Err)	F	p
Total seed rain /m <sup>2</sup> /yr	5,802.36 $\pm$ 562.89 <b>a</b>	3,876.92 $\pm$ 72.95 <b>a</b>	9,477.51 $\pm$ 867.45 <b>b</b>	15.3	<b>&lt;0.001</b>
Damaged seed rain /m <sup>2</sup> /yr	2,818.93 $\pm$ 282.40 <b>a</b>	2,144.37 $\pm$ 392.07 <b>a</b>	5,287.57 $\pm$ 514.36 <b>b</b>	16.5	<b>&lt; 0.001</b>
Damaged seed (%)	48	55	56	NS	NS
Intact seed rain /m <sup>2</sup> /yr	2,983.43 $\pm$ 302.24 <b>a</b>	1,732.54 $\pm$ 337.22 <b>b</b>	4,189.94 $\pm$ 439.10 <b>a</b>	11.4	<b>&lt; 0.001</b>
<i>S. molle</i> canopy area (m <sup>2</sup> )	62.12 $\pm$ 10.05	101.04 $\pm$ 27.95	134.77 $\pm$ 25.70	NS	NS
Seed production/tree/yr	384,865 $\pm$ 84318.5 <b>a</b>	522,210 $\pm$ 208589.3 <b>ab</b>	1,233,690 $\pm$ 253,357.5 <b>b</b>	5.42	<b>&lt; 0.01</b>
Bird droppings/m <sup>2</sup> /yr	4.10 $\pm$ 0.73	5.6 $\pm$ 0.94	6.50 $\pm$ 0.47	2.64	NS

**Table 3.2:** Annual rain of total, damaged and intact *Schinus molle* seeds below *Acacia tortilis* trees at three sites near Kimberley. Also shown are means for tree canopy area, and total number of seeds below a tree canopy. The annual density of bird droppings is an indication of tree use by birds. Statistical differences determined by one-way ANOVA, and Scheffé post-hoc multi-comparison test. Letters indicate significant differences between columns and significant p-values indicated in bold. D.f. = 2 (3 habitats); n = 10 (trees per habitat).

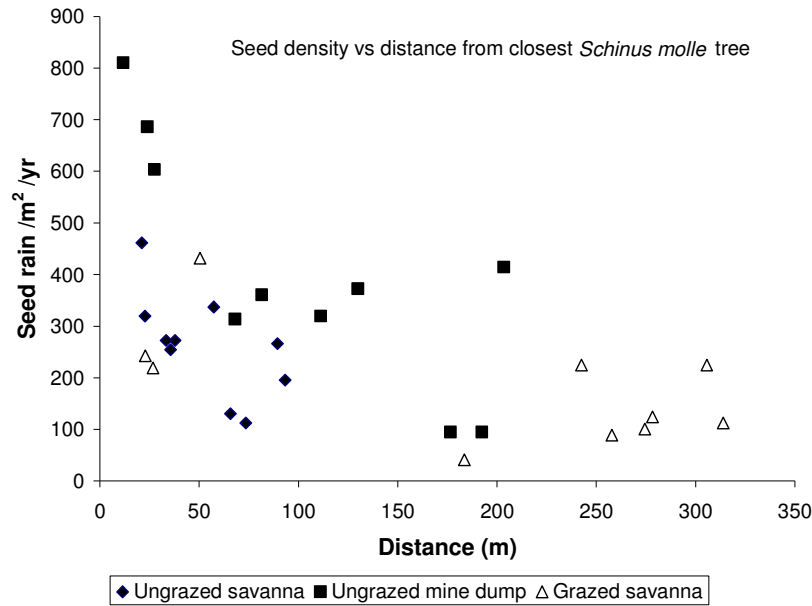
	Ungrazed savanna	Grazed savanna	Ungrazed mine dump	F	p
Seed rain /m <sup>2</sup> /yr	239.64 ± 31.72 <b>ab</b>	167.45 ± 35.67 <b>a</b>	382.84 ± 74.33 <b>b</b>	4.61	<b>&lt; 0.01</b>
Damaged seed rain /m <sup>2</sup> /yr	53.25 ± 8.22	47.33 ± 9.97	72.18 ± 14.56	1.33	NS
Damaged seed (%)	23	28	19	NS	NS
					<b>&lt; 0.001</b>
Intact seed rain/m <sup>2</sup> /yr	186.39 ± 24.51 <b>ab</b>	120.11 ± 27.15 <b>a</b>	310.65 ± 60.24 <b>b</b>	5.64	
<i>A. tortilis</i> canopy area (m <sup>2</sup> )	79.95 ± 9.70	93.06 ± 25.23	96.76 ± 16.35	0.23	NS
Seed dispersed /canopy/year	19,936.57 ± 4,392.55	17,508.80 ± 5,098.86	40,235.16 ± 15,942.37	1.56	NS
Bird droppings/m <sup>2</sup> /yr	21.00 ± 1.52	20.60 ± 1.65	22.10 ± 2.68	0.14	NS

**Table 3.3:** Total annual seed damage per square metre for seed beneath conspecific *Schinus molle* trees and seed dispersed below *Acacia tortilis* in semi-arid savanna (Chi-Square = 514.38; p < 0.0001).

Species	Intact seed	Damaged seed	Total
<i>Acacia tortilis</i>	1,043 (78.13%)	292 (21.87%)	1335
<i>Schinus molle</i>	15,051 (46.49%)	17,324 (53.51%)	32375



**Figure 3.1:** Fitted linear regression lines showing the relationship between tree canopy area and total annual density of the *Schinus molle* seed rain at three sites beneath conspecifics and *Acacia tortilis* trees. (a) *Schinus molle*: Ungrazed savanna ( $r^2 = 0.22$ ;  $n = 10$ ;  $p = 0.16$ ); Grazed savanna ( $r^2 = 0.51$ ;  $n = 10$ ;  $p = 0.01$ ); Ungrazed mine ( $r^2 = 0.04$ ;  $n = 10$ ;  $p = 0.54$ ) and (b) *Acacia tortilis*: Ungrazed savanna ( $r^2 = 0.07$ ;  $n = 10$ ;  $p = 0.43$ ); Grazed savanna ( $r^2 = 0.06$ ;  $n = 10$ ;  $p = 0.48$ ); mine dump ( $r^2 = 0.81$ ;  $n = 10$ ;  $p = 0.06$ ). The regression line was fitted only where relationship was significant.



**Figure 3.2:** Seed dispersal distances from the closest *Schinus molle* seed sources at three different sites. Linear regression: Ungrazed savanna (slope = -2.4;  $r^2 = 0.39$ ;  $p < 0.05$ ); ungrazed mine dump (slope = -2.6;  $r^2 = 0.64$ ;  $p < 0.005$ ); grazed savanna (slope = - 0.6;  $r^2 = 0.34$ ;  $p > 0.05$ ).

### *Seed bank and decay of buried seed*

I tested the longevity of buried *S. molle* seeds in relation to time, depth and direction of burial and the interactions of these factors with three-way analysis of variance. There was significant interaction effect between time and depth on seed survival (Table 3.4). Seed survival was low at both depths, and the number of intact seeds decreased over time. Seed buried between 0-5 cm depth tended to be significantly healthier than seed buried in between 5-10 cm depth (Table 3.4 and Figure 3.3). However, for both depths, all buried seed had died after one year (Figure 3.3). The results of the seed bank sampling showed a similar pattern, with very low recruitment recorded from the seed bank trays. A total of 12 *S. molle* seedlings were recorded from seed bank trays, with ten seedlings from the

depth of 0-5 cm and two seedlings from the depth of 5-10 cm after 14 months of irrigation and recording in the nursery. The time frame of emergence was two months maximum for both soil depths.

### *Population structure and seedling establishment*

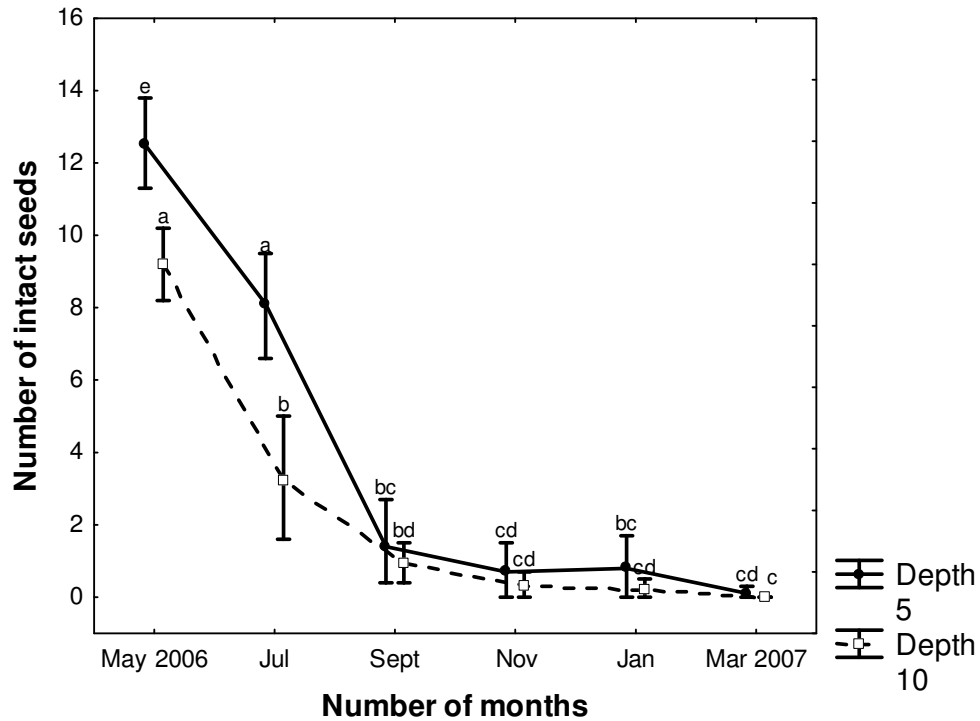
I recorded a total of 76 *S. molle* individuals in the 3 500 ha grazed savanna site, 401 in 200 ha ungrazed savanna and 426 on the 300 ha mine dump, giving minimum densities of 2.17, 200 and 142 trees/km<sup>2</sup>. The proportion of immature trees was significantly greater on the ungrazed mine dump than in the two savanna sites. Young plants (seedlings and saplings) made up 68% of the population on the mine dump, but <40% on the savanna sites (Table 3.5). Trees with small basal area were frequent and old trees infrequent at the mine dump and ungrazed savanna, but old trees were more common than young trees in grazed savanna (Figure 3.4a). The results also showed a significant positive regression between tree basal area and canopy cover for all the three habitats; however canopies on the grazed site were small in relation to basal area in comparison with the ungrazed sites (Figure 3.4b).

**Table 3.4:** Three-way factorial analysis of variance (ANOVA) for *Schinus molle* seed buried below tree canopies and interaction effects between months, direction and depth. Significant p-values indicated in bold (NS = non significant; \*\* = p< 0.05; \*\*\* = p < 0.0001).

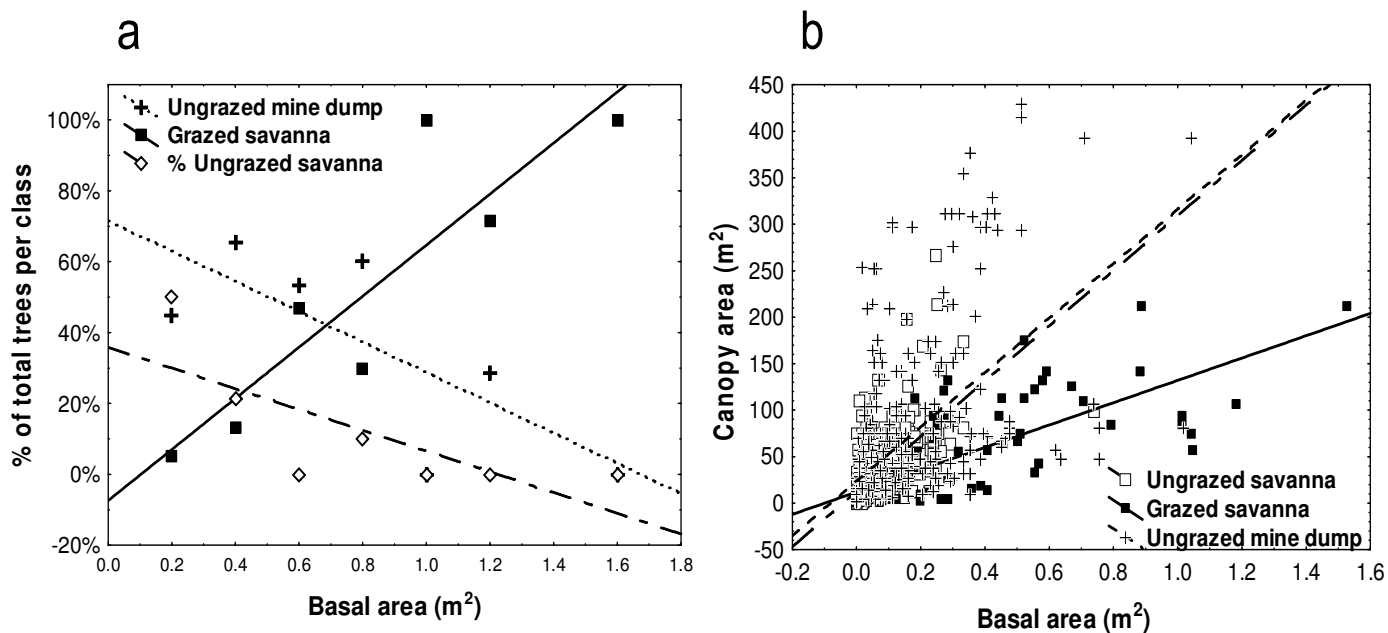
Factors	SS	Df	MS	F	P
Months	1859.875	5	371.975	139.4906	<b>&lt;0.001</b>
Direction	5.208	1	5.208	1.9531	NS
Depth	81.675	1	81.675	30.6281	<b>&lt;0.001</b>
Months*Direction	11.742	5	2.348	0.8806	NS
Months*Depth	97.275	5	19.455	7.2956	<b>&lt;0.001</b>
Direction*Depth	0.208	1	0.208	0.0781	NS
Months*Direction*Depth	5.142	5	1.028	0.3856	NS

**Table 3.5:** Number of young and mature *Schinus molle* under three land use types (Chi-Square = 113.70; df = 2;  $p < 0.0001$ ).

	Ungrazed savanna	Grazed savanna	Ungrazed mine dump
Young plants	129	24	288
Mature plants	272	52	138
Adult: seedling ratio	1.00:0.47	1.00:0.46	1.00:2.09
Total (N)	401	76	426



**Figure 3.3:** Interaction of time and soil depth (2-way ANOVA), on intact of *Schinus molle* seed in the soil seed bank. Different letters indicate significant differences between treatments. Means sharing the same letters are not significantly different. Vertical bars indicate SD.



**Figure 3.4:** Fitted lines for the proportions of *Schinus molle* sampled in various basal area classes in the three different habitats (land uses). (a) Basal area classes: ungrazed savanna ( $r^2 = 0.57$ ;  $p < 0.05$ ); grazed savanna ( $r^2 = 0.78$ ;  $p < 0.01$ ); mine dump ( $r^2 = 0.57$ ;  $p < 0.05$ ). (b) Regression between canopy area and stem basal area: ungrazed savanna ( $r^2 = 0.41$ ;  $p < 0.0001$ ); grazed savanna ( $r^2 = 0.56$ ;  $p = 0.0001$ ); mine dump ( $r^2 = 0.31$ ;  $p < 0.0001$ ).

## Discussion

### *Seed production and damage*

This study was designed to gain a better understanding of the ecological characteristics that may allow further invasion or act as a barrier to invasion by *S. molle* in semi-arid savannas of South Africa. *S. molle* produces large quantities of seed. The results showed that seed production was high at all three sites, with plants at the ungrazed mine dump having the highest seed production. Annual seed rain per unit area was also higher on the mine dump than in less disturbed ungrazed and grazed savanna. *S. molle* produces flowers and fruits throughout the year, when conditions are favourable (Howard and Minnich, 1989).

Contrary to the prediction of the enemy release hypothesis (Keane and Crawley, 2002), *S. molle* seeds experience seed predation in its introduced range in South Africa. Herbivory of *S. molle* seeds was not explicitly measured in this study; since I considered both insect-predated and rotten seeds to be damaged seeds. However, Iponga *et al.*, (2008a) showed that *S. molle* seed predation was higher in semi-arid savanna with summer rainfall than in the winter-rainfall region of South Africa and that an indigenous wasp, *Megastigmus transvaalensis* (Hussey) (Hymenoptera: Torymidae) that feeds on seeds of native *Rhus* species was the main seed predator of *S. molle* in both regions. Despite this, the study also showed that the proportion of damaged seeds was relatively low (<30%). Plants Populations with large seed crops have been shown to suffer from relatively large losses to seed predation (Hainsworth *et al.*, 1984; Sperens, 1997; Jennersten and Nilsson, 1993).

The results also showed that there was a higher proportion of damaged *S. molle* seed beneath *S. molle* canopies than beneath canopies of other tree species. This is not surprising, as other studies also found that seed and seedling damage leading to mortality was greatest under conspecific plants (Schupp, 1988a, b; Böhning-Gaese *et al.*, 1999; Hyatt *et al.*, 2003).

### *Seed dispersers and dispersal distances*

Bird-mediated dispersal of fleshy-fruited species exhibits a high spatial variability which often depends on vegetation structure (Kollmann, 2000). I assumed that *S.*



*molle* seed found in traps under trees of other species had been dispersed to such sites by birds such as cape glossy starling, crested barbet, olive thrush, pied barbet, pied starling, red-eyed bulbul, redfaced mousebird, and whitebacked mousebird, and which were observed consuming *S. molle* fruits in the study area. Due to dispersal of its fruits in this way (Howard and Minnich 1989; Corkidi *et al.*, 1991; Milton *et al.*, 2007), *S. molle* seedlings establish under tree canopies in semi-arid savannas of South Africa and mature individuals are often associated with other trees (Milton *et al.*, 2007; Iponga *et al.*, 2008b) or perch sites such as poles and fences.

Results showed that *S. molle* seeds were dispersed to distances of up to 320 metres from female trees. The density of dispersed seeds declined with distance from the closest *S. molle* seed source at all the sites. Although the dispersal curve was long-tailed, most seeds were deposited within 50 m from the nearest potential parent tree. This conforms with results of other studies of bird-dispersed seeds that showed that passerine birds move most seed less than 100 m from the source, but that seeds can be moved as far as one kilometre (Debussche *et al.*, 1982; Williams, 2006). Long-distance dispersal of *S. molle* seeds may depend on the acceptability of perch sites (Kollmann, 2000) and the fact that some birds retain seeds for a long time in the gut. Corkidi *et al.*, (1991) reported a gut retention time of 25 minutes for birds feeding on *S. molle* in Mexico. In arid savanna, where rainfall is unpredictable, many bird species show nomadic and erratic movement patterns (Tyler, 2001) which may affect seed dispersal distances.

A limitation of the present study is that the distance of seeds from the nearest female tree is a poor measure of seed dispersal distance (Nathan and Muller-Landau, 2000). The assumption that the nearest female tree is the maternal tree might lead to an underestimation of dispersal distances when seeds originated from plants further away the nearest tree (Nathan and Muller-Landau, 2000).

### *Seed bank and decay of buried seed*

A general pattern of decrease in number of intact seed over time was observed for buried seed at both depths, and no seeds remained viable before the end of the experiment. Although assessment of the viability of buried seeds was based solely on visual inspection, results suggest that *S. molle* is unlikely to maintain a persistent soil-

stored seed bank, and that viable seeds are likely to be found on the topsoil, a pattern similar to many species in deciduous forest tree (Pickett and McDonnell, 1989). A soil-stored seed bank is not essential for the spread of a species that continuously produces viable seed that are well dispersed by birds (Corkidi *et al.*, 1991) and that will germinate under moist conditions at any season of the year (Howard and Minnich, 1989). The implications for invasion management are that once the species has been cleared from an area, reestablishment will be slow, the rate depending on importation of seed by birds rather than on germination from a soil-stored seed bank.

### *Population structure and seedling establishment*

The demographic survey of *S. molle* in the three different sites indicated that propagule pressure (being the product of population density of adult trees and their annual seed production) appeared to be driving the rate of recruitment in this species. *S. molle* seedling and sapling densities in ungrazed savanna and the ungrazed mine dump were higher than for grazed savanna, as reflected by high density of young individuals, but adult: seedling ratios did not differ between savanna sites. Greater seed production and the higher seedling: adult ratio on the mine dump may be partly explained by the disturbance history. Highly disturbed areas such as mine dumps are generally considered vulnerable to invasion, probably due to greater availability of nutrients (Brown and Peet, 2003) and reduced competition from indigenous plant species (Pausas *et al.*, 2006).

## **Conclusions**

*Schinus molle* seed production was generally high in all the sites. Birds facilitated the movement of *S. molle* seeds away from conspecifics and to potential germination sites below canopies of other tree species (Iponga *et al.*, 2008a). Regeneration and spread of *S. molle* depends on continuous seed production and dispersal rather than a persistent seed bank. The study also demonstrated that land use may affect *S. molle* invasions. The study has shown that there were higher densities of young *S. molle* plants in the ungrazed mine dump and ungrazed savanna than in the grazed savanna. This reflected not only the pattern of seed dispersal below non *S. molle* trees in those

habitats but also suggested that propagule pressure may be fundamentally important in determining invasion patterns of *S. molle* in this semi-arid savanna. Very high levels of recruitment of *S. molle* on the mine dump suggested that dramatic population increases may be expected. It is presently unclear how land uses such as grazing intensity and habitat interactions could influence *S. molle* populations in semi-arid savanna in the long-term. The implications for invasion management are that it is important to prevent further planting and to clear existing plantings; once the species has been cleared from an area, re-establishment will be slow.

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# Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa

**Chapter 1:** General problem of biological invasion in South Africa landscape

**Chapter 2:** Dynamics of alien woody plant invasions: review of processes and ecological impacts

## Main objectives

**Chapter 3:** Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 4:** *Megastigmus* wasp damage to seeds of *Schinus molle* (Peruvian pepper tree) across a rainfall gradient in South Africa: Implication for invasion

**Chapter 5:** Seed set of the invasive alien tree *Schinus molle* (Anacardiaceae) in semi-arid savanna, South Africa: the role of pollination and selfing

**Chapter 6:** Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 7:** Performance of seedlings of the invasive alien tree *Schinus molle* under indigenous and alien host trees in semi-arid savanna

**Chapter 8:** Superiority in competition for light: a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Peruvian pepper tree) in South Africa

**Chapter 9:** Distribution of the invasive alien tree *Schinus molle* in western South Africa: current determinants and projections under scenarios of climate change and management.

**Chapter 10:** General conclusions and recommendations

## CHAPTER FOUR

### *MEGASTIGMUS* WASP DAMAGE TO SEEDS OF *SCHINUS MOLLE* (PERUVIAN PEPPER TREE) ACROSS A RAINFALL GRADIENT IN SOUTH AFRICA: IMPLICATIONS FOR INVASIVENESS

#### **Abstract**

Seed predation is a key factor affecting the recruitment and spatial distribution of plants. For alien plant species, the study of seed predation may lead to improved understanding of the mechanisms that limit or accelerate spread in a new region. This note assesses the intensity and pattern of insect seed predation of Peruvian pepper tree, *Schinus molle* L. in two regions of South Africa (the winter-rainfall Western Cape and the summer-rainfall Northern Cape provinces) by an indigenous wasp *Megastigmus transvaalensis* (Hussey) (Hymenoptera: Torymidae). Based on samples of 100 fresh ripe fruits randomly collected from 30 trees from each region, I found that a significantly higher proportion of *S. molle* fruits was damaged in the summer-rainfall region ( $75.33 \pm \text{S.E. } 1.39 \%$ ) than in the winter-rainfall region ( $32.80 \pm \text{S.E. } 2.08 \%$ ). Moreover, a greater proportion of seed damage was caused by insects in the summer-rainfall region. The seed wasp *M. transvaalensis* typically develops inside the seeds of indigenous *Rhus* species but has formed a new association with *S. molle* in both regions. The role of this predator in dampening the rate and impact of *S. molle* invasion in South Africa needs to be explored.

**Keywords:** Alien plants, biological control, biological invasions, new association, seed endophagy, *Rhus*



## Introduction

Biological invasions pose one of the biggest threats to biodiversity worldwide (Williamson, 1999). Invasive species have caused economic or ecological problems that are difficult and sometimes impossible to control. Understanding the reasons why some alien species become invasive may help to identify appropriate management strategies. One hypothesis often cited to explain invasion success is the enemy release hypothesis (Williams, 1954; Elton, 1958; Blumenthal, 2006), which attributes the success of alien species to the fact that they are freed from the limiting biotic mortality factors (e.g., diseases, herbivores and pathogens) when introduced to a new habitat. Escape from natural enemies, it is argued, may give alien species a competitive advantage over native species and lead to an increase of their populations, possibly leading to invasion (Blumenthal, 2006).

Recent studies have demonstrated that alien plant species have smaller pathogen and herbivore communities in their introduced ranges than in their native ranges (Mitchell and Power, 2003), and that species regulated by predators in their native habitat may experience a strong predator release effect in their new environment (Maron and Vilà, 2001; Keane and Crawley, 2002). For example, DeWalt *et al.*, (2004) found that enemies of the shrub *Clidemia hirta* (L) D. Don., in its native Costa Rica were absent from Hawaii where it was introduced. Furthermore, insect and pathogen exclusion facilitated *C. hirta* establishment in Hawaii, suggesting that the absence of these enemies may have contributed to its invasiveness in the new habitat.

Although seed predation has been studied extensively in natural systems (Schöning *et al.*, 2004; O'Rourke *et al.*, 2006), research on effects of habitat differences on seed predation of alien plants are limited, and have mainly focused on post-dispersal seed predation (Myster and Pickett, 1993; Forget *et al.*, 1999). Some studies in South Africa on *Sesbania punicea* (Cav.) Benth. (Hoffmann and Moran, 1998) and on other long-lived woody alien plants, such as *Prosopis* species (Zimmermann, 1991) show that satisfactory control of perennial weeds can be accomplished by a single species of agent that drastically reduces the fecundity of its host plant. Predators often are able to destroy almost all seeds set in a season (Blate *et al.*, 1998), and high rates of seed predation may play a key role in plant population dynamics (Maron and Simms, 2001). Hoffmann and Moran (1998) advocated that

agents that reduce seed-set should be used routinely as first line of attack in biological control of weeds.

Spatial heterogeneity in seed predation may result from seed predators being more abundant in some habitats than others (Thompson, 1982). In its native South American range, *Sesbania punicea* is utilized by at least 18 insect herbivore species that together conspicuously damage all part of the plant (Erb, 1980). In South Africa, *S. punicea* suffered negligible damage from a few local generalist insect herbivore species until the 1980s when three South American herbivore species were introduced (Hoffmann, 1990; Hoffmann and Moran, 1998). Together these caused 99.7% reduction in seed production and a significant decline in the density of *S. punicea* (Hoffmann and Moran, 1998).

This study investigates geographical differences in predation pressure on seeds of the introduced Peruvian pepper tree, *Schinus molle* L., in South Africa by examining how the intensity of seed predation differs across a range of sites in the summer- and winter-rainfall regions of the country.

## **Materials and methods**

### *Study species*

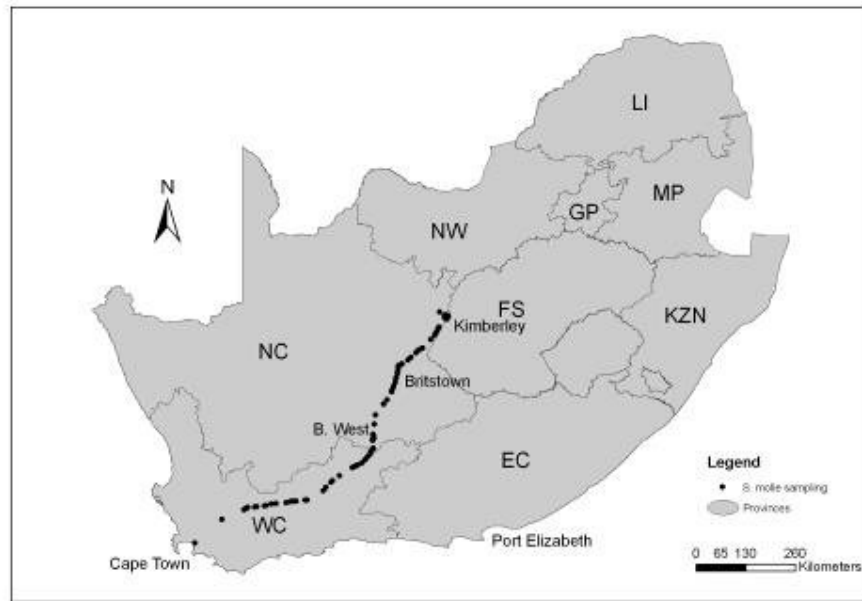
*Schinus molle* L., a shade-tolerant evergreen tree from Peru, was introduced into South Africa for use as an ornamental and shade tree in the middle 1800s (Potts, 1919). This species produces flowers and fruits throughout the year whenever conditions are favourable. Seeds are dispersed by birds, mammals, and water (Howard and Minnich, 1989; Silva *et al.*, 2005). The species is spreading in disturbed sites and in natural communities where it forms dense canopies that can completely shade out and displace native vegetation in the semi-arid savanna regions of South Africa (Milton *et al.*, 2007).

### *Field site and experimental design*

I sampled 30 trees each from summer and winter rainfall region. In total, 100 fresh, ripe seeds of *S. molle* (with red pericarps) were collected beneath each of 30 randomly

selected trees from the summer- and winter-rainfall regions (Western and Northern Cape provinces of South Africa). Samples were collected during a survey of *S. molle* populations along national and provincial roads and also on farms during February 2006 (summer). Trees were sampled over a distance of about 387.4 km in the winter and in the equinoctial rainfall region, between Stellenbosch and Beaufort- West (33° 56'S 18° 52'E; 32° 21'S 22° 35'E) and over 237.27 km in the late summer rainfall region, from Britstown to Kimberley (30° 35'S 23° 30'E; 28° 45'S 24° 46'E) on the road transect (Figure 4). Mean annual rainfall along the transect ranged from 800 mm in the SW near Stellenbosch to 400 mm in the NE near Kimberley, and was least in the centre of the transect near Touwsrivier (250 mm) which lies between the winter and summer rainfall zones (South Africa Weather Bureau, 2003). At each site, seeds were collected from a single randomly selected tree. The seeds were then placed in a paper bag, labelled with tree number and region of occurrence, and later examined in the laboratory for seed predation by counting the number of intact and damaged seeds under a dissecting microscope.

Insect-damaged seeds could be separated from other damaged seeds (rotten seeds) by the presence of insects inside the seeds or by emergence holes. Insect-damaged seeds were kept in a container for 1 year after the samples were collected and covered with a cotton screen for good aeration until insects emerged. Insects that emerged were photographed and samples were sent to the Department of Entomology and Nematology at the University of Florida. All the insects that emerged from seeds belonged to the same wasp species and produced emergence holes similar to those observed in the seeds collected. Because I counted emergence holes but did not dissect intact seeds, it is possible that I underestimated the full extent of seed predation.



**Figure 4:** Map of South Africa showing provincial boundaries and the major towns found along the line transect used for sampling. The dotted line = GPS location of *S. molle* presence. WC = Western Cape; NC = Northern Cape; EC = Eastern Cape; KZN = KwaZulu-Natal; MP = Mpumalanga; LI = Limpopo; GP = Gauteng Province; Bea West = Beaufort West.

### *Data analysis*

The percentages of insect-damaged seeds and of rotten seeds were compared between the winter and summer rainfall region populations. Seeds with insect emergence holes were considered to be insect damaged, and soft black seeds were considered to be rotten. One-way analysis of variance (ANOVA) was used to test for differences in seed damage between the regions after meeting the requirement of normality and homoscedasity of the data. The proportional contribution of insect endophagy and rotting to seed damage (characterized by breakdown of tissue causing the decay of flesh of the seeds) was compared for the two regions using contingency tables and the Chi-squared statistic (Statistica 6.1, StatSoft, Inc. 2003).

## Results

The native seed-feeding wasp *Megastigmus transvaalensis* Hussey (Hymenoptera: Torymidae) (see [http://creatures.ifas.ufl.edu/beneficial/m\\_transvaalensis.htm](http://creatures.ifas.ufl.edu/beneficial/m_transvaalensis.htm)) was identified as the main seed predator of *S. molle* in both regions. The total seed damage observed in *S. molle* was significantly greater in the summer-rainfall than in the winter-rainfall region for the localities sampled ( $p < 0.0001$ ;  $F_{1, 58} = 287.87$ ; Table 4.1), and was largely attributed to feeding damage by the developing larvae of *M. transvaalensis* (% of damage caused by insects  $1745/3000 = 58.17\%$ ; Table 4.2). There was no difference in the mean percentage of rotten seeds between the two regions ( $p = 0.764$ ;  $F_{1, 58} = 0.09$ ; Table 4.1). However, the relative proportion of insect-damaged seeds was significantly greater in the summer-rainfall population than in the winter-rainfall population (Chi-squared = 1300.12;  $P < 0.00001$ ; Table 4.2). Although *M. transvaalensis* is an African seed predator of *Rhus* spp., it apparently readily accepts some *Schinus* spp. as developmental hosts (Scheffer and Grissell, 2003). The ability of this seed wasp to exploit a novel host plant is consistent with the new host association principle (Hokkannen and Pimental, 1989).

**Table 4.1:** Percentages (mean  $\pm$  SE) of damaged, insect damaged and rotten seeds per sample (n=100 seeds) in summer and winter rainfall areas of South Africa.

Variables	Winter rainfall	Summer rainfall	F-value	P-value	N	Significance level
Total seeds damaged	32.80 $\pm$ 2.08	75.33 $\pm$ 1.39	287.87	0.0001	30	***
Insect damaged seeds	16.23 $\pm$ 1.93	58.16 $\pm$ 1.81	249.50	0.0001	30	***
Rotten seeds	16.56 $\pm$ 1.35	17.16 $\pm$ 1.45	0.09	0.764	30	NS

**Table 4.2:** Data used in Chi-square goodness of fit test, comparing the number insect damaged seeds, rotten seeds and healthy seeds between the two regions sampled (Chi-square = 1300.12;  $p < 0.0001$ ).

	Healthy seeds	Rotten seeds	Insect damaged seeds	Total
Winter rainfall	2016	574	487	3000
Summer rainfall	740	497	1745	3000

## Discussion

The study revealed that the native torymid wasp *M. transvaalensis* was the main endophagous seed predator of *S. molle* in both regions. The indigenous host plants of *M. transvaalensis* are four South African *Rhus* species (Anacardiaceae), *Rhus crenata* Thunb., *R. lancea* L.f., *R. pendulina* Jacq., and *R. pyroides* Burch. (Grissell and Hobbs, 2000; Cuda *et al.*, 2002). The high percentage of insect seed predation in the summer-rainfall region was probably due to the widespread occurrence of the indigenous *R. lancea* in sites where most of the sampling of *S. molle* populations was conducted (personal observation). This wasp is adventive in both Hawaii (Beardsley, 1971) and Florida, USA (Habeck *et al.*, 1989). In both of these US states, the wasp also attacks fruits of another *Schinus* species (*S. terebinthifolius* Raddi), with overall seed mortality caused by this wasp reported to be as high as 76% in Florida (Wheeler *et al.*, 2001) and 80% in Hawaii (Hight *et al.*, 2003). These levels of predation are similar to our results for *S. molle* in the summer-rainfall region of South Africa.

Although insect-damaged seeds were found in both regions, seed predation by this wasp was greater (in relative and absolute terms) in the summer–rainfall region. Reasons for the higher seed predation may include differences in abundance of the indigenous and alien hosts, or time of sampling in relation to the rainy season (in both the winter and summer rainfall areas). The wasp *M. transvaalensis* may be reducing the pre- and post-dispersal survival of *S. molle* seeds in the semi-arid savanna of South Africa and hence, the abundance and rate of spread of this invasive shrub.

However, as no control sites were available this hypothesis cannot be tested without manipulation of seed predation.

These results are contrary to some previous studies that have shown that alien plant species have fewer predators or pathogens in their introduced ranges and this may give them a competitive advantage over native species (Maron and Vilà, 2001; Keane and Crawley, 2002; Mitchell and Power, 2003). However, the results are in agreement with studies that have found that native predators do prey upon invaders in some systems (Trowbridge, 1995; Robinson and Wellborn, 1988; Baltz and Moyle, 1993, Creed and Sheldon, 1995). Particularly interesting is the study by Parker and Hey (2005); they found that an array of terrestrial and aquatic generalist herbivores prefer alien over native plants. The results also are consistent with those of Procheş *et al.*, (2008) who found heavy insect loads on alien woody plants in South Africa.

Although *S. molle* seed predation was higher in the semi-arid savanna region, the spread of *S. molle* is also greater in this area. This phenomenon may be due in part to certain aspects in the life history of this species, such as the ability to flower and seed after every major rainfall event. In some areas, *S. molle* may compensate for seed predation by prolific seed production. Many alien plant species and weeds have high growth rates and early reproduction, which may compensate for the effects of predation (Hönig *et al.*, 1992). Like many other invasive species, *S. molle* also has reproductive strategies that increase the likelihood of successful mutualisms with animals that function as seed dispersers (Richardson *et al.*, 2000). For example, its year-round production of small pink fruits facilitates its dispersal by a variety of indigenous birds (Milton *et al.*, 2007). However, other factors, which may include seedling establishment and survival in different microhabitats as well as climate change, may possibly explain the invasion success of *S. molle* in the semi-arid savanna of South Africa, but those factors require further investigation. Determining the extent to which seed predation reduces the invasive potential of *S. molle* is important for reducing the considerable impact of this species in areas currently invaded (Milton *et al.*, 2007; Iponga *et al.*, 2008) and for reducing its further spread. Such knowledge will be useful for implementing biological control of this species.

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# Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa

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**Chapter 10:** General conclusions and recommendations

## CHAPTER FIVE

### SEED SET OF THE INVASIVE ALIEN TREE SCHINUS MOLLE (ANACARDIACEAE) IN SEMI-ARID SAVANNA, SOUTH AFRICA: THE ROLE OF POLLINATORS AND SELFING

#### **Abstract**

For an introduced plant species to become invasive, it must be able to reproduce, even in an initially small population. Alien plants may be reproductively limited in their adopted habitats because of a lack of mutualistic pollinators. However, if plants are adequately served by native generalist pollinators, successful reproduction, naturalisation and expansion into exotic habitats may occur. *Schinus molle*, an emerging invasive plant in South Africa, is already showing signs of invasion in semi-arid savanna and along perennial rivers in arid regions. This species produces abundant flowers and seeds, but its self-compatibility and dependence on pollinators for seed set are unknown. This study investigates the extent to which seed production in *S. molle* is dependent upon pollinators and outcrossing with the objective of understanding whether pollination and seed set could be a barrier to the spread of *S. molle* in arid savannas of South Africa. Pollination experiments demonstrated that seed set was greater in female flowers exposed to natural pollinators than in those from which pollinators were excluded. Fruit set in inflorescences protected from external pollinators but artificially cross-pollinated, was greater than for protected inflorescences that received no artificial pollination. However, the fact that a few seeds were also found in treatments protected from pollinators and not treated with pollen may indicate that some *S. molle* flowers might be bisexual and capable of self-pollination. The results suggest that *S. molle* fruit set is mainly affected by insect pollination, but there is also the possibility of self-pollination and apomixis.

**Key words:** Biological invasions, breeding system, dioecy, Peruvian pepper tree, Pollination

## Introduction

Many plant species are deliberately or accidentally introduced into non-native habitats, but only a small fraction of these introduced species become invasive (Williamson, 1996; Richardson *et al.*, 2000a), and there is an imperfect understanding of why some introduced species become invasive while others fail (Enserink, 1999). One way to understand the traits that enable alien plant species to invade and persist outside their native range is to study key stages of the reproductive cycle of the plant, including pollination and seed dispersal. Pollination is the primary step in seed formation; therefore, where seed output is limited by pollination failure, I would expect levels of recruitment to the population from seed to be limited, unless recruitment is already constrained by microsite limitation (Wilcock and Neiland, 2002). Some processes, such as seed dispersal, have often been linked to that of seedling recruitment (e.g. Nathan *et al.*, 2000a,b; Holl, 2002; Milton *et al.*, 2007), but few studies have considered the preceding stage, i.e. that of pollination. Despite pollination being crucial to plant reproduction, the role of pollination mutualisms in facilitating or containing invasions has received little attention (Parker and Haubensak, 2002) except in recent papers by Herrera (2000), Picó and Retana (2000) and Richardson *et al.* (2000b).

Low levels of pollinator visitation have been shown to cause pollen limitation in a range of systems (Zimmerman and Aide, 1989; Thomson, 2001). For an introduced plant species to become invasive it must reproduce. For this reason, monoecious and self-compatible plants are more likely to be successful invaders because they can sire their own seeds if initial population sizes are small, limiting the availability of mates (Baker, 1955, 1967; van Kleunen and Johnson, 2007; van Kleunen *et al.*, 2008). Despite self-compatibility, pollinators may be required to move pollen from anthers to stigmas when introduced plants lack autonomous self-fertilization mechanisms (Parker, 1997).

Specialized pollination mutualisms (where a plant relies on a single species of pollinator) are rare in nature (Waser *et al.*, 1996; Richardson *et al.*, 2000b; Pellmyr, 2002). When a plant species requires a specialist pollinator, reproductive success may be constrained by the absence of specialist pollinators in the foreign habitat or biogeographical area (Richardson *et al.*, 2000b; Stout *et al.*, 2002). Reproduction of wind- and self-pollinated plant species is independent of mutualisms, but variation in

levels of pollinator visitation may promote or inhibit invasive plant spread in the new habitat for species that rely on vertebrate or invertebrate flower visitors (Baker, 1965; Valentine, 1978).

Even when potential pollinators are present, individual reproductive success of introduced plants, which at least initially grow as solitary individuals or in small populations, may be reduced by negative effects of small population size, i.e., allee effects (Stephens *et al.*, 1999). *Schinus molle* in semi-arid savanna of South Africa produces abundant flowers and seeds (Iponga *et al.*, 2008a), but its self-compatibility and dependence on pollinators for seed set is unknown. The main objective in this study is to understand whether pollination could be a barrier or accelerate the spread of *S. molle* in arid savannas of South Africa. In this study I ask the following specific questions: (1) Are *S. molle* inflorescences dependent on insects for pollination? (2) Do flowers of *S. molle* have the capacity for autonomous seed set?

## **Materials and methods**

### *Study site*

Field experiments were conducted at two sites, near Kimberley (28° 47' 24.6"S; 24° 46' 58.3"E, 1198 m above sea level) in the Northern Cape province of South Africa. Two study sites that differed in disturbance histories, namely military land currently managed as ungrazed savanna and an ungrazed mine dump were selected within the Kimberley area. Because the study was carried out on only one site of each land use type, comparisons of land use effects in this experiment may be considered as pseudo-replicated and differences among them cannot necessarily be attributed to particular management factors (see Milton *et al.*, 2007; Iponga *et al.*, 2008a,b for more details on the sites).

### *Species*

*Schinus molle* L. (Anacardiaceae), a shade-tolerant evergreen tree native to South America (Barkley, 1957), was introduced into South Africa for use as an ornamental and shade tree in the middle 1800s (Potts, 1919). It spreads in disturbed sites and in natural communities where it forms dense canopies that can completely shade out and

displace native vegetation in the semi-arid savanna regions of South Africa (Iponga *et al.*, 2008b). Although the species is considered to be dioecious, some flowers appear to be bisexual, because isolated female trees have been seen to produce large fruit crops, possibly because of apomixes (personal observation). The species produces flowers and fruits throughout the year whenever conditions are favourable. Flowers are visited by flies and small bees (Howard and Minnich, 1989), and seeds are dispersed by birds, mammals, and water (Howard and Minnich, 1989; Silva *et al.*, 2005; Milton *et al.*, 2007; Iponga *et al.*, 2008b, c). The interaction with invertebrate pollinators and vertebrate dispersers may thus be crucial in determining whether the invader can spread in the new habitat.

### *Field site and experimental design*

To test whether flowers of *S. molle* in its invasive range in South Africa can set seed in the absence of pollinators by apomixis (i.e., seed production without fertilization) or autonomous self-fertilization (i.e., self-fertilization without assistance of pollinators); I performed a bagging experiment. Twenty-four female trees were selected at each of the two sites. On 6 March 2002, I selected four inflorescences on each of the 24 trees (96 inflorescences per site). To exclude pollination, some inflorescences were covered with bags made of fine nylon mesh with mesh size of 0.3 mm to compare fruits set in the open and bagged inflorescences.

To test whether open-pollinated flowers are pollen limited, I also hand pollinated some inflorescences without bags. Furthermore, to test for any negative side effects of bagging on fruit set, I also hand pollinated some inflorescences with bags. Using a factorial design experiment, I developed the following four treatments on each tree:

- (1) B-P: The inflorescence was bagged to exclude pollinators and was hand pollinated using pollen from another tree (n = 24 per site);
- (2) B-NP: Bag + No hand pollination: The inflorescence was bagged to exclude pollinators but was not hand pollinated (n = 24 per site);
- (3) NB-P: No bag + hand pollination: The inflorescence not protected, but was hand pollinated using pollen from another tree (supplementation of pollen) (n = 24 per site);



- (4) NB-NP: No bag + No pollination: The inflorescence was not protected and was not hand pollinated (open inflorescence and with no hand pollination) (n = 24 per site);

Each treatment was randomly placed on a different aspect (N, S, E, and W) of the tree. The distance between the closest male and female tree were kept as far away as possible (20 to 200 m) to avoid pollen coming from the nearest male tree. I used a total of 24 female trees per site to have a balanced experiment in terms of the effect of aspect. I hand-pollinated, over a two-week period, all open flowers on selected bagged inflorescences on each tree with pollen from another tree. Hand pollination was done by picking the male flowers and brushing them on the female flowers. All the inflorescences were bagged before the buds opened to avoid any form of external pollination.

The unopened buds on each inflorescence were counted, and their transformation to ripe fruits tracked by weekly monitoring. The following variables were recorded: (1) number of unopened buds in each treatment; (2) number of flowers; (3) number of green fruits; and (4) number of red fruits per treatment inflorescence. *Schinus molle* inflorescences have very large numbers of flowers; to estimate flower numbers per treatment, I estimated the numbers of flowers and buds per inflorescence bunch by selecting ten inflorescences and counting the number of flowers per inflorescence branchlet and the number of branchlets per inflorescence.

### *Statistical analysis*

I used repeated-measure ANOVA to compare the number of flowers and fruits produced per treatment inflorescence over time period after checking for homogeneity and normality. I also used bootstrapping analysis for the non normal data. The effect of bagging on total fruits set over time was tested between different sites using repeated-measures ANOVA. Linear regression analysis was also performed to determine the relationship between the number of flowers at the start of the experiment and the total number of total fruits at the end of the experiment. I also tested the effect of aspect on fruit set over time for each treatment using repeated measures ANOVA (Statistica 6.1, StatSoft, Inc. 2003). To control for the fact that the

four inflorescences measured on the same tree were not independent, I included plant identity as a factor in the model.

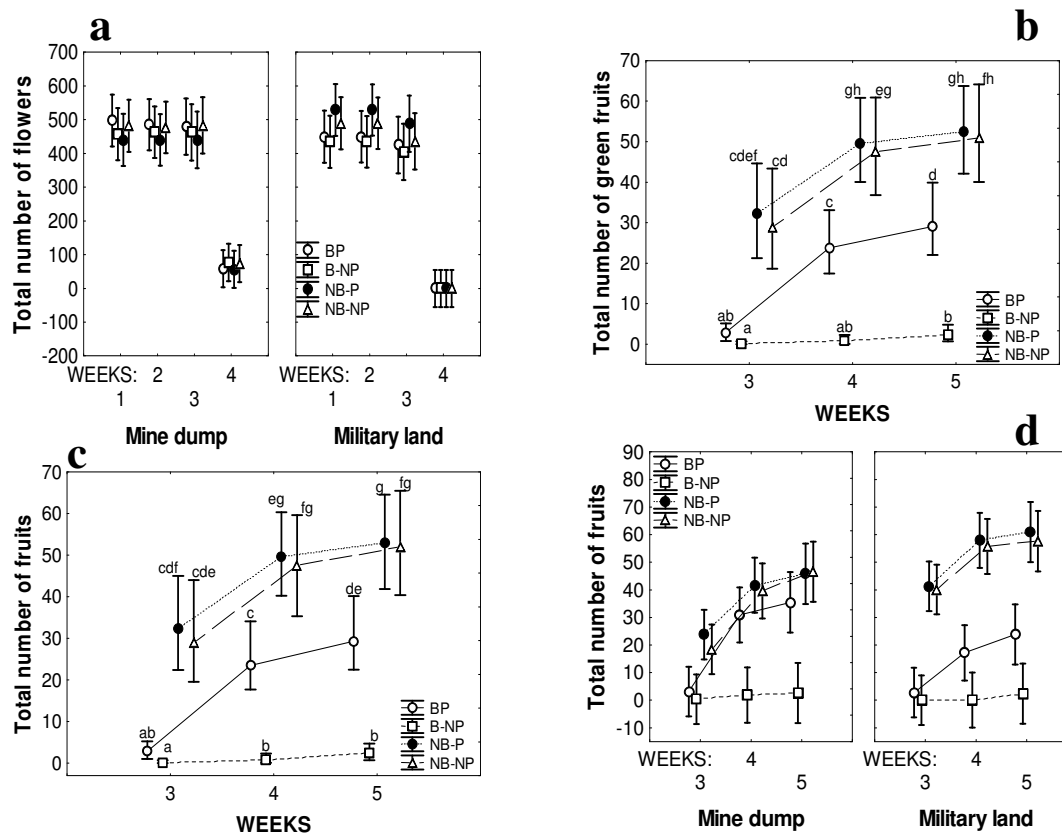
## Results

### *Flower and fruit production*

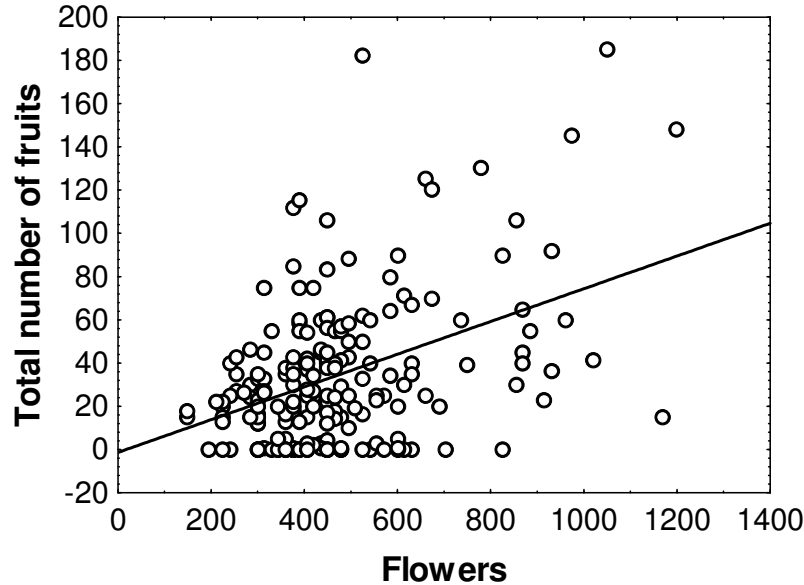
The overall process of flowering and fruiting, from inflorescence emergence to formation of unripe fruit, was completed within two weeks, but fruit development and maturation took an additional four to five weeks. The whole process, from flowering to fruit maturation, took about seven weeks. As indicated by the significant time-by-treatment interaction, the increase in the number of green and red fruits ( $F_{6, 376} = 9.76$ ;  $p < 0.0001$ ), was fastest for the inflorescences without bags and with hand pollination, followed by the inflorescences without bags and pollination and slowest for the bagged inflorescences with hand pollination. However, the bagged and unpollinated inflorescences showed the lowest numbers of green fruits and total fruits over time.

The number of flowers did not differ between treatments ( $F_{9, 552} = 0.61$ ;  $p > 0.05$ ; Figure 5.1 a) at both sites. The number of green fruits (Bonferroni test,  $p < 0.0001$ ; Figure 5.1b) and total fruit production (Bonferroni test,  $p < 0.0001$ ; Figure 5.1c) was significantly higher in bagged (inflorescences protected from insect visitation), hand pollinated treatments than in bagged treatments that were not pollinated (BP vs. B-NP) (Figure 5.1b, c). This indicates that pollinators may be required for seed production.

The results revealed that bagged inflorescences that were not pollinated (B-NP) set some fruits, although the fruit production was very low, and that fruit set increased significantly between census dates (Figure 5.1 b, c). Fruit production in unbagged pollen supplementation treatments did not differ significantly from the unbagged treatment without extra pollination (NB-NP vs. NB-P) (Figure 5.1b, c). Although the two sites generally show the same pattern of fruit set in all treatments, the hand-pollinated treatment appeared to be less effective on the military land than on the mine dump (Figure 5.1d). There was no difference in fruit set between different aspects of the tree canopy ( $F_{18, 35} = 1.54$ ;  $p > 0.05$ ). The proportion of flowers that set fruits was positively correlated with the total number of fruits ( $r^2 = 0.17$ ;  $p < 0.0001$ ;  $N = 48$ ; Figure 5.2).



**Figure 5.1:** Interaction effect of time (weeks) and pollination treatment of the repeated-measure ANOVA on the mean number of *Schinus molle* flowers per site (a); mean number of green fruits over time (b); mean number of total fruits set over time (c) and mean number of total fruits set per site (d). Different letters indicate significant differences between treatments and means sharing the same letters are not significantly different. Vertical bars indicate SD.



**Figure 5.2:** Fitted line of the linear regression between number of total fruit set and number of total flowers of *Schinus molle* ( $r^2 = 0.17$ ;  $p < 0.001$ ;  $N = 48$ ).

## Discussion

Many successful invasive flowering plants produce an abundance of flowers which are visited by a range of pollinators and secrete profuse volumes of nectar (Titze, 2000; Ghazoul, 2002). Pollination limitation thus seldom seems to be a major constraint for spread of introduced plants either because asexual propagation occurs or because wind or generalist pollinators can provide a pollination service (Richardson *et al.*, 2000b). The production of large numbers of seeds by an alien plant improves its chances of becoming invasive and of persisting and extending its range rapidly (Trakhtenbrot *et al.*, 2005). This study highlights concerns about the increase in seed production mediated either by external flower pollination or self-pollination. The results reveal that the overall process of flowering and fruiting, from flower emergence to seed maturation, was completed within approximately seven weeks. This suggests that phenological cycle of *S. molle* is completed quickly in semi-arid savanna in South Africa. The results showed that open pollinated inflorescences (with and without extra artificial hand pollination) had more fruits set when compared with bagged treatments that excluded natural pollinators. No difference in fruit set was

found between the two open pollination treatments which suggest that pollen abundance is not a limiting factor for fruit production in *S. molle*.

The results also showed that hand pollination of inflorescences in the pollinator exclusion treatment produced significantly improved fruit set relative to that of unpollinated inflorescences. However, some fruits were set in the absence of pollinators and hand pollination. The presence of fruit set in protected inflorescences might be due to the fact that, as has been observed for many alien plant species (van Kleunen *et al.*, 2008), some *S. molle* flowers may be bisexual and capable of self-pollination or apomixis. This suggests that flowers of *S. molle* may set fruit through self-pollination or by insect pollination - as a result of facilitated selfing and outcrossing, with insects mediating pollen transfer. Some studies have indicated that certain plant species may rely on the service of pollinators for reproduction even when they are self-compatible or self-pollinated (Atkinson, 1992; DeGroot *et al.*, 1997; van Kleunen *et al.*, 2005). These results seem to indicate that the ability of isolated *S. molle* plants to set seed as successfully as those in large populations is probably due to a combination of self-pollination and insects of pollination. For example, in *Betula apoiensis* trees on western and southern ridges of Mt. Apoi in Hokkaido, northern Japan, that received little pollen from other trees, inbred progeny are produced due to self-compatibility (Wang *et al.*, 1999; Nagamitsu *et al.*, 2006). However, self-pollination may contribute to population persistence by means of ensuring seed production under pollen limitation. The results also suggest that a combination of self-pollination combined with insect pollination may explain high *S. molle* seed production observed in South Africa even on isolated, apparently female trees. This hypothesis could be tested by genetic studies.

Fruit set in the absence of insect pollination might also be due to accidental contamination of the researcher's hands by pollen. During the process of counting flowers, pollen adhering to the investigators hands might have penetrated the bags and lead to the fertilization of the bagged flowers leading to the setting of a few fruits in that treatment. Hand pollination was effective and, in combination with the open pollinated treatments, indicates the important role played by pollination for fruits set. The regression analysis revealed that total number of flowers could be used to predict fruit set at both sites.

An increase in seed production may only be important if seed abundance is a limiting factor affecting population dynamics. In populations where seed banks already contain many seeds, an increase in the number of seeds produced may not actually affect population size or the spread of the species. In the case of *S. molle*, where there is no persistent seed banks (see chapter 3), invasion will depend on continuous fruit production. Other factors, such as dispersal mechanisms, germination success and resource availability, may influence *S. molle* population size and range. These factors have been investigated in previous studies, but still need further investigation and are thus interesting areas for future research.

In order to invade a new habitat, alien plants may rely on resident native pollinators or other methods of reproduction (Stout *et al.*, 2002; van Kleunen and Johnson, 2007; van Kleunen *et al.*, 2008). However, because alien plants are sometimes well served by native or generalist pollinators, spread is likely to occur in the new habitat (Stout *et al.*, 2006). For example, the Australian *Acacia* species introduced to South Africa, which rely on insect pollination, are successfully setting seed and spreading (Milton, 1982a, b; Nel *et al.*, 2004; Richardson and Kluge, 2008).

## **Conclusion**

Although other factors, such as resource limitation, may limit fruit set of *S. molle* in semi-arid savanna of South Africa, our results indicate that *S. molle* fruit set may be achieved through insect pollination, but there is also a possibility of self pollination. It is unclear whether our results are the result of accidental contamination of bagged inflorescences with pollen or because *S. molle* flowers may have self-pollination capacity. The generalisation about the effect of pollination of *S. molle* in South Africa should not be made from a limited number of studies. Although observation have shown that isolated trees have seen to produced large fruit crops, further research is still required.

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# Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa

**Chapter 1:** General problem of biological invasion in South Africa landscape

**Chapter 2:** Dynamics of alien woody plant invasions: review of processes and ecological impacts

## Main objectives

**Chapter 3:** Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 4:** *Megastigmus* wasp damage to seeds of *Schinus molle* (Peruvian pepper tree) across a rainfall gradient in South Africa: Implication for invasion

**Chapter 5:** Seed set of the invasive alien tree *Schinus molle* (Anacardiaceae) in semi-arid savanna, South Africa: the role of pollination and selfing

**Chapter 6:** Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 7:** Performance of seedlings of the invasive alien tree *Schinus molle* under indigenous and alien host trees in semi-arid savanna

**Chapter 8:** Superiority in competition for light: a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Peruvian pepper tree) in South Africa

**Chapter 9:** Distribution of the invasive alien tree *Schinus molle* in western South Africa: current determinants and projections under scenarios of climate change and management.

**Chapter 10:** General conclusions and recommendations

## CHAPTER SIX

### SOIL TYPE, MICROSITE, AND HERBIVORY INFLUENCE GROWTH AND SURVIVAL OF *SCHINUS MOLLE* (PERUVIAN PEPPER TREE) INVADING SEMI-ARID AFRICAN SAVANNA.

#### **Abstract**

Naturalization of *Schinus molle* (Anacardiaceae) has been observed in semi arid savanna of the Northern Cape Province of South Africa. However, with high dispersal ability, the species is expected to achieve greater densities and invade more widely. To predict patterns of future invasion in semi-arid savannas, I investigated the effects of soil type, microsite condition (microsite), and herbivory by large mammals on growth and survival of *S. molle* seedlings.

The study involved a field manipulation experiment over 14 months using a factorial block design to examine transplanted seedlings in different savanna environments. The experiments examine the effects of soil type (sandy and clay), microsite, and herbivores on seedling performance (establishment, growth and survival). Seedlings were grown in a greenhouse and individually transplanted into four treatment groups: in open grassland, under tree canopies, and with and without cages to exclude large herbivores (cattle and game). The same experiment was repeated in two different soil types: coarse sand and fine-textured clay soil.

Results suggest that protection provided by canopies of large indigenous *Acacia* trees facilitates *S. molle* invasion into semi-arid savanna. In the field, *S. molle* seedlings performed considerably better beneath canopies of indigenous *Acacia* trees than in open areas regardless of soil type. Whether exposed or protected from large herbivores, no seedlings planted in open grassland survived the first winter. Although, seedlings grew better and had higher survival rates beneath tree canopies than in the open sites, exposure to large herbivores significantly decreased heights and

canopy areas of seedlings compared with those protected from large herbivores. The effect was greater on clay soil than on sandy soil.

The results suggest that low temperature (frost), and possibly inter-specific competition with grasses, may limit *S. molle* seedling establishment, survival and growth away from tree canopies in semi arid savannas. Low soil nutrient status and browsing may also delay growth and development of this species. The invasive potential of *S. molle* is thus greatest on fertile soils where sub-canopy microsites are present and browsing mammals are absent.

**Keywords:** alien plants, biological invasions, invasive species, microhabitat, interspecific interaction, facilitation, transplanting, tree invasions.

## Introduction

Variation in the success of particular introduced plant species can be caused by numerous environmental features, including substrate type and climatic factors. Harsh climatic conditions such as frost or drought can prevent the establishment of seedlings of species from milder climates. On the other hand, unusual weather events, such as above-average rainfall, may trigger establishment and facilitate naturalization or invasion (Richardson *et al.*, 2000).

Success is also mediated by various biotic interactions. The availability of dispersal agents to move viable seeds to suitable microsites (Jordano and Herrera, 1995; Dean and Milton, 2000), the absence of superior competitors for a limiting resource (Canham, 1989; Iponga *et al.*, 2008), and limited damage by pathogens and predators (Hoffman and Moran, 1998) may all increase the probability of invasion or determine the spatial distribution of an invasive plant population in the landscape (Russell and Schupp, 1998). One of the most important mechanisms for facilitating plant establishment in semi-arid environments is the amelioration of stressful micro-climatic conditions (Callaway, 1995). In savannas, microsites beneath tree canopies are among the most favourable for the establishment of seedlings of certain trees and shrubs (Verdú and Garcia-Fayos, 1996; Flores and Enrique, 2003). One reason for this is that variations in ambient temperatures are buffered and relative humidity is greater in these microsites (Belsky *et al.*, 1989; Belsky, 1994). Few studies have

documented facilitation of alien trees by native trees, but Milton *et al.*, (2007) show that such facilitation can act as a potent mediator of invasion success.

*Schinus molle* (Anacardiaceae) is an evergreen, drought-tolerant tree native to semi-arid parts of South America. Since the 1800s it was widely planted on roadsides, in graveyards, and in gardens in South Africa as a shade tree. It has recently become naturalized at some sites in semi-arid savanna (Iponga *et al.*, 2008). It is already considered a major invader in South Africa (Nel *et al.*, 2004), but has the potential to expand its range considerably (Rouget *et al.*, 2004). The species is dioecious and flowers and fruits continuously throughout the year. Female trees produce large crops of small bright pink berries in bunches on pendulous stems, and the seeds are dispersed by birds, mammals, and water (Silva *et al.*, 2005). Where naturalized in South Africa, seedlings occur mainly beneath indigenous *Acacia* trees where seeds of *S. mole* and other fleshy-fruited plants are dispersed by birds (Milton *et al.*, 2007). Such sites are also used preferentially by large herbivores seeking shade. Therefore this study specifically investigates the ways in which the following factors, individually and in concert, potentially influence establishment, growth and survival of *S. molle* seedlings in semi-arid savanna: soil type; facilitation by large *Acacia* tree canopies; and herbivory by large mammals. I then consider the implications of those patterns for the prediction of the invasion potential of this species in semi-arid savanna of South Africa.

## **Materials and methods**

### *Study sites*

The study was carried out at Benfontein Game farm (28°50'S; 24°50'E), an 11,300 ha property owned by De Beers Consolidated Mines and located approximately 8 km south-east of town of Kimberley in South Africa's Northern Cape Province. The mean annual rainfall for Kimberley is 431±127mm and usually peaks in the late summer months (March and April). Precipitation is usually in the form of late afternoon thundershowers. Mean daily temperature maxima and minima range between 33° C and 18° C in January, and 19° C and 3° C in July (South African Weather Bureau, 2007), and the altitude is about 1200 m above sea level.

The vegetation in the area is Kimberley Thornveld, a component of the Eastern Kalahari bushveld bioregion (Mucina *et al.*, 2006), and consists of semi-arid open savanna. Much of the farm is covered by open grassland with dwarf “karroid” shrubland surrounding a large but ephemeral pan (temporary water body). Soils at Benfontein can be divided into three types. In the north-west the substrate of the pan substrate comprises calcium carbonate (calcrete). Away from the pan to the south-east a belt of red Kalahari sand overlies the calcareous tufa. Igneous intrusions (dolerite for hills along the southern and south-western boundaries) give rise to fine-textured soil in this section of the farm (Spottiswoode, 2005). Cattle (*Bos indica*) stocked at approximately 18 ha/LAU (1 LAU or Large Animal Unit is equivalent to one head of cattle weighing 450 kg) are confined to open woodland dominated by *Acacia erioloba* on the sandy soils at Benfontein. The remaining 8,300 ha of Benfontein, including the pan and the *Acacia tortilis* dominated savanna on finer-textured soils is managed as a game farm. Indigenous animals are stocked at approximately 15 ha/LAU and include springbok, *Antidorcas marsupialis* (ca 2,134 individuals); blesbok, *Damaliscus dorcas phillipsi* (115), black wildebeest, *Cannochaetus gnou* (253) and ostrich (259). Smaller antelope including steenbok, *Raphicerus campestris*, common duiker, *Sylvicapra grimmia*, and the mountain reedbuck, *Redunca fulvorufula* also occur at low densities throughout the area.

### *Method description and sampling*

#### *Experimental design*

Seedlings of *S. molle* were germinated in greenhouse at Stellenbosch University. Geminated seedlings were transplanted into 1000 ml plastic bags and maintained at ambient temperatures with daily watering until they reached a height 10-15 cm. Two hundred of these seedlings were then transported to Kimberley in March 2006 for use in transplanting experiments.

A total of 120 *S. molle* seedlings were transplanted to the savanna, 60 on sandy soil, and 60 on fine soil (Table 6.1). As the soil types were 20 km apart on opposite sides of the pan, the soil-type treatments could not be interspersed. Within each of the soil types, a factorial block design was used to examine effects of microsite and herbivory on seedling performance. Ten spreading *Acacia erioloba* trees were

selected as host plants on Kalahari sand and 10 *Acacia tortilis* trees were selected as hosts on fine-textured soil. Beneath each of these host trees, three *S. molle* seedlings were planted (approximately 2 m to the south, east and west of the host tree trunk). Plantings of three *S. molle* seedlings were made in open grassland beyond the canopies of each of the 20 host trees. Individual cages were placed around 60 seedlings to protect them from large browsing herbivores (15 each in open and subcanopy sites on sand and fine-textured soil).

### *Statistical analysis*

Seedlings were monitored monthly for 14 months for growth and survival, starting the first month after transplanting (March 2005) until the end of the experiment in April 2007. The following measurements were recorded monthly for each seedling: height, canopy diameter using a 50 m measurement tape, change in basal area (based on stem diameters measured with vernier callipers), and the number of branches produced by each plant.

The canopy area was calculated using the following formula for an ellipse (Bronstein and Semendjajew, 1991):  $\text{Cover} = (\pi/4) \cdot \text{canopy1} \cdot \text{canopy2}$  (1), where *canopy1* and *canopy2* are two perpendicular diameters of the plant as seen from above.

The experiment included time as an independent variable. Repeated measure analysis of variance (ANOVA) was used to test the main factors (soil type, microsite, herbivory) and their interactions on measured plant parameters (height, canopy area, change in stem basal area and number of branches) over time period after testing for normality and homogeneity of the data. ANOVA models significant at 0.05 were used and significantly different treatment means were separated using a Scheffé post-hoc test in Statistica (Statistica 6.1, StatSoft, Inc. 2003). For this paper only the results of heights and canopy areas were considered. The survival of all transplanted seedlings was calculated as the mean number of surviving seedlings per treatment. Seedlings that survived at each recording stage were expressed as a total of the original seedling population planted.

A generalized non-linear model, with a log link function to a Poisson distribution was used to test for differences in number of seedlings that survived



compared to dead seedlings between treatments (Herbivory and Microsite) for each soil type, since I used count data (Statistica 6.1, StatSoft, Inc. 2003). A survival analysis was done comparing two or more groups in the generalized non linear model module of Statistica, to compare cumulative proportion of seedlings that survived over time.

## Results

### *Seedling height and canopy cover*

At the end of 14 months, the heights of seedlings were significantly greater in the clay soil than the sandy soil (Table 6.4). *Schinus molle* seedlings grew significantly taller (Table 6.4) and had larger canopy areas (Table 6.4) beneath tree canopies compared to open areas. Position beneath tree canopies had a greater positive effect on the performance of seedlings than other factors. Canopy areas of seedlings, however, did not differ between the two soil types (Table 6.4).

A significant interaction effect was found between soil types and browsing, but only for seedling height (Table 6.1). However, height and canopy areas of seedlings in the shade were more negatively affected by large herbivores for seedlings in the shade than those in the open (Table 6.3 and 6.4 and Figure 6.1). Seedlings in cages were significantly taller and wider than uncaged seedlings but for shaded plants only; no difference was found for caged and uncaged seedlings for plants in the open areas (Figure 6.1). The results also indicated the same trend over time for all the interactions. A sudden decline in seedling heights and canopy areas was observed during winter season (July-September) for seedlings in the open areas, whether exposed or protected from large herbivores and for both soil types. There was also a greater recovery of canopy areas, in summer (October-January) for unbrowsed seedlings in the shade, compared with those in the open areas for both soil types (Figure 6.1).

**Table 6.1:** Allocation of *Schinus molle* seedlings to treatments. The numbers in the body of the table are the numbers of seedlings in each treatment.

Treatments	Sandy soil	Fine-textured soil
Host tree	<i>Acacia erioloba</i>	<i>Acacia tortilis</i>
Browser	cattle	mixed game
Subcanopy (caged)	15	15
Subcanopy (exposed to herbivores)	15	15
Grassland (caged)	15	15
Grassland (exposed to herbivores)	15	15
Total	60	60

**Table 6.2:** Results of repeated measure analysis of variance (ANOVA) of *Schinus molle* heights, and their different interaction effect between soil type, microsite, herbivory and time on transplanted seedling. Significance: NS = non significant; \*\* =  $p < 0.05$ ; \*\*\* =  $p < 0.0001$ . With SS = Sum of square; MS = Mean square; Df = Degrees of freedom.

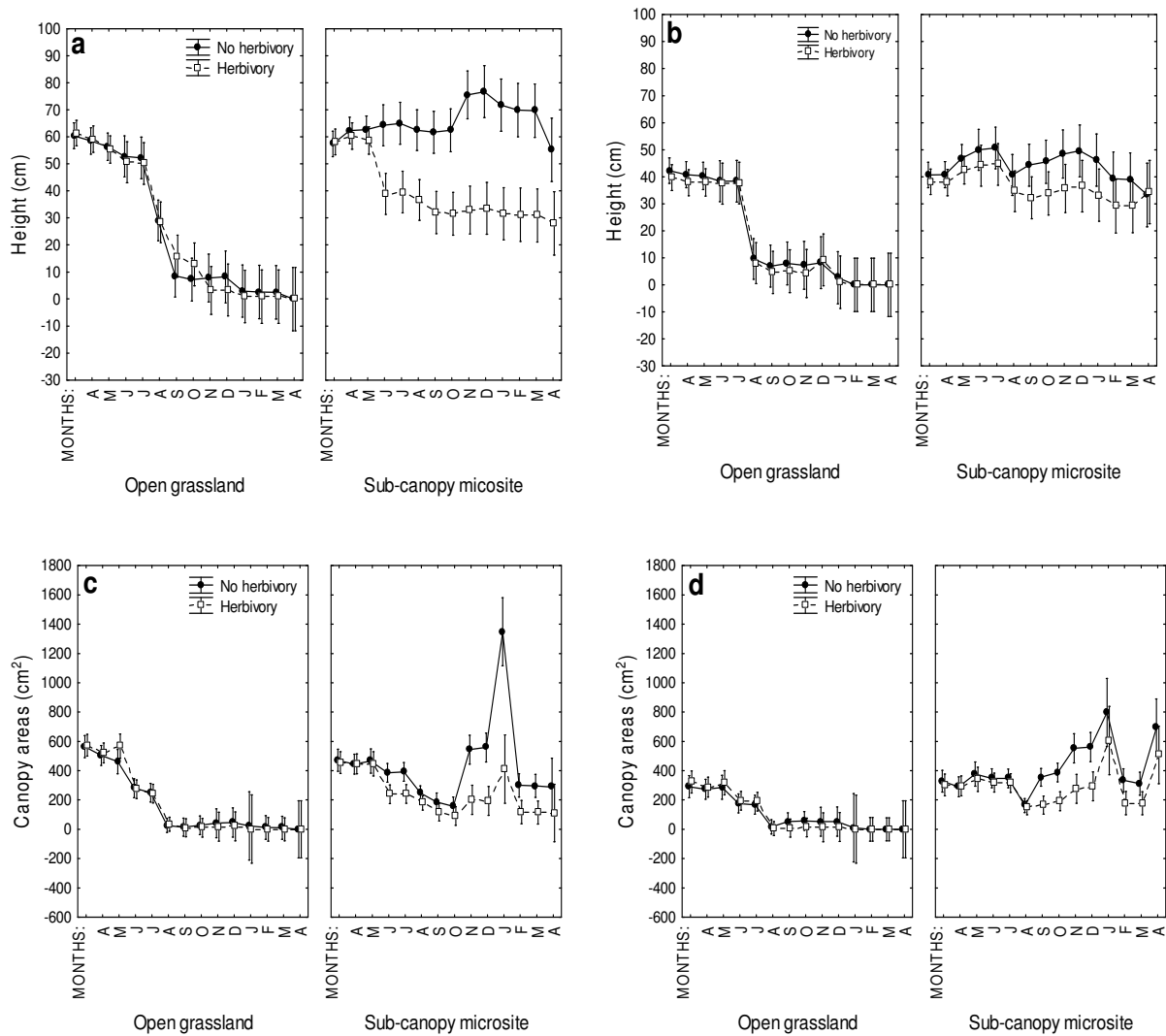
Treatments	SS	Df	MS	F-values	p-values	Significance level
{1} Soil type	43039	1	43039	22.556	<b>&lt;0.001</b>	***
{2} Microsite effect	271875	1	271875	142.485	<b>&lt;0.001</b>	***
{3} Herbivory effect	34683	1	34683	18.176	<b>&lt;0.001</b>	***
Soil type*microsite effect	1732	1	1732	0.907	0.342	NS
Soil type*herbivory effect	8367	1	8367	4.385	<b>0.038</b>	**
Microsite effect*herbivory effect	27944	1	27944	14.645	<b>&lt;0.001</b>	***
Soil type*microsite*herbivory effect	10369	1	10369	5.434	<b>0.021</b>	**
{4} MONTHS	235749	13	18135	132.728	<b>&lt;0.001</b>	***
Months *Soil type	12146	13	934	6.838	<b>&lt;0.001</b>	***
Months *microsite effect	129919	13	9994	73.144	<b>&lt;0.001</b>	***
Months *herbivory effect	8906	13	685	5.014	<b>&lt;0.001</b>	***
Months *Soil type*microsite effect	7720	13	594	4.346	<b>&lt;0.001</b>	***
Months *Soil type*herbivory effect	5039	13	388	2.837	<b>&lt;0.001</b>	***
Months *microsite effect*herbivory effect	8400	13	646	4.729	<b>&lt;0.001</b>	***
4*1*2*3	2740	13	211	1.542	0.095	NS

**Table 6.3:** Results of repeated measure analysis of variance (ANOVA) of *Schinus molle* canopy areas, and their different interaction effect between soil type, microsite, herbivory and time on transplanted seedling. Significance: NS = non significant; \*\* =  $p < 0.05$ ; \*\*\* =  $p < 0.0001$ . With SS = Sum of square; MS = Mean square; Df = Degrees of freedom.

Treatments	SS	Df	MS	F-values	p-values	Significance level
{1} Soil type	199852	1	199852	0.8877	0.348	NS
{2} Microsite effect	19529103	1	19529103	86.7464	<b>&lt;0.001</b>	***
{3} Herbivory effect	2718405	1	2718405	12.0749	<b>&lt;0.001</b>	***
Soil type*microsite effect	675016	1	675016	2.9984	0.086	NS
Soil type*herbivory effect	111693	1	111693	0.4961	0.482	NS
Microsite effect*herbivory effect	2582989	1	2582989	11.4734	<b>&lt;0.001</b>	***
Soil type*microsite effect*herbivory effect	152492	1	152492	0.6774	0.412	NS
{4} MONTHS	22852970	13	1757921	59.4109	<b>&lt;0.001</b>	***
Months*soil type	4864857	13	374220	12.6472	<b>&lt;0.001</b>	***
Months*microsite effect	18172969	13	1397921	47.2443	<b>&lt;0.001</b>	***
Months*herbivory effect	2774805	13	213447	7.2137	<b>&lt;0.001</b>	***
Months*soil type*microsite effect	1445395	13	111184	3.7576	<b>&lt;0.001</b>	**
Months*soil type*herbivory effect	1183377	13	91029	3.0764	<b>&lt;0.001</b>	***
Months*microsite effect*herbivory effect	1875614	13	144278	4.8760	<b>&lt;0.001</b>	***
4*1*2*3	972349	13	74796	2.5278	<b>&lt;0.001</b>	***

**Table 6.4:** Mean heights ( $\pm$  Std.Err) and mean canopy areas ( $\pm$  Std.Err) of surviving seedlings of *Schinus molle* after 14 months protected from large herbivores in sub-canopy microsites and in the open grassland. *P-values* obtained through Scheffé *post-hoc tests*.

Variables/Treatments	Soil types	sub-canopy microsite + No herbivory (Mean $\pm$ Std.Err)	Open area + No herbivory (Mean $\pm$ Std.Err)	p-values
Heights (cm)	Clay	65.52 $\pm$ 3.01 (15)	24.93 $\pm$ 3.01 (15)	<b>&lt;0.001</b>
Canopy areas (cm <sup>2</sup> )	Clay	434.68 $\pm$ 32.74 (15)	161.66 $\pm$ 32.74 (15)	<b>&lt;0.001</b>
Heights (cm)	Sandy	43.94 $\pm$ 3.01 (15)	17.34 $\pm$ 3.01 (15)	<b>&lt;0.001</b>
Canopy areas (cm <sup>2</sup> )	Sandy	417.59 $\pm$ 32.74 (15)	102.50 $\pm$ 32.74 (15)	<b>&lt;0.001</b>



**Figure 6.1:** Interaction effect of months, shading and soil type on mean heights and mean canopy areas of *Schinus molle*. Solid line = protected from large herbivory, and dotted line = exposed to herbivory. The graph (a) = heights for clay soil, (b) = heights for sandy soil, (c) = canopy areas for clay soil and (d) = canopy areas for sandy soil. Vertical bars show standard deviations from the mean.

### *Seedling survival*

The total mortality of seedlings after 14 months of experiment showed considerable variation across treatments for both soil types. Seedling survival (i.e. mean seedling survival at the end of the experiment) was significantly higher for seedlings beneath tree canopies than for those in the open areas, on both soil types (Table 6.6 and Figure 6.2). There were significant differences in survival of seedlings in subcanopy and open sites. Soil type and herbivory had no significant influence on survival (Table 6.6 and Figure 6.2). At the end of the experiment, all of the seedlings in the open area, whether exposed to or protected from large herbivores, had died and only seedlings beneath tree canopies remained alive. In contrast, beneath tree canopies, survival of seedlings protected from large herbivores was greater than for seedlings exposed to large herbivores on both soil types, but significant only for seedlings on the clay soil (Table 6.6).

Although seedling mortality in the sandy soil began later than on fine soil, mortality was also faster in the sandy soil than in the clay soil where seedling numbers declined more gradually (Figure 6.2a). Mortality occurred more quickly for seedlings in the open area, whether exposed to or protected from large herbivores, than for seedlings beneath tree canopies (Figure 6.2b). The results also show that seedling mortality in the open areas started in winter with a fast decrease until the end of the experiment when the all seedlings were dead; in contrast, below tree canopies mortality was low and gradual (Figure 6.2b; Table 6.7 ).

**Table 6.5:** Mean heights ( $\pm$  Std.Err) and mean canopy areas ( $\pm$  Std.Err) of surviving seedlings of *Schinus molle* after 14 months exposed to or protected from large herbivores in sub-canopy microsites. *P-values* obtained through Scheffé *post-hoc* tests.

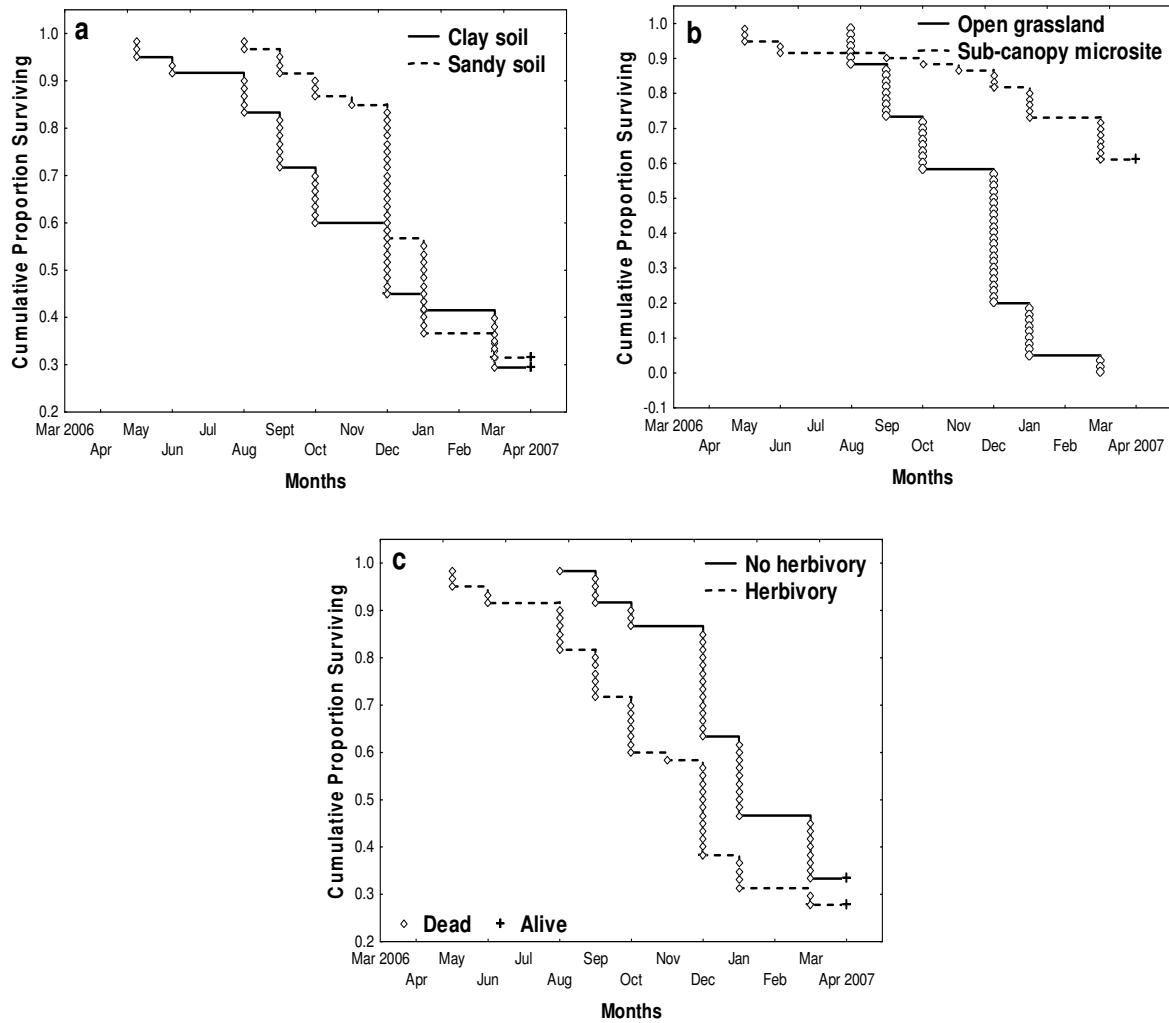
Variables/Treatments	Soil types	Herbivory + sub-canopy microsite (Mean $\pm$ Std.Err)	No herbivory + sub-canopy microsite (Mean $\pm$ Std.Err)	p-values
Heights (cm)	Clay	38.85 $\pm$ 3.01 (15)	65.52 $\pm$ 3.01 (15)	<b>&lt;0.001</b>
Canopy areas (cm <sup>2</sup> )	Clay	240.45 $\pm$ 32.74 (15)	434.68 $\pm$ 32.74 (15)	<b>&lt;0.001</b>
Heights (cm)	Sandy	36.12 $\pm$ 3.01 (15)	43.94 $\pm$ 3.01 (15)	0.263
Canopy areas (cm <sup>2</sup> )	Sandy	294.09 $\pm$ 32.74 (15)	417.59 $\pm$ 32.74 (15)	0.144

**Table 6.6:** Log link function to a Poisson distribution of the mean ( $\pm$  Std.Err) number of seedlings of *Schinus molle* that survived at 14 months for different treatment interactions (Chi-Square = 0.000; p = NA).

Soil types	Microsite effect	Herbivory effect	Mean percentage $\pm$ Std.Err.
Clay	Open area	No herbivory	0 (15)
Clay	Open area	Herbivory	0 (15)
Clay	Sub-canopy	No herbivory	0.73 $\pm$ 0.12 (15)
Clay	Sub-canopy	Herbivory	0.47 $\pm$ 0.13 (15)
Sandy	Open area	No herbivory	0 (15)
Sandy	Open area	Herbivory	0 (15)
Sandy	Sub-canopy	No herbivory	0.60 $\pm$ 0.13 (15)
Sandy	Sub-canopy	Herbivory	0.67 $\pm$ 0.13 (15)

**Table 6.7:** Descriptive statistics of survival analysis for each group. Clay soil vs. sandy soil (p = 0.08; z = -1.74); Open grassland vs. tree sub-canopy (p < 0.001; z = -6.73); Herbivores vs. No herbivores (p < 0.05; z = 2.81).

Treatment Groups	Dead	Percent Dead (%)	Alive	Percent Alive (%)	Total N
Clay soil	42	70.00	18	30.00	60
Sandy soil	41	68.33	19	31.67	60
Open area	60	100.00	0	0.00	60
Sub-canopy	23	38.33	37	61.67	60
No herbivory	40	66.67	20	33.33	60
Herbivory	43	71.67	17	28.33	60



**Figure 6.2:** Cumulative proportion of *Schinus molle* seedlings that survived over time. The graphs show: (a) = clay soil vs. sandy soil; (b) = open grassland vs. sub-canopy microsite; (c) = protected from large herbivory vs. exposed to large herbivory. The cross (+) = proportion of seedling that survived and, (0) = no seedling survived.



## Discussion

### *Microsite effect*

The results clearly indicate that sub-canopy microsite, protection of seedlings from large herbivores and fine-texture soil; together improve *S. molle* seedling performance in semi arid savanna. However, canopy cover of large *Acacia* trees seems to be the most important factor determining the survival of *S. molle* seedlings despite the fact that the species is known to be drought tolerant (Howard and Minnich, 1989). The results showed that *S. molle* seedlings grew better in the subcanopy sites than in the open grassland and suggested that those facilitation processes occur across both clay and sandy soil. The good performance of seedlings underneath tree canopies could be associated with the microclimate condition created by the canopy underneath of *Acacia* trees, which often act as a nurse plant for fleshy-fruited shrubs in semi arid savannas (Milton *et al.*, 2007).

Tree and shrub canopies buffer temperature changes beneath them, so that the difference between minimum and maximum temperatures is less below tree canopies than in open grassland (Belsky *et al.*, 1989). During winter, the minimum temperatures remain higher below tree and shrub canopies than in the open (Davies *et al.*, 2007; Drezner, 2007). Seedlings in the open areas may experience more frequent and more severe frosts than their counterparts beneath tree canopies (Shumway, 2000). In summer the shading effects of the canopy might decrease light penetration, reduce solar radiation and lower soil surface temperature, thereby reducing desiccation and increasing higher relative humidity, which potentially can enhance *S. molle* seedling establishment and growth (Belsky, 1994; Scholes and Archer, 1997). This is also consistent with the argument that light reduction below pioneer trees could be responsible for the unusually high success of tree seedlings that have been observed to recruit near established trees in the grasslands (Scholes and Archer, 1997; Weltzin and McPherson, 1999; Van Auken, 2000; Teague *et al.*, 2001).

Although most seedling shoot dieback began during the winter, implicating extreme cold or frost in the mortality of *S. molle* seedlings in open sites, further experiments are required to discriminate between the effects of temperature amelioration, and of reduced radiation or transpiration rates, on seedling survival.

It is also possible that competition from grass may be the cause of the sudden decline of seedling performance in the open areas. Studies in old field grasslands have shown that grass competition could reduce growth and survival of woody plant seedlings in a grass dominant environment (Iponga *et al.*, 2005). However, given that winters are dry and grasses generally dormant in winter, the competition hypothesis seems less plausible than the facilitation hypothesis in explaining mortality patterns. Because this experiment did not measure competition and physical factors directly, it is not clear which one of those may have the more negative effect on seedling performance in the open areas.

### *The effect of large herbivores*

The results showed that seedlings exposed to large herbivores were significantly shorter than those protected from large herbivores for both soil types, beneath tree canopies and in the open, and that this effect was more marked on fine-textured soils and beneath tree canopies. Herbivores are well known to reduce seedling performance and cause plant mortality (Pitt *et al.*, 1998; Iponga *et al.*, 2005). Seedlings exposed to large herbivores experience more trampling and browsing damage in the shade, because those microsites are preferentially used by large herbivores for resting and browsing food (Belsky *et al.*, 1989, Dean *et al.*, 1999). However, it was not possible to tell which species of herbivores caused more damage to *S. molle* seedlings.

Seedlings in the open areas exposed to or protected from large herbivores did not differ significantly in size. The reason is probably that herbivore damage was obscured by other sources of variation among seedlings such as frosting caused by lower temperatures during winter season, or drought in summer. The ability of introduced plants to establish and spread may depend not only on the structure of the resident biotic community, but also the local abiotic conditions or their joint effects (Michell *et al.*, 2003; DeWalt *et al.*, 2004). These results contrast with several studies that have indicated a positive relationship between grazing intensity and degree of invasion in grassy woodland systems (Prober and Thiele, 1995; Abensperg-traun *et al.*, 1998) and have suggested that removal of stock is a common management approach for reducing the rate of invasion in those ecosystems (Elix and Lambert, 1997). Higher densities of large game on the clay substrate may have contributed to lower seedling performance, which, in turn, may have contributed to lower the risk of

*S. molle* invasion in those areas. This again indicates that herbivores can exert considerable control over *S. molle* seedling performance beneath tree canopy.

### *How do substrate textures affect seedling performance?*

Particle size and organic matter content in the soil, affects water holding capacity, aeration, resistance to root penetration, and nutrient availability (Freitas and Mooney, 1996; Reich *et al.*, 1997), all of which have been shown to influence seedling survival (Peters, 2004). Sandy substrates in the semi-arid and arid parts of South Africa are nutrient poor relative to finer-textured soils (Milton *et al.*, 1992). Soil phosphorous and other nutrients adhere to clay particles and are less mobile in clay than in sand (Allcock, 2002). Nutrient-enriched patches beneath trees would therefore be more persistent on clay than on sand, and possibly more prone to alien invasion for this reason (Vinton and Burke, 1995).

Moreover, *S. molle* is probably sensitive to water availability at the establishment stage, and fine-texture soils have better water-holding capacity than coarse sandy soil (Nambiar *et al.*, 1979; Gordon *et al.*, 1989; Freitas and Mooney, 1996; Reich *et al.*, 1997). The ability of newly planted seedlings to perform well can be related to their water status (Mena-Petite and Muñoz-Rueda, 2005). The rainfall in the Kimberley area is extremely variable, both in time and in spatial distribution; it usually peaks in the late summer months with March and April being the wettest months (South African Weather Bureau, 2007). There is a distinct arid period during winter and a humid period during summer months. The sudden drop of seedling performance observed in winter in the open area during this experiment could be associated with post planting water and nutrient stress due to the lack of water in winter; which may cause lack of continuity between soil and roots immediately after planting, and increase the time needed to produce adequate amounts of new roots to resume water and nutrients uptake. Grossnickle (2000) found that, until the root system has grown sufficiently to offset transpiration loss with water uptake, seedlings may continue to suffer water stress and exhibit high mortality rates.

### *Interaction effects*

Significant three-way interactions between soil types, microsite and herbivory effect were found for heights, but not canopy areas, of seedlings. This significant three-way interaction was probably due to the interaction between microsite and herbivory effect on seedling performance, where seedlings in the clay soil experience more herbivory damage than the sandy soil for seedlings beneath tree canopies. This suggested that seasonal and inter-annual fluctuations in physical conditions may influence seedling performance in semi-arid savanna. Tree recruitment in semi-arid savannas occurs in occasional favourable spells (Higgins *et al.*, 2000; Jeltsch *et al.*, 2000) that maintain tree populations in environments generally unfavourable for seedling establishment and survival, but favourable for adult plants.

Large *Acacia* trees in semi-arid savanna are focal points for animal activity (Dean *et al.*, 1999, Radford *et al.*, 2001), because they supply nest sites for birds, shade and food resources for animals. Soil beneath trees is enriched by fallen nests, birds dropping and dung deposition by large herbivores, (Dean *et al.*, 1999), so that plants growing beneath tree canopies are often more nutritious than plants in surrounding habitat (Belsky *et al.*, 1993). Productive, nutritious plants tend to attract more herbivorous animals to patches near trees, reinforcing nutrient enrichment in those areas, but may also cause seedling mortality indirectly due to trampling effects. Our results support the notion that large trees may elevate plant nutrient concentrations beneath their canopies improving productivity of sub-canopy plants, a phenomenon reported in other African savannas (Roos and Alsopp, 1997).

### *Survival*

Although there was a considerable variation of seedling survival across treatment and sites after transplanting of *S. molle* seedlings, survival was always higher for seedlings in tree sub-canopy microsites than those in the open habitats for both soil types. Large *A. tortilis* trees appear to have the greatest influence on *S. molle* survival in semi-arid savannas with frosty winters, and thus facilitate the invasion of this species into savanna. It is therefore unlikely that *S. molle* will invade treeless ecosystems or habitats that are subject to frost and drought. However, management-induced bush thickening or invasion of these savannas by trees (such as *Prosopis* sp.) that establish

in open microsites could promote *S. molle* invasion in grassland (Siemann and Rogers, 2003).

## Conclusion

This study demonstrated that the control of invasion of *S. molle* in semi-arid savannas is complex and may simultaneously depend on multiple biotic and abiotic variables. The results show that height and canopy area decreased in the winter in the open areas but not under tree canopies and that herbivory caused height and canopy area reductions beneath tree canopies but not in the open area where all seedlings died. Soil type did not affect these general patterns. I conclude that physical factors (probably frost) damage seedlings in the open, whereas biotic factors (probably herbivory) damage seedlings beneath canopies. Under the current climate and vegetation, no recruitment of *S. molle* is likely to occur in open areas in semi-arid savannas at altitudes of 1 000 m or more above sea level. The possibility of *S. molle* plants being facilitated by tree canopies in semi-arid savanna has to be taken into consideration when assessing the probability for further invasion. Our study also indicated that large herbivores could control the distribution of this species and that *S. molle* is less likely to spread on sandy substrates.

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# Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa

**Chapter 1:** General problem of biological invasion in South Africa landscape

**Chapter 2:** Dynamics of alien woody plant invasions: review of processes and ecological impacts

## Main objectives

**Chapter 3:** Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 4:** *Megastigmus* wasp damage to seeds of *Schinus molle* (Peruvian pepper tree) across a rainfall gradient in South Africa: Implication for invasion

**Chapter 5:** Seed set of the invasive alien tree *Schinus molle* (Anacardiaceae) in semi-arid savanna, South Africa: the role of pollination and selfing

**Chapter 6:** Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 7:** Performance of seedlings of the invasive alien tree *Schinus molle* under indigenous and alien host trees in semi-arid savanna

**Chapter 8:** Superiority in competition for light: a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Peruvian pepper tree) in South Africa

**Chapter 9:** Distribution of the invasive alien tree *Schinus molle* in western South Africa: current determinants and projections under scenarios of climate change and management.

**Chapter 10:** General conclusions and recommendations

## CHAPTER SEVEN

### PERFORMANCE OF SEEDLINGS OF THE INVASIVE ALIEN TREE *SCHINUS MOLLE* UNDER INDIGENOUS AND ALIEN HOST TREES IN SEMI-ARID SAVANNA

#### **Abstract**

I assessed the importance of host trees in influencing invasion patterns of the alien tree *Schinus molle* (*Anacardiaceae*) in semi-arid savanna in South Africa. Recruitment of *S. molle* is dependent on trees in its invaded habitat, particularly *Acacia tortilis*. Another leguminous tree, the invasive alien mesquite (*Prosopis* sp.), has become common in the area recently, but *S. molle* rarely recruits under canopies of this species. Understanding the association between these species is needed to predict invasion dynamics in the region. I conducted experiments to test whether: i) seedling survival of *S. molle* is better beneath *A. tortilis* than beneath mesquite canopies; (ii) growth rates of *S. molle* seedlings are higher beneath *A. tortilis* than beneath mesquite. Results showed that growth and survival of *S. molle* seedlings did not differ significantly beneath the native *A. tortilis* and the alien *Prosopis* species. This suggests that microsites provided by canopies of mesquite are as good for *S. molle* establishment as those provided by the native *Acacia*. Other factors, such as the failure of propagules to arrive beneath mesquite trees, must be sought to explain the lack of recruitment beneath mesquite.

**Keywords:** Biological invasions, facilitation, invasion dynamics, invasive species, microsites for establishment.

## Introduction

The invasion of woody plants into grasslands or savannas is often initially slow, especially for fleshy-fruited alien plants (Scholes and Archer, 1997; Briggs *et al.*, 2002). In the initial phase, isolated trees represent focal points for bird activity, and therefore for recruitment of bird-dispersed indigenous and alien plants (Flores-Flores and Yeaton, 2000; Dean *et al.*, 2002; Milton *et al.*, 2007). Once founder trees mature and propagule pressure increases, subsequent displacement of grassland vegetation can occur rapidly (Van Auken, 2000; Briggs *et al.*, 2002). Abundant seed input (high propagule pressure) can play a role in accelerating invasions by woody plants, particularly for bird-dispersed species (Berlow *et al.*, 2002). More specifically, species with bird-dispersed seeds can potentially infiltrate natural nucleation processes, thereby disrupting crucial processes in savanna ecosystems (Milton *et al.*, 2007).

*Schinus molle* L. (Anacardiaceae; Peruvian pepper tree), an alien tree from South America, recently started invading natural semi-arid savannas near Kimberley in South Africa's Northern Cape province. In this area, *S. molle* usually occurs in association with, and frequently overtops, the native tree *Acacia tortilis* (Fabaceae: Mimosoidea) (Milton *et al.*, 2007; Iponga *et al.*, 2008 b), but seldom occurs in association with another widespread and common tree in the area, the invasive alien mesquite (*Prosopis* sp. – a hybrid of several *Prosopis* species; also Fabaceae: Mimosoidea). This pattern could be due to: (1) the failure of seeds of *S. molle* to arrive below mesquite canopies; (2) the inability of *S. molle* seeds to germinate below mesquite canopies; or 3) the failure of *S. molle* seedlings to survive beneath mesquite trees because of environmental conditions below the canopy of this species. This study addresses potential reasons for point 3 mentioned above, and compares the performance of *S. molle* seedlings planted under the canopies of the two trees species to determine whether either species is facilitating or limiting recruitment of *S. molle* seedlings.

## Material and Methods

The experiment was conducted between March 2006 and April 2007 on 50-80 year old diamond mining tailings on the De Beers Mine near the town of Kimberley (-

28.76091178; 24.79271270) in the Northern Cape province, South Africa. The climate is semi arid with the mean annual rainfall of  $431 \pm 127$  mm. The mean monthly temperature range is from 35°C to 18°C in January and from 20°C to 3°C in July (South Africa Weather Bureau, 2007). Over the past 50 years the alien tree *Schinus molle* has been grown as a shade tree, and planted at many picnic sites along national and provincial roads in South Africa (see Milton *et al.*, 2007 for more details). Both *Acacia tortilis* and *Prosopis* sp. are deep-rooted, microphyllous leguminous trees belonging to the Mimosoideae that occur in semi-arid savanna. Umbrella Thorn Acacia (*Acacia tortilis*) is a medium to large microphyllous tree native primarily to savannas of Africa. *Prosopis* is a genus of about 45 species of leguminous spiny trees and shrubs native to subtropical and tropical regions of the Americas. Several *Prosopis* species introduced to regions outside their native ranges for agroforestry purposes have become invasive (Richardson *et al.*, 2004). In southern Africa the most invasive forms are hybrids of *P. glandulosa*, *P. juliflora* and *P. velutina* (Zimmerman, 1991).

To test the effect of host tree type on seedling performance, ten trees each of *Acacia tortilis* and *Prosopis* sp. (hereafter acacia and mesquite) with approximately the same canopy size, separated from each other by a distance of approximately 20 m were randomly selected on an old mine tailings of De Beers Mine in Kimberley. Seedlings of *S. molle* were grown in a greenhouse at Stellenbosch University. When seedlings reached a height 80 to 100 mm they were transplanted into the field, three seedlings beneath the canopy of each host tree at different directions (S, N, and E) relative to the tree trunk. A total of 60 seedlings were transplanted in the site, 30 under canopies of each of the two tree species. The performance of each seedling was recorded monthly for 15 months in terms of height, canopy area, stem basal diameter (measured with vernier callipers), and number of branches produced per seedling.

Canopy area was calculated using the following formula for an ellipse (Bronstein and Semendjajew, 1991):  $Cover = (\pi/4) \cdot canopy1 \cdot canopy2$  (1), where *canopy1* and *canopy2* are two perpendicular diameters of the plant as seen from above. One-way analysis of variance (ANOVA; Statistica 6.1, StatSoft, Inc. 2003) was used to test separately the effect of host tree (acacia vs. mesquite) after testing for normality and homogeneity of the data, followed by bootstrapping on the measured seedlings parameters (plant height, canopy area, change in stem basal area and

number of branches) at the end of the experiment. Seedling survival at each recording stage was examined in terms of the proportion of seedlings that survived relative to the total number of planted seedlings planted per host tree. Because I used count data, a generalized non-linear model, with a log-link function to a Poisson distribution was used to test for differences in number of seedlings that survived compare to dead seedlings between host tree type (acacia and mesquite) (Statistica 6.1, StatSoft, Inc. 2003).

## Results

*Schinus molle* seedling performance was not significantly different when planted below canopies of acacia and mesquite trees (Table 7.1). The proportion of *S. molle* seedling survival was the same beneath canopies of the two species: 40% (Table 7.2).

**Table 7.1:** Mean heights ( $\pm$  Std.Err), mean canopy areas ( $\pm$  Std.Err), mean number of branches ( $\pm$  Std.Err) and mean stem basal diameter ( $\pm$  Std.Err) of surviving seedlings of *Schinus molle* after 14 months beneath *Acacia tortilis* and *Prosopis* sp.. *P-values* were obtained through one-way ANOVA.

Variables / treatments	<i>Prosopis</i> sp.	<i>Acacia tortilis</i>	<i>p-values</i>
Height (cm)	39.84 $\pm$ 3.46	45.79 $\pm$ 3.60	0.24
Canopy areas (cm <sup>2</sup> )	215.71 $\pm$ 47.54	299.44 $\pm$ 49.49	0.23
Number of branches	2.07 $\pm$ 0.65	2.91 $\pm$ 0.68	0.38
Stem basal diameter (mm <sup>2</sup> )	0.32 $\pm$ 0.02	0.35 $\pm$ 0.02	0.29

**Table 7.2:** Log link function to a Poisson distribution of the mean ( $\pm$  Std.Err) number of seedlings of *Schinus molle* that survived for 14 months for different host tree types (*Acacia tortilis* and *Prosopis* sp.) (Chi-Square = 0.000; p = NA).

Treatments	Dead	Percent Dead (%)	Alive	Percent Alive (%)	Total N
<i>Prosopis</i> sp.	17	56.66	13	43.33	30
<i>Acacia tortilis</i>	18	60.00	12	40.00	30

## Discussion

In semi-arid savannas of South Africa, microsites provided by large acacia trees increase the growth and survival of alien *S. molle* seedlings (Iponga *et al.*, 2008 b). Similar patterns have been reported from grasslands in other parts of the world. For example, shading has been shown to increase the growth of seedlings of both the alien tree *Sapium sebiferum* and the native tree *Celtis laevigata* in Texas (Siemann and Rogers, 2003). Our study was designed to examine the performance of *S. molle* seedlings planted beneath *Acacia tortilis* and *Prosopis* sp., similar trees in the sub-family Mimosoideae, one native and one alien. Given that Milton *et al.* (2007) showed that fleshy-fruited aliens were confined to sub-canopy sites and that there were more beneath native acacias than beneath alien mesquite trees in the savanna. Our expectation was that *S. molle* seedlings performance and survival would be much reduced beneath mesquite canopies relative to that beneath acacia canopies. Possible causes of differences in the sub-canopy environmental between acacia and mesquite might include shade density, root competition or allelopathic influences. This would explain why association between mature *S. molle* and mesquite trees was much less common than that between acacia and *S. molle*. However, results of the transplanting experiment revealed no such differences in seedling performance and survival beneath the two host trees.

Since microsites provided by the two dominant tree species in the region afford similar opportunities for seedling survival and growth, I need to seek other explanations for the failure of mesquite trees to act like acacia in facilitating *S. molle* invasion. The most obvious explanations are: a lack of propagules arriving below mesquite canopies; or high predation of seeds below mesquite canopies. Dean *et al.*, (2002) suggested that the canopy architecture of invasive mesquite in the Northern Cape discourages utilization of these trees by local birds. Importantly, most branches of mesquite trees are angled too steeply to provide good perches for birds. Bird species richness and diversity in woodlands dominated by native *Acacia* differed substantially from woodlands invaded by alien mesquites, with a general trend of fewer species and fewer individuals in mesquite-invaded woodland (Dean *et al.*, 2002). Research is required to determine the implications for seed dispersal of *S. molle*, and thus its invasion dynamics, in mesquite-invaded ecosystems. Such work is currently reported in this thesis.



The seed predation hypothesis was not tested in this study. However, the seeds of the indigenous *Acacia* spp. are heavily parasitized by indigenous bruchid beetles (Coleoptera) and seeds of *Prosopis* spp. are now parasitized by two endophagous Coleoptera introduced for biological control (Zimmermann, 1991). On the other hand, damage to *Schinus molle* seeds is caused mainly by a southern African wasp species limited to Anacardiaceae (Iponga *et al.*, 2008 a). A study of the dispersal of *S. molle* seed in semi-arid savannas in South Africa showed that birds can move seeds distances of up to 320 metres from female trees, but that most seeds were deposited within 50 m of putative source trees (Iponga *et al.*, 2009). It is unlikely that the wasp would parasitize seeds dispersed by birds beneath mesquite more frequently than seeds dispersed to acacia subcanopy sites, particularly as native species of Anacardiaceae are more abundant beneath acacia than mesquite in this woodland (Milton *et al.*, 2007).

I have rejected the seedling performance hypothesis for explaining lack of *S. molle* association with mesquite. Of the alternative explanations, poor dispersal of seeds to mesquite canopies by birds is probably the most convincing. Although Milton *et al.*, (2007) showed that *S. molle* can germinate below mesquite tree this savanna, the seed germination and seed predation hypotheses have not yet been tested.

In conclusion, I believe that invasion of southern African arid savanna by mesquite will have a negative to neutral effect on the rate of invasion of this ecosystem by *S. molle*. However, where mesquite trees are invading grasslands where few other perches are available to birds, the alien host might provide microsite conditions that would advance the invasion of *S. molle* or other fleshy-fruited alien tree species.

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# Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa

**Chapter 1:** General problem of biological invasion in South Africa landscape

**Chapter 2:** Dynamics of alien woody plant invasions: review of processes and ecological impacts

## Main objectives

**Chapter 3:** Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 4:** *Megastigmus* wasp damage to seeds of *Schinus molle* (Peruvian pepper tree) across a rainfall gradient in South Africa: Implication for invasion

**Chapter 5:** Seed set of the invasive alien tree *Schinus molle* (Anacardiaceae) in semi-arid savanna, South Africa: the role of pollination and selfing

**Chapter 6:** Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 7:** Performance of seedlings of the invasive alien tree *Schinus molle* under indigenous and alien host trees in semi-arid savanna

**Chapter 8:** Superiority in competition for light: a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Peruvian pepper tree) in South Africa

**Chapter 9:** Distribution of the invasive alien tree *Schinus molle* in western South Africa: current determinants and projections under scenarios of climate change and management.

**Chapter 10:** General conclusions and recommendations

## CHAPTER EIGHT

### SUPERIORITY IN COMPETITION FOR LIGHT: A CRUCIAL ATTRIBUTE DEFINING THE IMPACT OF THE INVASIVE ALIEN TREE SCHINUS MOLLE (PERUVIAN PEPPER TREE) IN SOUTH AFRICAN SAVANNA

#### **Abstract**

Invasion of ecosystems by woody alien plant species is a widespread phenomenon. Interspecific competition has often been suggested as a mechanism for replacement of one species by another, but this is rarely tested. I investigated the potential of an invasive alien tree to transform vegetation by quantifying the relative abilities of the alien tree *Schinus molle* and dominant native trees *Acacia tortilis* and *Rhus lancea* to compete for light when growing in association within a South African semi-arid savanna. Due to dispersal of its fruits by birds, seedlings of *S. molle* establish under tree canopies. Using canopy symmetry as an index of ability to compete for light, I found that the alien *S. molle* consistently out-competes the dominant native tree species. The results also show that pod production of *A. tortilis* was higher when it grew alone compared to when it grew with *S. molle* or *R. lancea*. The percentage of dead branches was higher on *A. tortilis* trees growing in association with the *S. molle*. The outcome is that the alien tree will gradually increase in abundance, changing woodland structure and ecosystem processes. Our findings provide evidence for the role of competition in the process of alien plant invasions. I suggest that *S. molle*, previously considered a benign naturalized species in South Africa, should be declared a noxious weed in some parts of that country.

**Keywords:** Biological invasions, coefficient of tree symmetry (TS), shade, symmetry technique, woodland structure

## Introduction

Invasive alien plants (*sensu* Richardson *et al.*, 2000) have caused substantial changes to the structure and functioning of ecosystems in many parts of the world. By replacing native species and altering vegetation structure, plant invasions potentially drive further changes in community pattern, soil nutrient status, species interactions, ecosystems services and disturbance regimes (Hobbs and Mooney, 1986; Richardson and Van Wilgen, 2004; Traveset and Richardson, 2006). The tendency of invasives to become spatially or numerically dominant in their adopted ranges may contribute to homogenization of biotas (McKinney and Lockwood, 1999).

Spatial patterns in plant communities have been attributed to a range of processes, including interactions between individuals of different plant species, localized dispersal abilities, and disturbance regimes. One interaction with the potential to affect species distribution in communities invaded by alien species is competition for resources at local scales (Pauchard and Shea, 2006). The effects of the invaders on disturbance regimes or other ecosystem processes are generally much more dramatic than any effect attributable to competitive interactions among individuals (e.g. Brooks *et al.*, 2004). Nonetheless, competitive interactions are crucial in some cases and need to be better understood to facilitate effective management strategies.

Schwinning (1996) stated that resources can be divided in proportion to the biomass of competing individuals (relative symmetric competitors), or they can be divided so that large competitors get more than their proportional share (asymmetric competition). In reviewing the mechanisms underlying the impacts of alien plant invasion in terrestrial systems, Levine *et al.*, (2003) found that competition for resources was often hypothesized to be important but that its role was seldom verified through experimentation.

Light and water are among the most limiting resources for plant life, as they are essential for the acquisition of carbon and mineral nutrients (Townsend *et al.*, 2000). Whereas competition for direct sunlight is generally asymmetric, competition for soil resources is generally symmetric (Yokozawa and Hara, 1992). Two interacting plants may compete for resources and this may lead to the exclusion of one by the other. However, the interactions between pairs of species are often mediated by other

species, and the indirect effects of such interactions often result in a reduction in the competitive ability of one of the directly interacting species, altering the fitness of both the interacting individuals (Kareiva, 1994; Miller, 1994).

Particular architectural features, such as the growth form of the plant, the size, angles, distributions, and spatial relations of its leaves and branches may give alien plants an advantage in certain habitats (Morris *et al.*, 2002). Consequently, plant architecture and structure may be important for interpreting plant performance and competitive ability when plants are growing close to one another (Morris *et al.*, 2002).

Two species can coexist if they have neutral or positive effects on one another (MacArthur and Levins, 1967). Coexistence often occurs when, for example, each of the interacting species is a superior competitor for different resources in the habitat (Bolker and Pacala, 1999). Nevertheless, one species could out-compete the other if it can grow faster or deplete a limiting resource more rapidly or efficiently (Schwinning, 1996). In this way, differences in competitive ability may explain the dominance in some plant communities.

The genus *Schinus* L. (Anacardiaceae) is native to South America and includes approximately 29 species (Barkley, 1957). Members of the genus have been introduced to many parts of the world outside their natural ranges as ornamentals and for spice production (Morton, 1978). One of the *Schinus* species introduced to South Africa is *S. molle* L., a long-lived and drought tolerant hardy evergreen tree native to the arid zone of Peru. Introduced in the mid 1800's, the species has been planted in villages and on farms since around 1900 and along national and provincial roads in South Africa over the past 50 years. Unlike many other alien trees introduced to South Africa (Richardson *et al.*, 1997), *S. molle* has, until recently, shown little sign of becoming invasive. It is, nonetheless, included in a recent, objectively derived, list of "major invaders" in South Africa (Nel *et al.*, 2004). Bioclimatic analyses suggest that the species has the potential to expand its range in South Africa (Rouget *et al.*, 2004).

Wilson *et al.*, (2007) showed that the extent of invasiveness of woody plants in South Africa is determined by a complex interplay of many factors, including the traits of the species, their residence time, the extent of human-mediated dissemination, and the locality of initial plantings relative to the most favourable sites for the species in the entire region. Consequently, the current limited extent of invasion by *S. molle*

may be an artefact of the observation timescale and initial planting sites. In South Africa, *S. molle* invades savanna and grassland and has also naturalised along drainage lines and roadsides in semi-desert Karoo (Henderson, 2001).

This study investigates the ability of *S. molle* to compete for light with the dominant native trees *Acacia tortilis* (Forssk.) Hayne (Fabaceae: Mimosoidea) and *Rhus lancea* L.f. (Anacardiaceae) in a semi-arid savanna in South Africa. Since the study species are trees with long life cycles, it was impractical to study interactions directly in manipulative experiments (Richardson *et al.*, 2004). However, the widespread coexistence of the study species over large areas provides a useful natural experiment for gaining insights in this regard. *Schinus molle* trees frequently grow in association with indigenous trees where their seeds are dispersed by birds (Milton *et al.*, 2007). If the alien species is able to over-top indigenous tree species and to outcompete them for light, then the alien species would become structurally dominant, possibly altering the functioning of the ecosystem. Our aim was to ascertain whether this occurs in *S. molle*-invaded ecosystems.

Using canopy symmetry as an index of ability to compete for light, I tested the hypothesis that the evergreen native *R. lancea* and alien *S. molle* would both out-compete the microphyllous and semi-deciduous *A. tortilis* for light, but that *S. molle* would not be able to displace the evergreen native *R. lancea*. I expected symmetry to be correlated with other indicators of fitness including canopy health and seed production.

## Material and Methods

### *Study site*

The study was conducted in semi-arid savanna vegetation near the town of Kimberley in the Northern Cape Province of South Africa, (28° 48' S, 24° 46' E, altitude 1198 m above sea level). Kimberley has warm, relatively moist summers, and cold, dry, winters. The annual rainfall (1961-1990) averages 414 mm and mean daily temperature ranges between 18° C and 33° C in January, and 3° C and 19° C in July (South African Weather Bureau, 2007). The vegetation is classified as Kimberley Thornveld, a component of the Eastern Kalahari bushveld bioregion (Mucina *et al.*, 2006), and is characterized by C<sub>4</sub> grasses and scattered trees. The study took place on



approximately 200 ha comprising the Diskobolos Military Base (Aleksanders Fontein) and part of the adjacent farm Rooifontein, 2 km south of Kimberley. Here the landscape is flat, lacking hills or drainage lines, and soils fine textured. Tree cover varies from 5-15% at landscape level. The dominant tree species, *Acacia tortilis*, usually has an understorey of fleshy-fruited shrubs (*Ehretia rigida*, *Lycium* spp., *Solanum* spp.) and tree saplings including the native species *Rhus lancea* and *Ziziphus mucronata*, and more recently the invasive alien tree *Schinus molle*.

### *Study species*

*Schinus molle* is dioecious and female trees produce large crops of small bright pink berries arranged in bunches on pendulous stems. These are eaten and dispersed by birds in California (Nilsen and Muller, 1980) and in South Africa (Milton *et al.*, 2007), and young plants generally establish below perch sites, mainly other trees. Most *S. molle* saplings and trees are thus rooted below the canopies of dominant native trees, as are *R. lancea* trees, the seeds of which are also bird-dispersed. Seeds of mammal- or wind-dispersed *Acacia* species, including *A. tortilis*, generally establish in the open grassland away from tree canopies (Yeaton and Romero-Manzanares, 1986; Milton and Dean, 1995).

Fleshy-fruited tree species appear to outlive and succeed their *Acacia* host trees (Milton and Dean, 1995). The outcome of interactions between the invader and the host tree are thus crucial for determining whether the invader can maintain its position and also for determining the impact of the invader. Growth inhibition on the shaded part of a tree canopy would result in the formation of an increasingly lopsided or asymmetrical canopy. I therefore assumed that trees showing large asymmetry in canopy radius from a vertical median, or any sign of distortion, are less competitive for light.

### *Coefficient of tree symmetry*

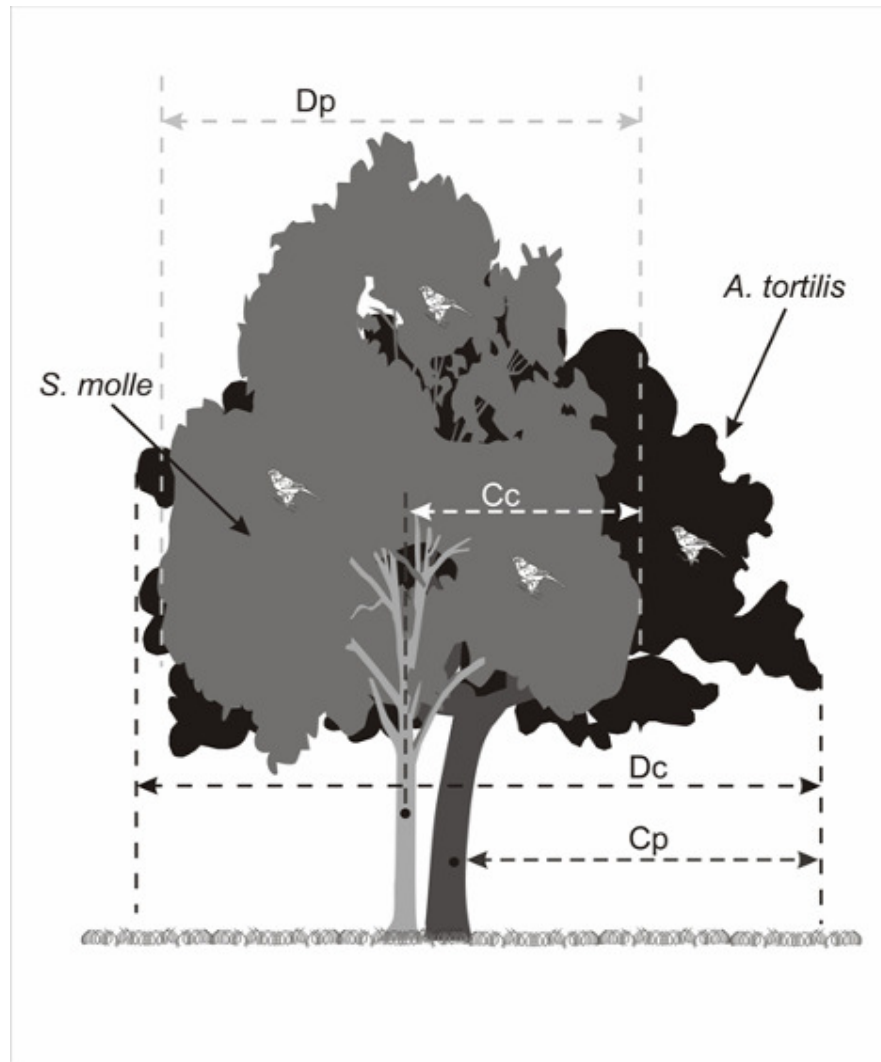
I applied the technique developed by Flores-Flores and Yeaton (2000). This compares the asymmetry or distortion of canopies of trees that are growing in association with one another by means of an index, the coefficient of tree symmetry (TS) that indicates

which individual of a pair of contiguous trees is competing more successfully for light. The technique, developed to predict the outcomes of competition between species pairs (*Acacia-Larrea*, *Prosopis-Acacia*, *Opuntia-Yucca*) in the southern Chihuahua Desert, Mexico (Flores-Flores and Yeaton, 2000), confirmed outcomes previously inferred from tree mortality (Yeaton and Romero-Manzanares, 1986).

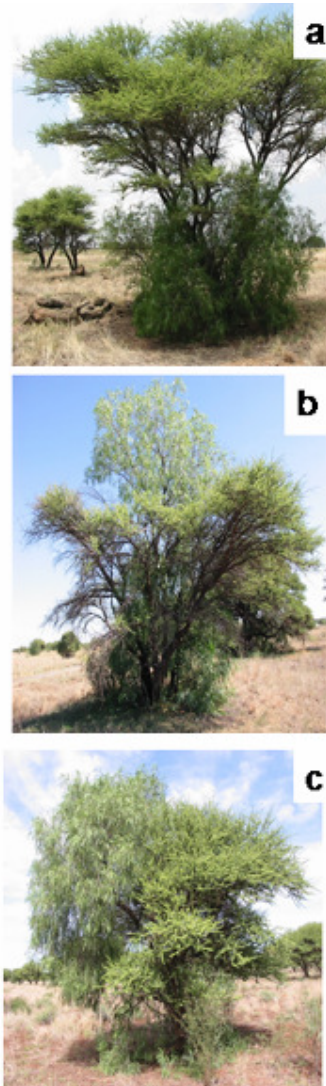
The sampling method requires that canopies of two individual trees of different species be in contact. In the plain determined by the two tree trunks, the longest diameter of the complete canopy of two trees combined according to Figure 8.1 ( $D_c$  or  $D_p$ ) is measured. This is complemented with the measurement of the distance from the centre of each single or multi-stemmed plant ( $C_p$ ) to the edge where there is no contact. The assumption is that there will be a tendency for more growth in this direction (Figure 8.1). TS, the coefficient of tree symmetry is calculated as:

$$TS = D_c/C_p$$

The more even the canopy of the tree, the closer TS will be to 2 (i.e. for a perfectly symmetrical tree,  $TS = 1.0/0.5 = 2$ ). The smaller the TS ratio, the weaker is the ability of a species to out-compete its neighbour for light. If one tree is being affected strongly by its neighbour it will have a  $TS = 1$  (i.e.  $D_c = C_p$ ). In this case, the whole canopy is escaping the effect of competition and the canopy is completely asymmetrical. Over time, such a tree will probably be replaced by the neighbour that is competing more strongly for light. In this way, an index of the likelihood that a species with a tall dense canopy will replace one with a lower more open canopy can be calculated and some inference can be made about whether this will happen in the medium or long term. The weaker competitor for light will possibly die or fall over due to the asymmetrical growth of the canopy (Figure 8.2).



**Figure 8.1:** Schematic representation of light competition assessment between *Schinus molle* (alien) and *Acacia tortilis* (native) in semi-arid savanna in South Africa. The coefficient of tree symmetry (TS), an index developed by Flores-Flores and Yeaton (2000), is calculated by dividing the longest diameter of the complete canopy of a given tree ( $D_p$  for *S. molle*,  $D_c$  for *A. tortilis*), by the distance from its trunk to the canopy edge that is not in contact with its neighbour ( $C_c$  for *S. molle*,  $C_p$  for *A. tortilis*). The coefficient of tree symmetry (TS) is calculated as  $D_c/C_p$ , and the lower this value, the weaker the ability of the tree to compete for light.



**Figure 8.2:** The succession scenario between *Schinus molle* (alien) and *Acacia tortilis* (native) in semi-arid savanna in South Africa. Following seed deposition by birds, *S. molle* will germinate under the canopy of *A. tortilis* (a), *S. molle* will grow in almost perfect symmetry and overtop the host tree (b), then due to the shading effect by *S. molle*, *A. tortilis* will develop canopy distortion as it grows toward light and away from its neighbour (c). The asymmetrical canopy of *A. tortilis* might cause the tree to fall, for example, due to a strong wind.

## *Sampling*

To understand whether *S. molle* will out compete indigenous savanna trees (*A. tortilis* and *R. lancea*), whether *A. tortilis* trees have symmetrical canopies when growing alone and whether *R. lancea* may also out compete *A. tortilis* in semi-arid savannas, 171 pairs of tree species were sampled around Kimberley. Canopies of the individuals in each of the tree pairs selected for study were in physical contact. A total of 123 pairs of *S. molle* and *A. tortilis* were sampled, and 48 pairs of *S. molle* and *R. lancea* were sampled. Fifty-one pairs of *A. tortilis* and *R. lancea* close to one another were sampled, as were 100 *A. tortilis* trees growing alone. TS was calculated for each tree.

## *Plant health and fitness*

To assess whether competition for light with *R. lancea* or *S. molle* increases mortality rates for *A. tortilis*, I recorded the status (% of dying *A. tortilis* with and without *R. lancea* and *S. molle*) of 100 *A. tortilis* growing alone, 51 pairs of *A. tortilis* growing with *R. lancea*, and 68 pairs of *A. tortilis* and *S. molle*. The health and fitness quantification was only done for *A. tortilis* due to its dominance in the woodland. Other reasons were that *A. tortilis* plays the role of a nucleus founding species (Pausas *et al.*, 2006; Milton *et al.*, 2007) facilitating the recruitment of bird dispersed plants in these savannas (Dean *et al.*, 1999).

The percentage of canopy dieback (0%; <25%; 26-50%; 51-75% and > 75%) was used as an indication of tree health. As an additional indication of health, I also examined the abundance of pods on *A. tortilis* by recording, in categories, the percentage of the canopy covered by pods (0%; <25%; 26-50%; 51-75% and > 75%). Basal diameter of *A. tortilis* alone, and growing with *R. lancea* and *S. molle* was measured to determine: (a) at what stage fleshy-fruited trees began to be associated with *A. tortilis*, and (b) whether competition from *R. lancea* or *S. molle* caused *A. tortilis* to die at a smaller size than when this species grew alone.

## *Statistical analysis*

One-way analysis of variance (ANOVA) was used after checking the normality and homogeneity of the data; this was followed by bootstrapping analysis to test the non-normal data. Then, differences in TS between pairs of tree species were tested

separately and differences in means were illustrated graphically using a significance level of  $p < 0.05$ . A Scheffé post-hoc test was also done to determine significant effects between TS of trees in pairs (STATISTICA 6.1, StatSoft, Inc.; Anon.2003).

To understand the impact of the alien *S. molle* on indigenous trees, the analysis compared the coefficient of tree symmetry (TS) of *A. tortilis* and *S. molle* in the pair and the TS *R. lancea* and *S. molle* in the pair. There could be also exclusion between two indigenous species growing together. The difference between *A. tortilis* and *R. lancea* TS values were therefore also tested when the two species were growing together. The analysis also tested the difference between TS of *A. tortilis* growing alone with the TS of *A. tortilis* growing with *S. molle* and *A. tortilis* growing with *R. lancea*. Then another comparison was also made between TS of *A. tortilis* growing alone with those of *A. tortilis* with *S. molle*, *A. tortilis* with *R. lancea*, and *R. lancea* with *S. molle*.

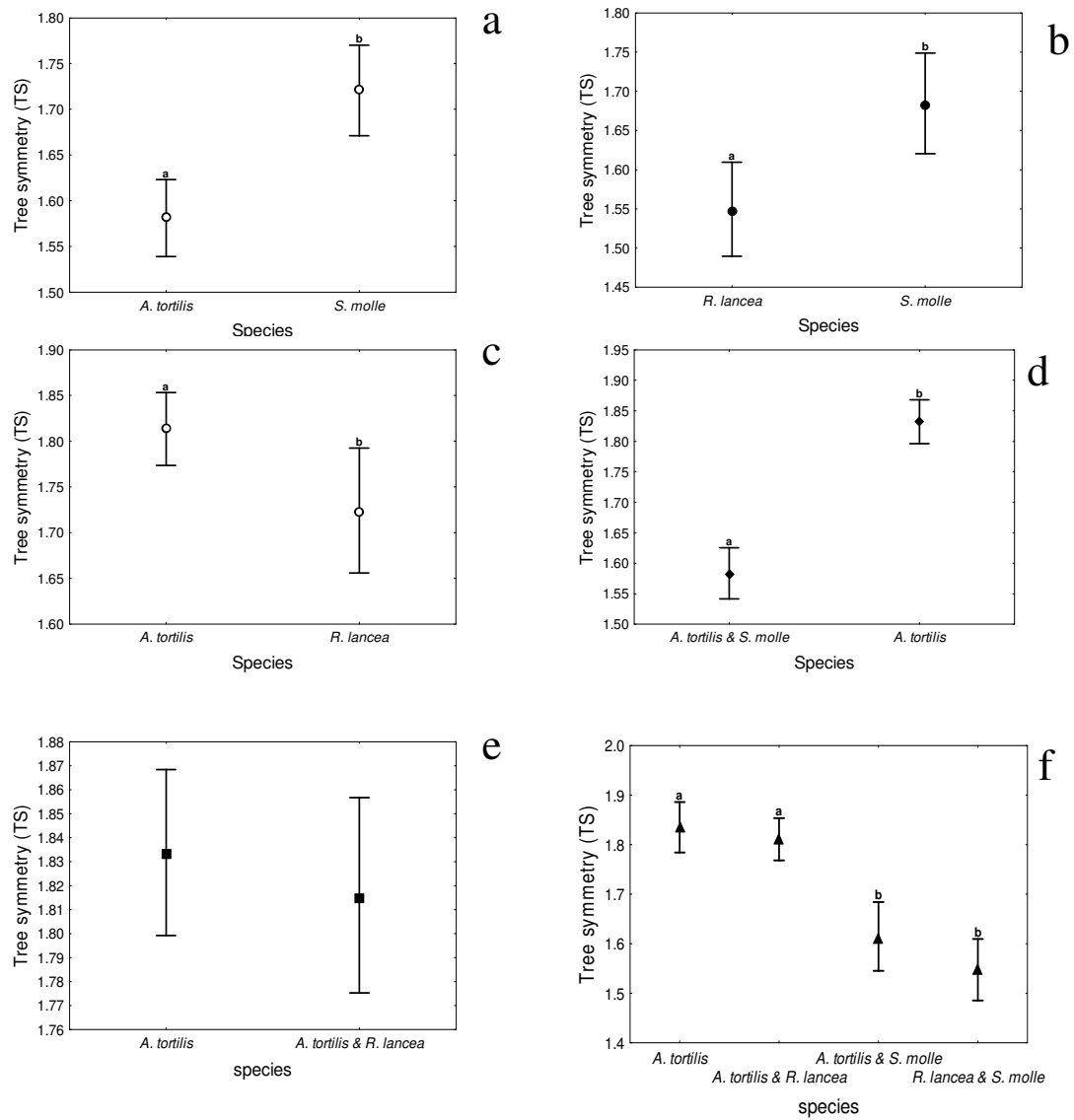
To reject the null hypothesis that all the measures (percentage of dead branches and presence of pods) used to assess *A. tortilis* performance, have the same uniform distribution when this species is growing alone or with *S. molle* or *R. lancea*, I used a Chi-square goodness of fit test to test this hypothesis for each of the five percentage category classes (Gotelli and Ellison, 2004:376). I used linear regression, between *A. tortilis* basal area and the proportion of the population of *A. tortilis* growing with *R. lancea* or with *S. molle*, to determine whether the association with fleshy-fruited trees increased as *A. tortilis* aged. I assumed that stem basal area increased with tree age.

## Results

### *Coefficient of tree symmetry*

The results showed that the mean coefficient of tree symmetry (TS) of *S. molle* was significantly higher than both *A. tortilis* ( $F_{1, 244} = 17.999$ ;  $p < 0.0001$ ; Figure 8.3a) and *R. lancea* ( $F_{1, 94} = 7.284$ ;  $p < 0.005$ ; Figure 8.3b), indicating that *S. molle* is causing asymmetrical canopy growth in both those species. However, the distortion was greater for *R. lancea* than for *A. tortilis* ( $F_{1, 100} = 5.155$ ;  $p < 0.05$ ; Figure 8.3c) when these two species grew together.

*Acacia tortilis* growing alone in the woodland had a significantly higher TS than when this species grew with *S. molle* ( $F_{1, 221} = 74.854$ ;  $P < 0.0001$ ; Figure 8.3d). However, no difference was found between *A. tortilis* growing alone and when it grew with *R. lancea* ( $F_{1, 149}$ ;  $p = 0.533$ ; Figure 8.3e). The results also show that the TS of indigenous trees (*A. tortilis* and *R. lancea*) when growing in association with non-indigenous *S. molle* were significantly lower than the TS of *A. tortilis* growing alone and *A. tortilis* growing with *R. lancea*. On the other hand, *A. tortilis* experiences significantly greater impact when growing with *S. molle* than when growing with *R. lancea* (Scheffe post-hoc test,  $p < 0.0001$ , Figure 8.3f).



**Figure 8.3:** Mean coefficient of tree symmetry (TS) of *Acacia tortilis* (native) vs. *Schinus molle* (alien) (a); *S. molle* vs. *Rhus lancea* (native) (b); *A. tortilis* vs. *R. lancea* (c); *A. tortilis* growing alone vs. *A. tortilis* growing with *S. molle* (d); *A. tortilis* growing alone vs. *A. tortilis* growing in association with *R. lancea* (e) ; and *A. tortilis* growing alone vs. *A. tortilis* growing with *R. lancea*, vs. *A. tortilis* growing with *S. molle*, vs. *R. lancea* growing with *S. molle* (f). Vertical bars indicate standard deviations from the mean and different letters above the bars indicate significant differences.



### *Plant health and reproductive performance*

The presence of pods appeared to be a good indicator of health and performance of *A. tortilis* in semi-arid savannas. Solitary *A. tortilis* trees produced more pods than those growing with *S. molle* (Chi square = 117.13, df = 4,  $P < 0.001$ ) or with *R. lancea* (Chi square 16.679, df = 4,  $p < 0.01$ ), but *S. molle* clearly depressed pod production more severely than did *R. lancea* (Table 8.1).

Association with *S. molle* appears to cause branch mortality of *A. tortilis* since a greater proportion of *A. tortilis* trees growing with *S. molle* were found in high classes of percentages of dead branches (51-75% and >75%) than those growing alone (Chi-Square = 70.636, df = 4,  $p < 0.0001$ ). Proximity to the native *R. lancea* did not significantly increase branch mortality of *A. tortilis* (Table 8.2).

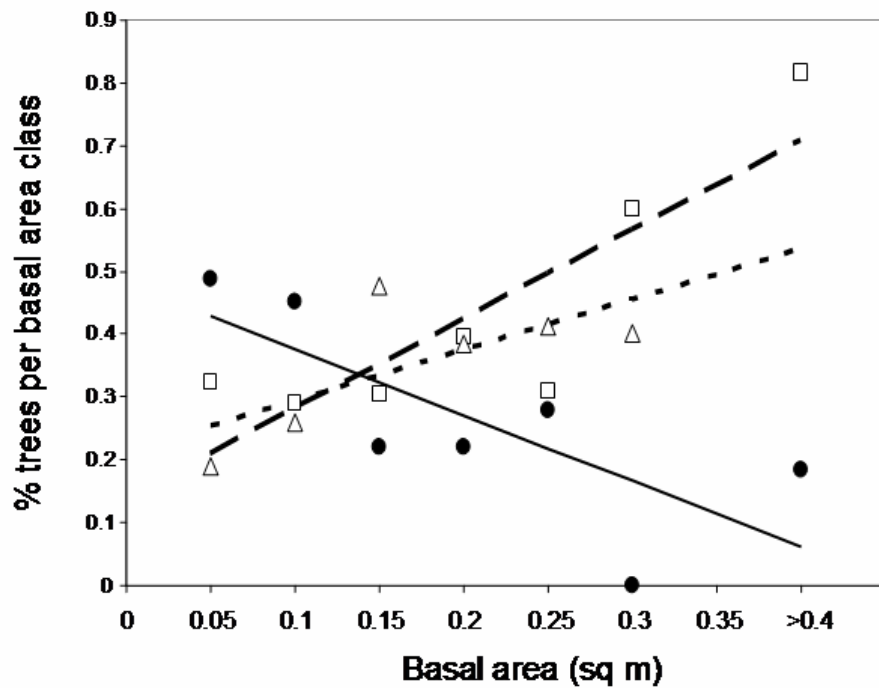
The proportion of *A. tortilis* growing alone decreased significantly with stem basal area class, whereas the proportion of *A. tortilis* growing in association with fleshy fruited trees tended to increase with stem basal area (Figure 8.4). The increase in *A. tortilis* association with *S. molle* with size was significant ( $r^2 = 0.737$ ;  $p < 0.05$ ), whereas association with *R. lancea* was non significant.

**Table 8.1:** Number of *Acacia tortilis* in each pod abundance category (0%->75% cover of canopy by pods) for *A. tortilis* growing alone, or growing with *Schinus molle* and with *Rhus lancea*. Bold type highlights numbers larger than 10.

Canopy cover of pods (%)	<i>A. tortilis</i> alone	<i>A. tortilis</i> with <i>S. molle</i>	<i>A. tortilis</i> with <i>R. lancea</i>
0%	4	6	2
<25	7	<b>18</b>	8
26-50	<b>25</b>	<b>22</b>	7
51-75	<b>31</b>	<b>17</b>	<b>20</b>
>75	<b>33</b>	5	<b>14</b>
Totals (N)	100	68	51

**Table 8.2:** Number of *Acacia tortilis* in each branch mortality category (0 %-> 75% volume of canopy comprising dead branches) on *Acacia tortilis* growing alone, with *Schinus molle* and with *Rhus lancea* for different percentage classes. Bold type highlights numbers larger than 10.

Branch mortality category (%)	<i>A. tortilis alone</i>	<i>A. tortilis with S. molle</i>	<i>A. tortilis with R. lancea</i>
0%	5	1	0
<25	<b>56</b>	<b>17</b>	<b>26</b>
26-50	<b>36</b>	<b>27</b>	<b>21</b>
51-75	2	<b>18</b>	4
>75	1	5	0
Totals (N)	100	68	51



**Figure 8.4:** Fitted lines for the proportions of *Acacia tortilis* trees in various basal areas growing alone (filled circle,  $n = 100$ ,  $r^2 = 0.580$ ,  $P < 0.05$ ; solid line), or growing in association with *Schinus molle* (open square,  $n = 68$ ,  $r^2 = 0.737$ ,  $P < 0.05$ ; dashed line) and or *Rhus lancea* (open triangle,  $n = 51$ ,  $r^2 = 0.497$ , n.s. ;dotted line).

## Discussion

Competition for light is often seen as one of the most important mechanisms whereby invasive alien plants cause changes in invaded communities (Hobbs and Mooney, 1986; Hutchinson and Vankat, 1997; Richardson *et al.*, 2000). This study was designed to examine the impact of non native *S. molle* distribution on two indigenous tree species (*A. tortilis* and *R. lancea*) in semi-arid savanna of South Africa, and also to test whether *S. molle* will be a better competitor for light when growing with *A. tortilis* and *R. lancea*. If *S. molle* is able to out-compete the native host, this could have a marked influence on vegetation structure in the long-term. Vegetation structure and tree architecture influence bird perching, foraging and nesting behaviour, which

in turn influence ecosystem functioning (Dean *et al.*, 2002; Seymour, 2006; Milton *et al.*, 2007).

This change in canopy symmetry of those indigenous species caused by competition with an alien species is probably due to their intolerance of shading by *S. molle*. As a result, canopies of both species, when growing in association with *S. molle*, will develop asymmetrically as shoots extend sideways to capture light. The results also indicate that *S. molle* is a stronger competitor for light since its canopy remains symmetrical as it overtops native neighbours.

Studies have suggested that large plants can pre-empt light from smaller neighbours by overtopping and shading them (Diggle, 1976; Hara, 1984) and as competition for light increases, there are greater advantages to be gained by investing in vertical crown expansion than through horizontal crown expansion to minimize shading by neighbours (Poorter and Werger, 1999; Baruch *et al.*, 2000). The arrangement of branches and leaves of plants can be closely linked with environmental conditions, particularly with regard to light (Poorter and Werger, 1999).

Our results show that *S. molle* can out-compete the dominant native trees in semi-arid savanna. I also show that the pod production of *A. tortilis* was higher when it grew alone than when it grew with *S. molle* or *R. lancea*. The percentage of dead branches was also high on *A. tortilis* trees growing with the alien *S. molle*. The performance of *A. tortilis* growing with *S. molle* could be limited due to the low light interception, which could increase the percentage of dead branches and decrease pod production. The process of replacement of native by alien trees is at an early stage at our study site, as shown by the size-class distribution of the population. It seems certain that invasive *S. molle* trees are poised to cause a marked change in the composition of these plant communities.

A limitation of this study was that I tested only the individual performance of canopy structure of pairs of plants. Other competitive interactions, such as for water and nutrient uptake, may interact with those for light to mediate the outcome of the results. However, for well-established mature trees such factors are probably less important since competition for water and nutrients are most important at the seedling stage (Walters and Reich, 2000; Bakker and Wilson, 2001; Iponga *et al.*, 2005).

Canopies of pairs of trees where *S. molle* was not emerging or overtopping the neighbouring indigenous species were not measured.

A degree of shade tolerance is generally necessary for tree species to establish (Walters and Reich, 2000). Fleshy-fruited seedlings recruit below the canopies of trees because they are dispersed to such sites by birds. As birds disperse the seeds of fleshy-fruited species *Rhus* and *Schinus* their seedlings are commonly associated with trees used as perches (Smith *et al.*, 1994; Dean *et al.*, 1999, 2002; Seymour, 2006; Milton *et al.*, 2007). For this reason it would be expected that *R. lancea* would have similar levels of shade tolerance to *S. molle*. Nevertheless, it is clear that *S. molle* is able to out-compete both indigenous trees for light. The results also suggested that *R. lancea* may have less impact on the dominant *A. tortilis* than *S. molle* in the semi-arid savannas.

It is probable that the *Acacia* tree in each tree pair sampled would have established before the fleshy-fruited neighbour arrived. This assumption is made because large *A. tortilis* were more frequently associated with fleshy-fruited trees and because seeds of fleshy-fruited tree species are usually dropped below perch sites. For this reason *S. molle* seedlings would have established and grown in the shade of *A. tortilis* before emerging from the host tree canopy. I cannot make the assumption for *R. lancea*-*S. molle* pairs, that the alien partner always established beneath the indigenous member of the pair. However, I have observed that *S. molle* can reach reproductive maturity beneath or within the canopies of tall indigenous savanna trees (Milton *et al.*, 2007). *Schinus molle* is mesophyllous and evergreen (Howard and Minnich, 1989), in contrast to *A. tortilis* which is microphyllous and semi-deciduous losing >80% of leaves in dry winters (Milton, 1987) and *R. lancea* which is mesophyllous and evergreen, but sheds all its old leaves in late spring when new leaves are forming (Palmer and Pitman, 1972). Moreover, the leaves of *S. molle* do not appear to suffer insect or fungal damage (S.J.Milton personal observation), whereas leaves of *R. lancea* are damaged by fungi (Crous *et al.*, 2003), that may reduce their ability to compete for light. Greater photosynthetic potential may possibly explain the competitive ability of *S. molle*.

Most light competition experiments have been between tree or shrub seedlings and grasses, or involved the manipulation of light in the laboratory (Siemann and Rogers, 2003). Field experiments on light competition are difficult to perform.

However, the response of the alien plant species reported by this study may correspond with that reported in many other studies that found high above-ground productivity of alien plants compared with indigenous species (e.g. Lawrence and Ratzlaff, 1989).

## Conclusions

I have shown that the performance of two dominant native tree species in semi-arid savannas of South Africa is influenced by alien trees (*S. molle*), that grow in association with them as a result of directed dispersal of its seeds by birds. The ability of *S. molle* to compete strongly for light, and the fact that such competition may lead to changes in vegetation composition, may contribute to the growth of *S. molle* populations and to the transformation of large areas from grassy open savanna with scattered *Acacia*, to less grassy woodland dominated by *S. molle*. This could have cascading effects including the disruption of pollinator and disperser mutualisms, changes in bird communities and reduction of grazing value for cattle and game. Consequently, *S. molle* may pose a threat to the conservation of this vegetation type. A comprehensive strategy for the management of this invasive species is urgently needed.

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# Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa

**Chapter 1:** General problem of biological invasion in South Africa landscape

**Chapter 2:** Dynamics of alien woody plant invasions: review of processes and ecological impacts

## Main objectives

**Chapter 3:** Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 4:** *Megastigmus* wasp damage to seeds of *Schinus molle* (Peruvian pepper tree) across a rainfall gradient in South Africa: Implication for invasion

**Chapter 5:** Seed set of the invasive alien tree *Schinus molle* (Anacardiaceae) in semi-arid savanna, South Africa: the role of pollination and selfing

**Chapter 6:** Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 7:** Performance of seedlings of the invasive alien trees *Schinus molle* under indigenous and alien host tree in semi-arid savanna

**Chapter 8:** Superiority in competition for light: a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Peruvian pepper tree) in South Africa

**Chapter 9:** Distribution of the invasive alien tree *Schinus molle* in western South Africa: current determinants and projections under scenarios of climate change and management

**Chapter 10:** General conclusions and recommendations

## CHAPTER NINE

### DISTRIBUTION OF THE INVASIVE ALIEN TREE SCHINUS MOLLE IN WESTERN SOUTH AFRICA: CURRENT DETERMINANTS AND PROJECTIONS UNDER SCENARIOS OF CLIMATE CHANGE AND MANAGEMENT

#### **Abstract**

Determining the potential range of invasive alien species under current conditions and likely patterns of change under scenarios of climate change and different management interventions is needed for planning effective long term intervention strategies.

I examined the distribution of the invasive alien tree *Schinus molle* (Peruvian pepper tree; Anacardiaceae) in South Africa, where it was planted over large areas. Localities of planted and naturalized trees were mapped along 5380 km of roads. A correlative modelling approach was used to produce profiles of present and future environmental conditions characterizing its planted and naturalized ranges. A cellular automata simulation model was used to estimate the dynamics of *S. molle* under future climates and different management scenarios.

Correlative models were successful in assessing both planted and naturalized known distributions of *S. molle*. The model for planted individuals yielded a larger potential range than the model for naturalized plants. Both models identify arid biomes as the most suitable. The potential range of *S. molle* is predicted to shrink progressively with future climate changes. The spread model identified the areas most susceptible to invasion in the future, and indicates that doubling the number of planted trees along roads would considerably increase the spread rate. Fine-scale differences in the spread rate of *S. molle* were observed along a rainfall gradient.

*Synthesis and applications.* Bioclimatic modelling combined with the spread model indicates that management efforts should be focussed in the Nama-karoo,

succulent karoo, and Albany Thicket biomes. Although some of the potential range of *S. molle* (defined based on current conditions) is predicted to become less favourable, the species might persist where it is well established long after conditions for recruitment have deteriorated. Some areas where the species is not widely naturalized (notably the fynbos biome) are predicted to become more favourable. *Schinus molle* should be declared a noxious weed in parts of the country.

**Key-words:** biological invasions; cellular automata simulation model; bioclimatic models; climate-change scenarios; generalized boosted model (BRT); management scenarios.

## Introduction

Successful invasion of an introduced species depends on many factors, including the climate and physical environment, features of the recipient ecosystem, life-history traits of the invader, and the availability and abundance of propagules (Richardson and Pyšek, 2006). Many management initiatives are underway around the world to tackle problems associated with invasive alien species. These range from local-scale efforts to eradicate particular species to systematic management programs at the scale of landscapes or regions. Limited resources and the rapid escalation in the extent of invasions make it essential to prioritize species and areas for management (Nel *et al.*, 2004).

For individual invasive species, a major challenge is to determine the potential range of suitable environmental conditions. This influences the importance attached to the species and its priority for management attention at different temporal and spatial scales (Rouget *et al.*, 2004). A problem is that many invasive species have had short residence times and have yet to sample all potentially invadable habitats. Several studies have tried to determine the potential distributions using species-distribution models (also called bioclimatic modelling); this involves correlating the presence/absence of a species with environmental conditions to determine its potential range (Guisan and Zimmermann, 2000). Recent studies have emphasized the crucial role of human factors in shaping the geographic ranges of invasive plant species (Thuiller *et al.*, 2006). The sites of introduction, in relation to the overall suitable range, and propagule pressure are key determinants of invaded range (Wilson *et al.*,

2007). The importance of these factors is generally difficult to determine since records of failed introductions are generally poor. Alien trees planted for ornamentation offer good opportunities for gaining insights regarding the role of human activities in shaping distribution range. The modelling tools mentioned above, together with spatially-explicit data of likely climate change, enable us to incorporate multiple factors to forecast changes in distribution as input to objective management plans for invasive species.

In this paper I examine the distribution of planted versus naturalized individuals of the alien tree *Schinus molle* over large parts of South Africa. My aims are: to produce accurate profiles of environmental conditions (biophysical and those related to human activities) that characterize the two types of range of this species: planted, and naturalized (self-established individuals); to predict changes in distribution due to climate change and management. The modelling approach comprises three main steps: (1) determining correlates of distribution for planted and naturalized individuals of *S. molle* using boosting regression trees; (2) estimating changes in distribution of naturalized plants under scenarios of climate change based only on climate-related variables; and (3) assessing effects of management strategies using a simple cellular-automata simulation model.

## **Materials and methods**

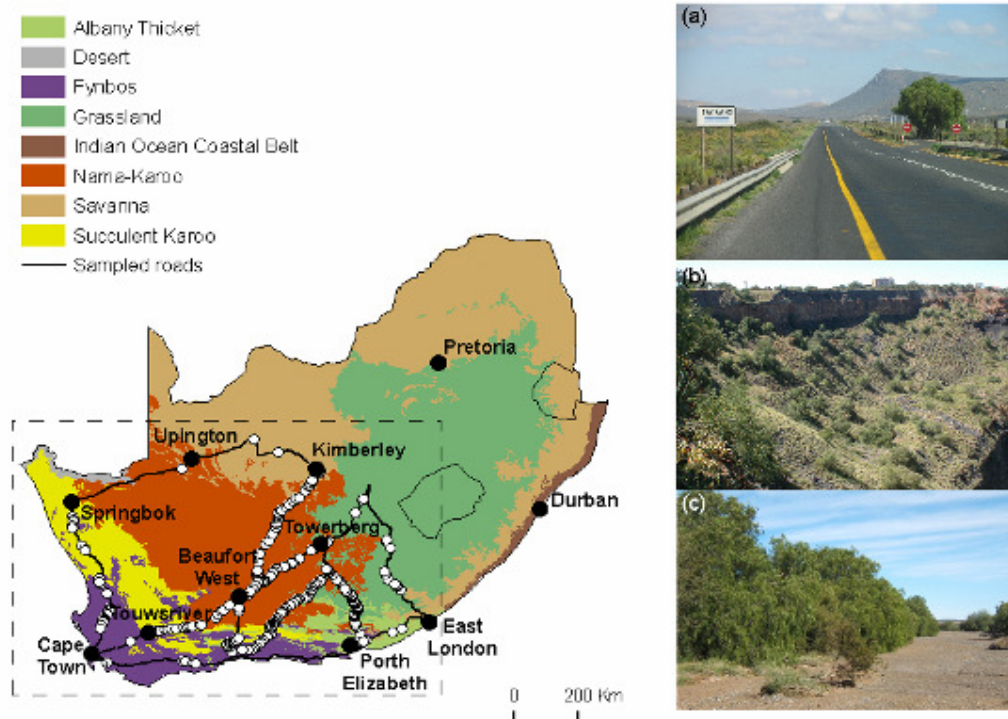
### *Potential distribution of Schinus molle: planted vs. naturalized individuals*

#### *Species occurrence and data collection*

*Schinus molle* L. (Peruvian pepper tree; Anacardiaceae), a long-lived and drought-tolerant evergreen tree, was introduced to South Africa in around 1850 from arid central South America. Especially since 1950 the species has been widely planted as a shade tree along major roads. Unlike many other alien trees introduced to South Africa (Richardson, 1998), *S. molle* has, until recently, shown little sign of becoming invasive. In the last two decades it has become highly invasive in semi-arid savannas (Iponga *et al.*, 2008c) and it is now listed as a major invader (Nel. *et al.*, 2004). Preliminary bioclimatic modelling suggested that this species could spread over a much larger part of South Africa (Rouget *et al.*, 2004). The species is dioecious, and

fruits are produced throughout the year and are dispersed by birds, mammals, and water (Milton *et al.*, 2007 and references therein).

The range of the species was recorded during a survey along 5380 km of roads in regions where *S. molle* is known to occur in high density: mainly the Eastern Cape, Free State, Northern Cape and the Western Cape provinces. *Schinus molle* is known to occur in other provinces (Henderson, 2001), but at very low density. Because of the incomplete sampling in eastern and north-eastern regions, I restricted the predictions to western South Africa (Figure 9.1). I recorded all planted and self-established (naturalized *sensu* Pyšek *et al.*, 2004) individuals along the roads. I also surveyed areas of radius 100m around each planted and naturalized individual to search for self-sown plants. Sometimes more than one individual was recorded at each location. Planted and naturalized individuals were recorded at 384 localities (2212 individuals) and 317 localities (1575 individuals) respectively.



**Figure 9.1** South Africa, showing roads (black lines) that were surveyed for the presence of planted and naturalized individuals of *Schinus molle*. White dots indicate where the species was recorded [the density of planted and naturalized individuals is shown in panels P1 and N1 in Figure 9.2]. Shading shows major terrestrial biomes (Mucina *et al.*, 2006). The dashed line encloses the study domain. Photographs show: trees planted along a road (a); self-sown individuals growing in Kimberley's Big Hole (b); and naturalized individuals along a river (c). Photo credits: D.M. Richardson (a), D.M. Iponga (b) and S.J. Milton (c).

### *Environmental variables*

I used climatic, topographic and land use variables that are known to influence the distribution of plant species in South Africa (Thuiller *et al.*, 2006; Wilson *et al.*, 2007). The climatic parameters used were: minimum temperature of the coldest month (*mtc*), growing degree days (*gdd10*; annual temperature sum above 10°), mean annual precipitation (*map*), and annual potential evapotranspiration (*pet*). These variables were derived from Schultze (1997) at a resolution of 1' x 1' (~1.6 km x 1.6 km at this latitude). Distance to major rivers (scale 1:500.000) (*driv*), "human



footprint” (*hfoot*) (Sanderson *et al.*, 2002), and biomes (*biome*) (Mucina & Rutherford 2006) were also used in most analyses (Table 9.1). The human footprint represents the degree of human-mediated modification of environments, through agricultural practices, urbanization and other factors, and it is thought to influence the distribution of *S. molle* in South Africa.

Others variables were also used to determine the importance of history in naturalization of *S. molle*: distance to the nearest planted individual (*dsp*), and a proxy for propagule pressure (*propres*), computed by dividing pixels at 1’x1’ into 100 smaller pixels and counting the number of pixels occupied by planted individuals. The variables were resized at 1’ x 1’ grid resolution to match the climatic data set in ArcGIS 9.3 (ESRI).

### *Correlative modelling approach*

I used the boosted regression trees (BRT; Ridgeway, 1999; Friedman, 2001; Friedman and Meulman, 2003) to estimate the potential range of *S. molle*. To elucidate ecological differences between planted and naturalized individuals of *S. molle* across its South African range (step 1), I first distinguished between occurrences corresponding to planted individuals (Planted) and naturalized individuals (Naturalized). Since absence data were not available, I generated random pseudo-absences at localities along the surveyed roads without confirmed presence of the species. Each occurrence dataset was then divided into training (70%) and testing (30%) sets to calibrate and evaluate model performance, respectively.

To reduce uncertainty due to the re-sampling procedure, I calibrated 10 replicate BRT models for each occurrence dataset by randomly creating 10 different sets of both training and testing occurrences. Each set of 10 replicate predictions were averaged at equal proportions to produce a unique ensemble estimate of the area suitable for *S. molle*. Additionally, BRT also estimated the relative importance of each environmental variable included into each replicate model by accounting for the rest of the variables (e.g. Thuiller *et al.*, 2006). As in the final ensemble predictions, I also computed the averaged influence of each environmental variable to understand their importance in explaining the potential distribution of planted and naturalized populations of *S. molle*.

Since naturalization of *S. molle* is also influenced by other non-environmental factors, I calibrated two extra models to explore the importance of the history of the invasion in explaining the current distribution of the species. The first model was calibrated incorporating all the previously mentioned environmental data as well as the distance to planted species and propagule pressure (NatDsp). The second model used only propagule pressure (NatPropres) (Table 9.1). Occurrence data set aside from model development (30%) was used to calculate the area under the curve (AUC) of the Receiver Operator Characteristic (ROC), which evaluates model performance independently of the arbitrary threshold of the prediction (Thuiller *et al.*, 2006). Following the scale of Swets (1988), prediction was considered random when it did not differ from 0.5, poor when it was in the range 0.5-0.7, and useful when in the range 0.7-0.9. Predictive accuracy greater than 0.9 was considered good to excellent (1= perfect). AUC values under 0.5 reflect counter predictions (omission and commission rates higher than correct prediction).

### *Potential distribution of naturalized individuals of Schinus molle under climate change*

To estimate changes in the potential distribution of *S. molle* with climate change (step 2), I determined a climatic envelop based only naturalized occurrence data and a reduced set of climatic data available for both present and future conditions (NatCc) (Table 9.1). As described previously, I developed 10 replicate models and projected them onto present-day conditions (to test the performance of the models) and two scenarios (A2 and B2) of future climates for 2050 and 2100 derived from the Hadley Centre for Climate Prediction and Research (see details in Thuiller *et al.*, 2005).

### *Spread of Schinus molle under different management strategies*

These previous climate-change predictions for both present and future climates were then incorporated into a simulation model to predict the range expansion of naturalized individuals of *S. molle* under different management scenarios. I used a cellular automata model following these simple rules:

- The cell size was 1' x 1'
- One time-step represents 10 years (time needed for one individual to reach maturity, Iponga *et al.*, 2008b), and I assumed that all plants were mature at the beginning of a time-step;
- Each individual produced in one time-step a maximum of 50 surviving offspring, based on seed production and seedling survival of this species (Iponga *et al.*, 2008a, b). This reproduction was dependent on the suitability of the cell, with no reproduction taking place 0.42 (based on the model built with naturalized distribution including only climate variables, NatCc), and production of 50 offspring with a suitability of 1.0, with linearly interpolation for intermediate value; These suitability thresholds were determined by analyzing the suitability values for the localities with naturalized individuals: 95% of them were found in areas with suitability levels between 0.42 and 1.
- I assumed that 10% of the offspring establish in neighbouring cells, independent of their occupancy status, and distributed these equally into all eight neighbouring cells. All dispersers arriving in a cell were then summed and rounded upwards.
- Each cell could hold a maximum of 341,874 individual plants, equal to one plant per 10 m<sup>2</sup>, based on our observations of maximum densities. Surplus individuals were discarded.

The different management scenarios tested were: a business-as-usual (NM) (i.e. scenario with no further plantings and no control operations); doubling the number of planted individuals along surveyed roads (P) (i.e. further planting for shade and amenity use); removing only planted individuals along the surveyed roads (C) (i.e. a pro-active management strategy aimed at removing sources of propagules); and removing all planted and all naturalized individuals in a cell (1' x 1') (CC). To determine the number of cells and the number of trees planted per cell under scenario P, I selected at random empty cells along the sampled roads and “planted” a randomly drawn number of trees following a Poisson distribution with  $\lambda = 6$  (as determined by plotting the frequency distribution of planted individuals found in the field) until the number of planted individuals was doubled.

To have a general pattern of occupancy of *S. molle* in different management scenarios, I calculated the change in occupied cells between NM (no management) and other management scenarios under both climate-change scenarios for 2050 and 2100 by subtracting the occupancy layers of NM scenarios from the occupancy layers of the other three management scenarios and summed up all cells. A positive value indicates more cells occupied than in the NM scenario, a negative number indicates fewer. The management scenarios were also tested under three climate-change scenarios (A2, B2, and no change). As suitability maps for the climate-change scenario were only available for 2000, 2050 and 2100, the suitability maps for the intermediate years (in ten year steps) were linearly interpolated. I selected three regions, centred on the towns of Towerberg (Nama-karoo biome), Touwsriver (succulent karoo biome) and Kimberley (savanna biome), to illustrate differences at fine spatial scales, after running the spread models. These regions were selected because they fell along a rainfall gradient (winter rainfall; all-year rainfall; summer rainfall) and because all had high numbers of *S. molle* individuals at present.

## Results

### *Potential distribution of Schinus molle: planted vs. naturalized individuals*

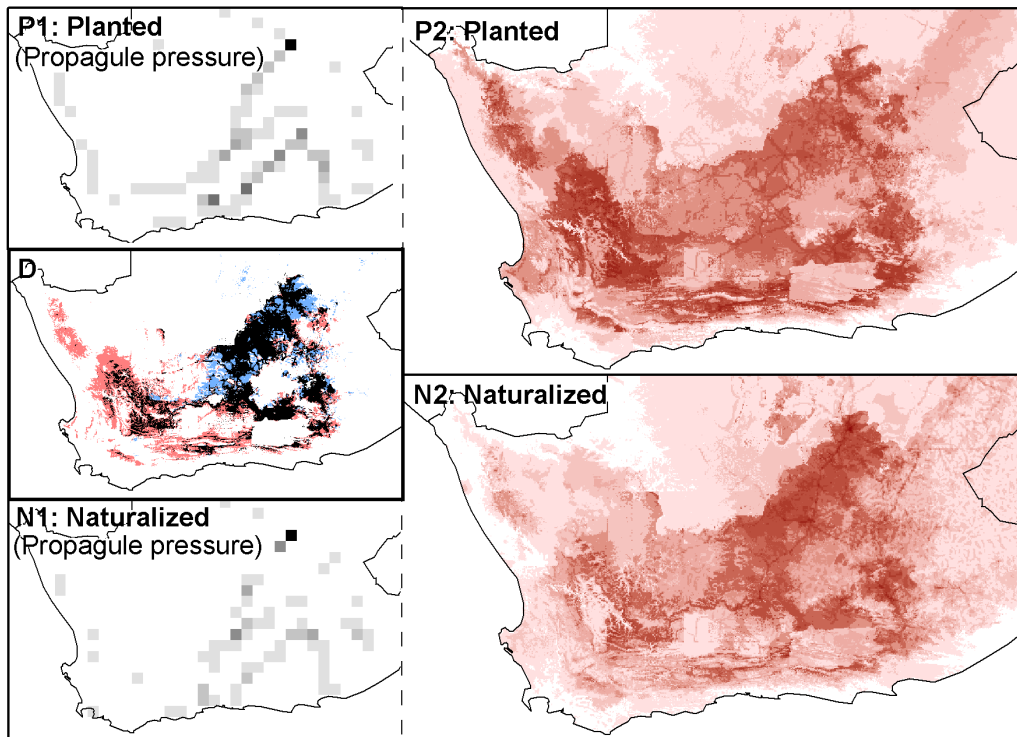
Models were successful in generating both planted and naturalized present-day known distributions of *S. molle* in the western part of South Africa, with AUC values of 0.91 (Planted) and 0.94 (Naturalized) (Table 9.1). These models were calibrated incorporating climatic and topographical variables. For Planted, the most influential variables for predicting *S. molle* environmental suitability were: minimum annual precipitation (*map*), mean annual evapotranspiration (*pet*) and mean temperature of the coldest month (*mtc*). For Naturalized the most important variables were: mean temperature of the coldest month (*mtc*), mean annual precipitation (*map*), annual potential evapotranspiration (*pet*), and distance to rivers (*driv*) (Table 9.1). When propagule pressure (*propres*) and distance from naturalized individuals to planted trees (*dsp*) were added to the model estimating the distribution of naturalized individuals (NatDsp and NatPropres), *dsp* emerged as the most important and sole

variable explaining the present-day distribution of *S. molle*. *Propres* also emerged as important when *dsp* was omitted (Table 9.1).

Unsurprisingly, the model Planted yielded a larger potential range of suitable conditions than Naturalized (Figure 9.2; P2 and N2, respectively). The models revealed that the largest area of suitable habitat for the establishment of *S. molle* without human assistance occurs in the Nama- and succulent-karoo biomes, followed by savanna, grassland, and Albany thicket biomes (Figure 9.4). Despite reasonable propagule pressure (Table 9.3 and Figure 9.2; P1) little area in the fynbos biome was found to be suitable for establishment of this species under current conditions (Figure 9.4).

**Table 9.1** The relative influence of variables in different models used to predict bioclimatic suitability for *Schinus molle* under current conditions and under climate-change scenarios. Environmental variables: *mtc* = minimum temperature of the coldest month; *gdd10* = growing degree days (annual temperature sum above 10°C); *map* = mean annual precipitation; *pet* = annual potential evapotranspiration; *driv* = distance to major rivers; biome; *hfoot* = human footprint (representing the total ecological footprint of human populations, see text); *propres* = proxy for propagule pressure (computed using ArcGIS 9.3 (ESRI), by dividing pixels at 1'x1' (1.6 km x 1.6 km) into 100 smaller pixels and counting the number of pixels occupied by planted species (sources of propagules); *dsp* = distance to the nearest planted individual. Bioclimatic models: Planted = model based on the distribution of mapped planted individuals; Naturalized = model based on the distribution of naturalized plants; NatDsp = model built with naturalized distribution including distance to the nearest planted individual; NatPropres = model built with naturalized distribution including a proxy for propagule pressure; NatCc = model built with naturalized distribution including only climate variables; AUC = area under the curve of a receiver-operating (predictive power of each model).

Model	Variables relative influence (%)									AUC
	<i>mtc</i>	<i>gdd10</i>	<i>map</i>	<i>pet</i>	<i>driv</i>	<i>biome</i>	<i>hfoot</i>	<i>propres</i>	<i>dsp</i>	
Planted	14.7	4.8	35.6	33.1	1.2	6.7	3.8	--	--	0.91
Naturalized	28.1	6.7	18.3	17.7	15.6	5.2	8.4	--	--	0.94
NatDsp	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.0	99.7	1.00
NatPropres	1.5	0.9	6.6	9.3	20.4	8.3	5.6	47.5	--	0.98
NatCc	31.2	12.3	31.4	25.1	--	--	--	--	--	0.93



**Figure 9.2** Predicted environmental suitability for *Schinus molle* modelled using locations of planted (P2) and naturalized (N2) individuals (for extent of sampling area, see Figure 9.1). Environmental suitability maps were generated using generalized boosted models using climatic, topographic and land-use variables as inputs (see text). Red and darker shades indicate higher suitability and propagule pressure respectively. Maps P1 (planted) and N1 (naturalized) show the number of planted/naturalized individuals in each cell (i.e. propagule pressure). D shows areas suitable only for planted (red), only for naturalized individuals (blue), and areas suitable for both (black).

**Table 9.2** Predicted change in the number of cells occupied by *Schinus molle* under different climate-change and management scenarios for year 2050 (A) and 2100 (B). Changes were computed as the difference in the number of cells under no management (NM) and other management scenarios (P, C, CC) by subtracting the occupancy layers (value 1 = occupied; 0 = not occupied) of NM scenario from the occupancy layers of the other three management scenarios and summing up all resulting values. Positive values indicate increased occupation with management; negative numbers indicate reduced occupation. Percentages are given in brackets. Climate-change scenarios: N (no climate-change); A2 (temperature rise by 2.8°C in 2080); and B2 (temperature rise by 2.1°C in 2080). Management scenarios: P (doubling the number of planted individuals along surveyed roads); C (removing only planted individuals along the surveyed roads); and CC (removing all planted and all naturalized individuals in a call from the planted one).

A) Year: 2050

Climate-change scenario	Management scenarios			
	NM	P	C	CC
N	6414	+ 934 (14.56%)	- 35 (0.54%)	- 71 (1.10%)
A2	4256	+ 806 (18.93%)	- 28 (0.65%)	- 58 (1.36%)
B2	5326	+1042 (19.56%)	- 35 (0.65%)	- 72 (1.35%)

B) Year: 2100

Climate-change scenarios	Management scenarios			
	NM	P	C	CC
N	14365	+1265 (8.80)	- 22 (0.15%)	- 37 (0.25%)
A2	6860	+1288 (18.77%)	- 33 (0.48%)	- 90 (1.31%)
B2	9471	+ 1603 (16.92)	- 39 (0.41%)	- 85 (0.89%)



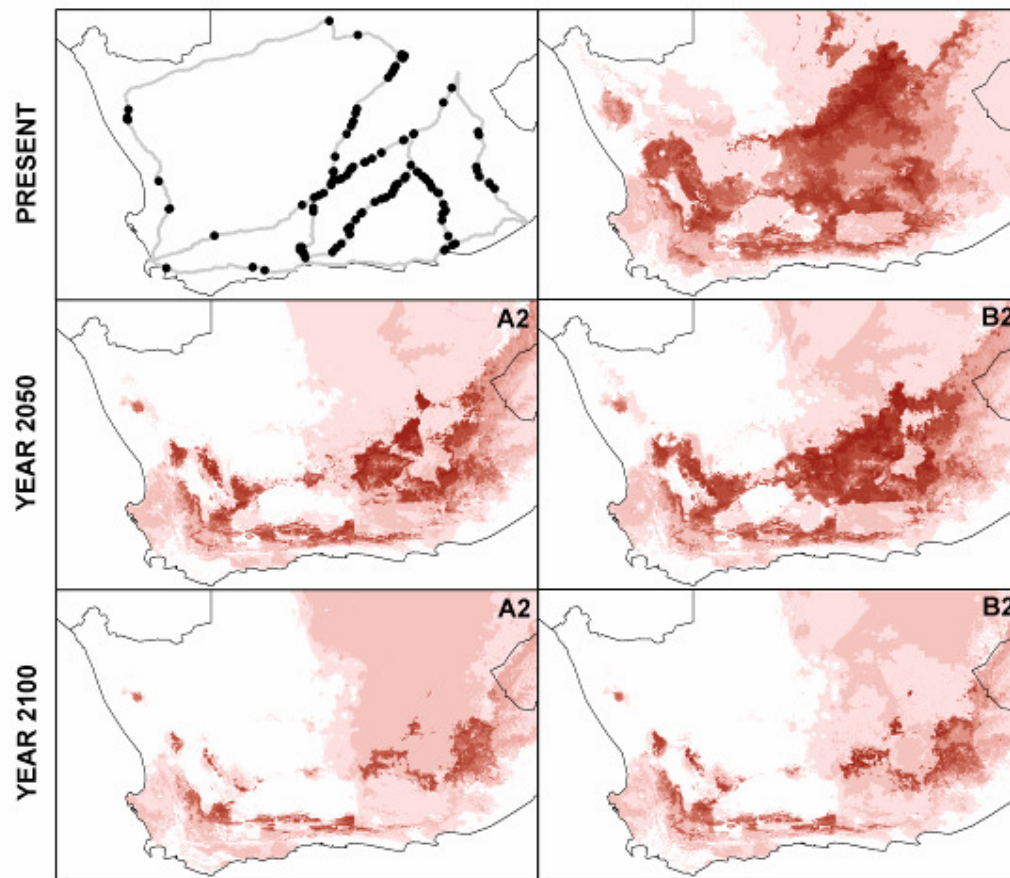
**Table 9.3** Number of cells (1.6km x 1.6km) in each biome sampled during the field survey (Sampled), containing planted individuals (Plant) and containing naturalised individuals (Nat). Percent indicate the percentage of cells in relation to each biome's size (Size, presented as number of cells). The invasion ratio is calculated as the number of cells with naturalized plants (Nat) divided by the number of cells with planted individuals of *Schinus molle* (Plant).

Biomes	Size	No. of cells			Percent			Invasion ratio
		Sampled	Plant	Nat	Sampled	Plant	Nat	
All	421877	3083	244	132	0.73%	0.06%	0.03%	0.54
Savanna	136014	330	20	15	0.24%	0.01%	0.01%	0.75
Grassland	119810	393	13	14	0.33%	0.01%	0.01%	1.08
Nama-karoo	88185	979	114	62	1.11%	0.13%	0.07%	0.54
Coastal Belt	5249	0	0	0	0.00%	0.00%	0.00%	NA
Desert	2404	12	0	0	0.50%	0.00%	0.00%	NA
Succulent karoo	29657	293	30	18	0.99%	0.10%	0.06%	0.60
Fynbos	29588	841	39	9	2.84%	0.13%	0.03%	0.23
Albany Thicket	10970	235	28	14	2.14%	0.26%	0.13%	0.50

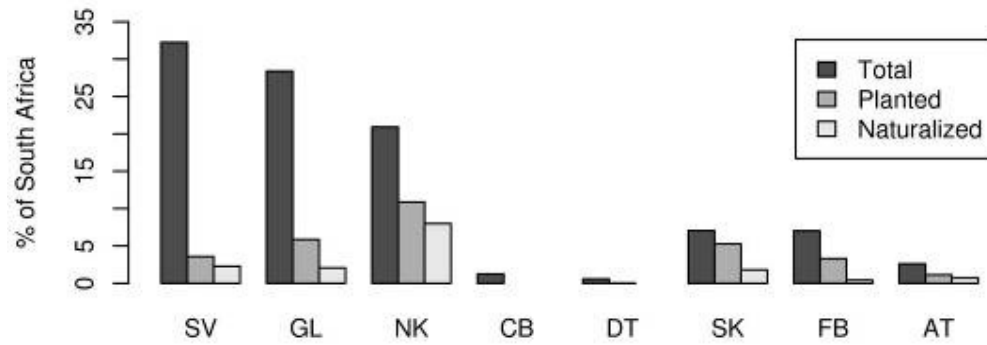
### *Potential distribution of naturalized individuals of Schinus molle under climate change*

Since our aim was to assess the potential of the species to occupy natural areas in the future under climate-change scenarios A2 and B2, I based our predictions only on naturalized occurrence data and climatic data (layers of potential changes in human-activity factors were not included; see Methods). The model calibrated using present-day occurrence and climatic data performed excellently (AUC=0.93) (Table 9.1), and showed little difference in terms of suitable areas to the model using a broad set of environmental layers (Figure 9.3).

The potential range of *S. molle* was generally predicted to shrink progressively under both scenarios of climate change. The area predicted as suitable for the species now (32.4%) is expected to undergo a considerable reduction: 16.7 % suitable area under scenario A2 and 23.5 % suitable area under scenario B2 in 2050; and 6.4% and 8.4% under scenarios A2 and B2 respectively in 2100 (Figure 9.3). This decrease in the area suitable for *S. molle* is expected to affect all biomes, but to be less pronounced in the grassland and fynbos biomes (Figure 9.5, blue lines).



**Figure 9.3** Predicted environmental suitability (for naturalization) of *Schinus molle* in South Africa under two scenarios of climate change (A2 and B2) for the years 2050 and 2100. Predictions were generated using only climatic variables as inputs (see Methods). Darker red shades indicate higher suitability values. The panel at top left shows the current distribution of *S. molle* used to calibrate the model (black dots), and the surveyed roads without confirmed presence of the species (grey line). The panel at top right shows modelled habitat suitability using current climatic conditions.



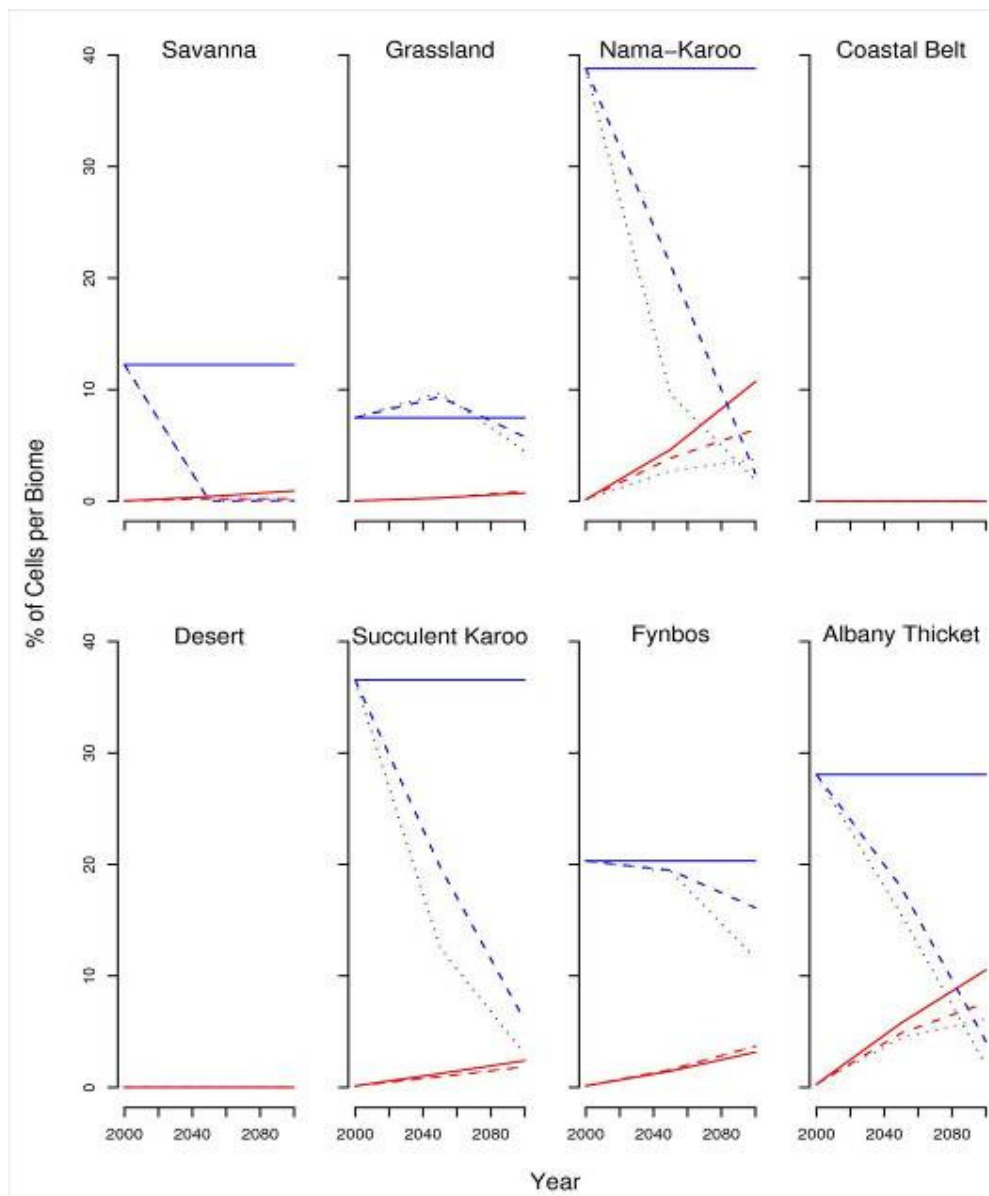
**Figure 9.4** The proportion of the total area of South Africa occupied by each biome, and the area predicted to be suitable for planted and naturalized individuals of *Schinus molle*. Biomes: SV = savanna; GL = grassland; NK = Nama-karoo; CB = Indian Ocean Coastal Belt; DT = desert; SK = succulent karoo; FB = fynbos; AT = Albany Thicket [The distribution of biomes is shown in Fig. 1]. Cell classified as “suitable” if the suitability value is larger than a threshold suitability value (the value above which 95% of individuals occur). Thresholds for planted and naturalized trees are 0.2911517 and 0.4058979, respectively.

### *Spread of Schinus molle under different management strategies*

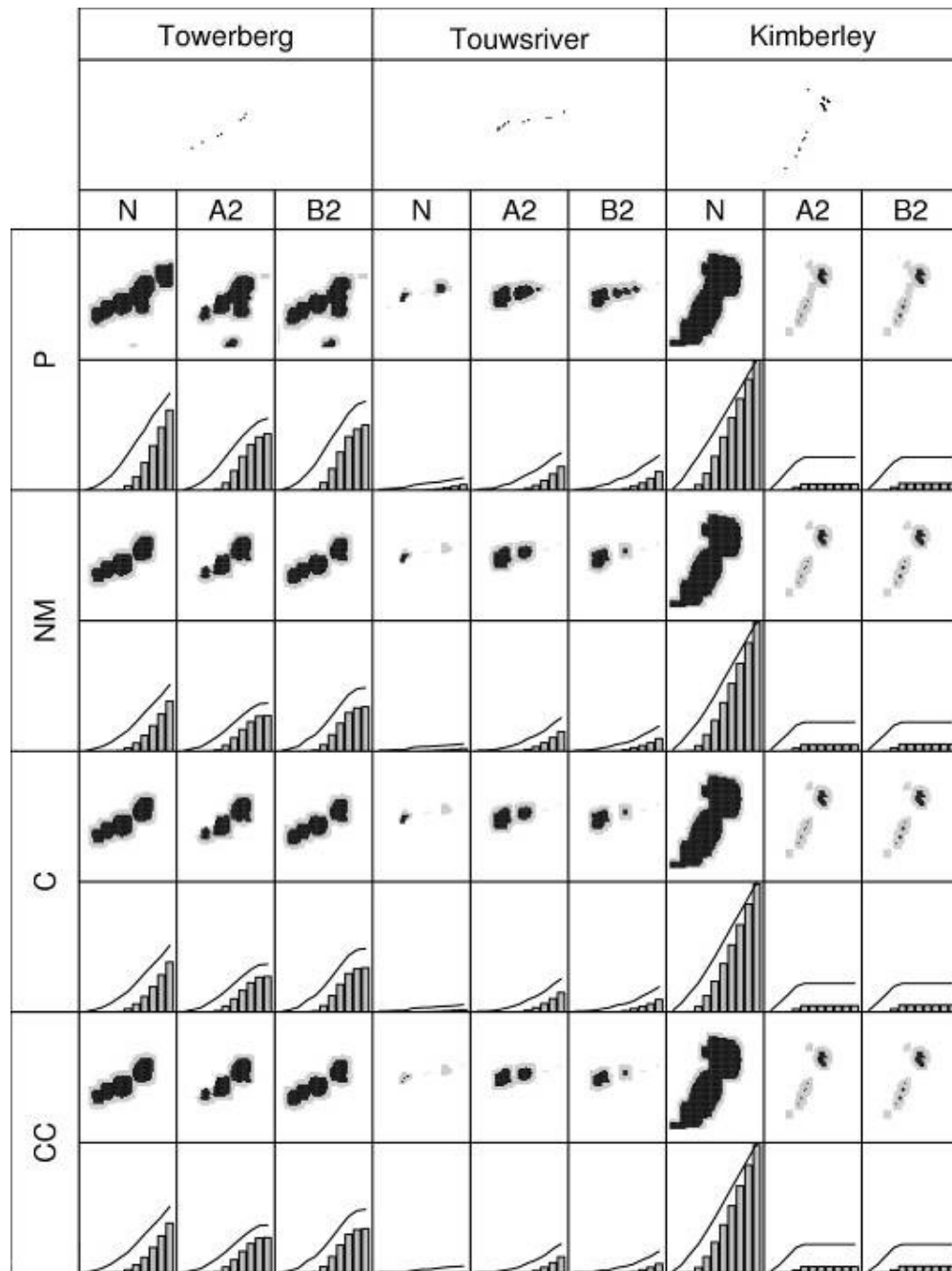
According to the predictions of the spread model, however, more than 10% of Albany Thicket and Nama-karoo respectively will be invaded under both climate-change scenarios (Figure 9.5, red line). Less area (<5% of the total area of the respective biome) is predicted for the fynbos and succulent karoo biomes with climate-change. Savanna and grassland biomes showed very low potential spread under climate-change scenarios (Figure 9.5, red line).

Differences in the total number of occupied cells with no management and under three scenarios of active management suggest that *S. molle* will increase its distribution (more cells occupied) under all management scenarios (Table 9.2). Unsurprisingly, highest cell occupancy occurred under management scenario P for all climate-change scenarios for both 2050 and 2100, while scenario CC generated the lowest cell occupancy (Table 9.2).

Different patterns were, however, observed at fine-scales for different scenarios. Under the no-change scenario (current climate condition), the number of occupied cells increases exponentially over time under all management scenarios and in all three regions, especially around Towerberg and Kimberley. Doubling the number of planted individuals at random along the roads (scenario P) led to increased spread, especially around Towerberg. Although the Kimberley area shows a high numbers of occupied cells under the no-change-in-climate scenario, it shows little increase of spread under both A2 and B2 climate-change scenarios (Figure 9.6). On the other hand, Touwsriver shows reduced spread under all climate and management scenarios. Although cell occupancy was highest under management scenarios NM and P, the management scenarios C and CC show no clear difference in all regions and all climate scenarios.



**Figure 9.5:** The percentage of cells per biome suitable for *Schinus molle* (suitability > 0.42) (blue lines) and invaded as predicted by the spread model (red lines) in different biomes. Solid lines indicate no climate change (N); dotted and dashed lines show climate-change scenarios A2 and B2, respectively.



**Figure 9.6:** Spread of *Schinus molle* under scenarios of climate change and management in three regions of South Africa (each 100km\*100km in size): Towerberg (coordinates of centre point: 24.53°E; 30.83°S), Touwsriver (20.28°E; 33.30°S), and Kimberley (24.76°E; 28.96°S). Maps show the distribution of the species in the year 2100; darker shades indicate high numbers of individuals in that pixel. Histograms show the number of cells occupied by plants per year and lines indicate numbers of individuals in the area. Time (from 2000 to 2100, in intervals of 10 years)

is shown on the x-axis. Three climate-change scenarios are shown in the three columns (N = no change, A2 and B2 are two widely accepted emission scenarios developed by the Hadley Centre for Climate Prediction and Research; for details see Thuiller *et al.*, 2005). Four management scenarios are shown in the rows (NM = no management; P = doubling the number of planted individuals at random along the roads; C = removing all planted individuals; CC = removing all planted and naturalized individuals in cells which have at least one planted individual). The maps in the first row indicate the original occurrence data on the site.

## Discussion

### *Potential distribution of Schinus molle: planted vs. naturalized individuals*

A large part of western South Africa is potentially suitable for growth and naturalization of *S. molle*. The area identified as suitable for growth of planted individuals is larger than the area identified as suitable for naturalization of the species. Differences in the two predicted ranges (Figure 9. 2 D) are instructive. Areas suitable for growth of planted individuals but not naturalization represent areas where environmental conditions currently prevent establishment. The larger area in P2 than in N2 (Figure 9. 2) is attributable to the role of nurturing by humans of planted trees (e.g. by watering, nutrient supplementation, and removal of competing vegetation) which improves growth and survival (Iponga *et al.*, 2008b). Areas shaded in red in Figure 9. 2 D indicate zones where (presumably largely abiotic) barriers preclude invasion by thwarting recruitment. The main focus of this study is on areas that are susceptible to invasion by *S. molle* – areas shaded in blue and black in Figure 9. 2 D under prevailing climatic and management conditions. The delineation of these areas is influenced by the interplay of climatic variables with other factors that define the dimensions of human intervention such as distance from planted trees and the density of planted plants, both of which affect propagule pressure (Rouget and Richardson, 2003; Foxcroft *et al.*, 2004).

At the biome level, the models show that the Nama- and succulent karoo biomes are clearly most affected by *S. molle* naturalization. Although *S. molle* has also been planted in the fynbos biome, naturalization in this biome is sparse (Figure 2 N).



Preliminary modelling by Rouget *et al.*, (2004) also showed that arid areas were most vulnerable for further invasion of this species. Not all arid areas that were sampled face naturalization and invasion by *S. molle*; localised areas, mostly in the succulent- and Nama-Karoo biomes and along the Eastern Cape coast, are affected. Mean annual temperature of the coldest month (*mtc*), mean annual precipitation (*map*) potential evapotranspiration (*pet*) and proximity to rivers (*driv*) are most important variables explaining the naturalized distribution of *S. molle* in the region. Proximity to rivers together with propagule pressure explained local patterns. In the more arid areas, *S. molle* invades mostly along perennial and ephemeral rivers. River beds probably act as conduits for seed dispersal and also provide additional water and shelter from temperature extremes which helps seedling establishment. Invasions could continue even with climate change as long as the rivers flow periodically.

Observations in the field suggest that *S. molle* can spread in natural habitats without human intervention because of its population dynamics and ability to infiltrate naturally-occurring dispersal networks (Milton *et al.*, 2007; Iponga *et al.*, 2008c). All indications are that this species is still at an early stage of invasion, and probably not at equilibrium with environmental conditions. Consequently, models calibrated using this limited set of occurrence data probably underestimate the potential naturalized distribution of *S. molle* in western South Africa. The species is expected to expand its range when established individuals mature and act as new seed sources. This limitation must be kept in mind, but I believe that the broad-scale prediction of *S. molle*'s potential range using the set of environmental variables applied in this study are reasonably robust.

### *Potential distribution of naturalized individuals of Schinus molle under climate change*

It is widely held that climate change will exacerbate problems with invasive species (Dukes and Mooney, 1999), but the many ways in which changes could affect the ranges of species, and the many complex interactions that could potential facilitate or hinder shifts, make accurate predictions very difficult (Thuiller *et al.*, 2007). The models suggest that under both climate-change scenarios examined the area suitable for *S. molle* naturalization is predicted to shrink substantially in the Nama-karoo, succulent karoo and Albany Thicket biomes. Climate change will not only alter the

suitability for individual species, but is likely to reshuffle species composition and possibly change ecosystem functioning. Such changes will certainly affect environmental suitability in ways other than simply through altered climatic tolerance. Nonetheless, it is unlikely that such changes will counter the overall deterioration of opportunities for recruitment and spread over the next century.

Limitations of this study include the many uncertainties inherent in climate-change scenarios, the coarse spatial resolution of the analysis, and uncertainties in the modelling techniques (Thuiller, 2004; Pearson *et al.*, 2006). The relatively coarse scale may also mask potential refuges for species and environmental heterogeneity under climate-change scenarios, especially in areas where the sampling effort was low, leading to potential underestimation of range expansion. There are also uncertainties related to lags associated with biotic processes. Extensive habitat fragmentation, effects of rising CO<sub>2</sub> concentrations, changing soil conditions and fire regimes, and altered biotic interactions mean that predictions must be viewed with caution. Nonetheless, the result suggest that regions such as Kimberley (currently a “hotspot” of *S. molle* invasions in South Africa) might be affected relatively early by climate change, but that the region will become less suitable for naturalization over time. This provides managers with a conundrum; *S. molle* invasions in this region are currently regarded as a serious conservation threat requiring urgent action (Milton *et al.*, 2007; Iponga *et al.*, 2008c). But, is such action justified if the threat is likely to diminish over the next century?

### *Spread of Schinus molle under different management strategies*

To determine the pattern of spread of *S. molle* in South Africa I combined information from climatic suitability under scenarios of climate change and management by means of a simulation spread model. Results indicates that Nama-Karoo and Albany Thicket and to a lesser extent succulent karoo and fynbos biomes may experience an increase of *S. molle* spread under present and future climatic conditions, even if there was a consistent decline of potential suitability in both future climate-change scenarios beyond 2050 for those biomes. This suggests that although the conditions may not be favourable beyond 2050, the species may have time to expand substantially during the next few decades, and that this may facilitate the spread observed in some biomes. Most importantly, *S. molle* could persist outside its potential future ranges in the near

to medium term because the species is relatively long lived and produces large quantities of seed. *Schinus molle* may also be more flexible with regard to its bioclimatic constraints than has been assumed in the spread model, and could persist outside areas predicted to be suitable. Immediate management intervention should focus in those biomes.

For the overall assessment of *S. molle* spread in the western part of South Africa, results suggest that the savanna, grassland and fynbos biomes might be considered low-risk areas for *S. molle* spread under scenarios of climate change, whereas Nama-karoo and Albany Thicket biomes should be considered high-risk areas. Climate change seems to improve conditions for *S. molle* naturalization in some parts of South Africa, but might create barriers for establishment and spread in other regions. The areas around the towns of Kimberley and Touwsriver are predicted to become less susceptible to invasion by *S. molle* compared to Towerberg. However, Towerberg, showing different patterns of range increase under all climate-change scenarios, may emphasise the risk of invasion faced by the Nama-karoo biome. However, to be really effective in controlling the invasion of *S. molle* in South Africa, all plants should be removed. Removal of planted and naturalized individuals should start in the areas identified as being at the highest risk of invasion with or without climate change. Removal operations should then move to the Kimberley area which has large propagule sources. Although the models predicted very low suitability under climate-change scenarios around Kimberley, I cannot predict with confidence the future condition of those areas with high invasion levels at present.

## Conclusions

To be really effective in controlling the invasion of *S. molle*, all plants should be removed. Removal of only some plants (e.g. large planted trees along roads) will have little influence because the naturalized plants will soon become seed sources. Clearing of *S. molle* should be prioritized in those areas where environmental suitability is predicted to increase under climate change (e.g. arid areas of the western part of South Africa). In areas where decreased environmental suitability is predicted, management could be limited to sensitive sites and areas where invasive stands are already having severe impacts on ecosystems (see Iponga *et al.*, 2008c for discussion). *Schinus molle* has been considered a relatively “safe” alien tree until recently. However, its ability

to disrupt natural ecosystems has been clearly documented. Despite the evidence provided in this paper which suggests that much of its current range in western South Africa will become less favourable for the species under climate change, the species is already well established over large areas (where it will persist long after conditions for establishment have deteriorated). Also, several areas where the species is currently not widely naturalized (notably fynbos and grassland areas) are predicted to become more favourable. Consequently, I recommend that the species should be declared a noxious weed in parts of the country, notably the Eastern Cape, Northern Cape and Western Cape.

The approach followed in this study offers a useful means for objectively planning long-term intervention strategies for emerging invasive species. However, it also is important to be realistic about all uncertainties when making predictions and keep them in mind when interpreting the results. Climate matching is thus a useful approach to identify areas at risk of introduction and establishment of newly or not-yet-introduced species, but may not predict the full extent of invasions. It is clear that more realistic models of the impacts of climate change on *S. molle* environmental suitability and range shifts are needed to address the complex interactions between many factors affecting *S. molle* distribution other than climate, including biotic interactions, evolutionary change and dispersal capacity.

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# Invasive potential of the Peruvian pepper tree (*Schinus molle*) in South Africa

**Chapter 1:** General problem of biological invasion in South Africa landscape

**Chapter 2:** Dynamics of alien woody plant invasions: review of processes and ecological impacts

## Main objectives

**Chapter 3:** Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 4:** *Megastigmus* wasp damage to seeds of *Schinus molle* (Peruvian pepper tree) across a rainfall gradient in South Africa: Implication for invasion

**Chapter 5:** Seed set of the invasive alien tree *Schinus molle* (Anacardiaceae) in semi-arid savanna, South Africa: the role of pollination and selfing

**Chapter 6:** Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna

**Chapter 7:** Performance of seedlings of the invasive alien tree *Schinus molle* under indigenous and alien host trees in semi-arid savanna

**Chapter 8:** Superiority in competition for light a crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Peruvian pepper tree) in South Africa

**Chapter 9:** Distribution of the invasive alien tree *Schinus molle* in western South Africa: current determinants and projections under scenarios of climate change and management

**Chapter 10:** General conclusions and recommendations



# CHAPTER TEN

## GENERAL CONCLUSIONS AND RECOMMENDATIONS

### General discussion

Predicting the invasive potential and dynamics of alien plant species remains a difficult task. Using the case of the Peruvian pepper tree, *Schinus molle*, in South Africa, this thesis aimed to examine in detail the ecological processes and potential for a tree species which, although introduced a century ago and producing abundant seeds, only recently started to display invasive tendencies. The main objectives of the research were to refine predictions about the spatial limits and potential rates of spread for the species and to gain a better understanding of its potential distribution and impact in South African ecosystems under a range of scenarios of climate and land-use changes. Invasion patterns were studied in detail in semi-arid savannas. Other studies then compared these patterns with those observed in other southern African biomes – the aim being to gain the best possible understanding of the potential of the species as an invader for the whole of South Africa. The main hypothesis that was tested was that physical and ecological barriers exist which limit the invasion of *S. molle*, preventing it from reaching the potential distribution in South Africa shown from simple climate-envelope models. Understanding was gained of why the species is not spreading as fast or as far as predicted in preliminary studies.

Instead of being under purely climatic control, the invasive potential of an introduced plant species is also affected by its capacity to set viable seed, to disperse, to germinate, establish as a seedling, and to reach reproductive maturity. The level of dissemination of the species by humans (e.g. planting and seed dispersal) is also crucial. Of primary interest in this study were the ways in which biotic versus abiotic factors affected one or more of the species' life-history stages. In chapters 3 to 5 of the thesis I considered how pollinators, seed dispersers, seed predators, and pathogens influence the abundance of viable seed (including production, viability and dispersal). Conditions, including temperature maxima and minima and humidity were investigated in chapters 6 and 7. In chapter 8, I investigated competitive interactions between established *S. molle* trees and indigenous woody plants for light and other

resources. Finally, in chapter 9, I explored future invasion scenarios including habitat suitability for *S. molle* establishment under present conditions and under scenarios of climate change and management.

This study demonstrated that seed production and seed rain density of *S. molle* was high throughout its introduced range (384,864 - 1,233,690 seeds/tree/year; 3,877 – 9,477 seeds/m<sup>2</sup>/yr). Seed rain quality was, however, much reduced by an indigenous endophagous predator. Although *S. molle* did not maintain a persistent seed bank, dispersal of seed by birds facilitated the movement of *S. molle* seeds to a variety of microhabitats, and reduced seed damage away from seed-production sources. Seed production, dispersal and establishment of *S. molle* in the semi arid-savannas were not dependent upon disturbance (chapter 3). The assessment of the intensity and pattern of seed predation in South Africa reveals that the seed damage was mostly caused by an indigenous wasp *Megastigmus transvaalensis* (Hussey) (Hymenoptera: Torymidae) that normally develops in seeds of an indigenous *Rhus* species (Anacardiaceae) but has formed a new association with *S. molle* in both winter- and summer-rainfall regions. The role of this predator in dampening the rate and impact of *S. molle* invasion in South Africa needs further study (chapter 4).

Investigation of pollination demonstrated that fruit set in inflorescences protected from external pollinators but artificially cross pollinated, was greater than for protected inflorescences. However, the fact that a few seeds were also found in treatments protected from pollinators and not treated with pollen, suggests that some *S. molle* flowers might be bisexual and capable of self-pollination. Generalizations about the pollination requirements of *S. molle* cannot be made from a study at one location, and further research is required in South Africa (chapter 5).

Transplantation experiments (chapter 6) showed that *S. molle* seedlings performed considerably better beneath canopies of indigenous *Acacia* trees than in open areas regardless of soil type, and that exposure to large herbivores significantly decreased heights and canopy areas of seedlings compared with those protected from large herbivores. It was clear that protection provided by canopies of large indigenous *Acacia* trees facilitates *S. molle* invasion into semi-arid savanna. Whether exposed or protected from large herbivores, no seedlings planted in open grassland survived the first winter. The results suggest that low temperature (frost), and possibly inter-specific competition with grasses, may limit *S. molle* seedling establishment, survival

and growth away from tree canopies in semi arid savannas. The invasive potential of *S. molle* is thus greatest on fertile soils where sub-canopy microsites are present and browsing mammals are absent; this emphasises how microsite type characteristics need to be considered for management and monitoring of *S. molle* distribution in South Africa in general.

Having shown that recruitment of *S. molle* is dependent on indigenous microphyllous leguminous trees in this woodland, particularly *Acacia tortilis* (Fabaceae: Mimosoidea) as establishment microsites, I asked whether, another leguminous tree, the invasive alien mesquite (*Prosopis* sp.; also Fabaceae: Mimosoidea), might serve a similar function. Although mesquite has become common in arid savannas in southern Africa, *S. molle* rarely recruits under canopies of this species (Milton *et al.*, 2007). Understanding the association between these species was needed to predict invasion dynamics in the region. An additional transplantation experiment demonstrated that canopies of mesquite provide just as good microsites for *S. molle* establishment as those of the native acacia. Other factors, such as the failure of propagules to arrive beneath mesquite trees, must therefore be sought to explain the lack of recruitment beneath their canopies. The second possible reason for the lack of association between *S. molle* and invasive mesquite observed in the woodland is the finding of Dean *et al.*, (2002) that birds used invasive mesquite less frequently than indigenous *Acacia* species in the Northern Cape. They suggested that most branches of mesquite trees are angled too steeply to provide good perches for birds (chapter 7).

I showed in chapters 6 and 7 that seeds of *S. molle* are dispersed by birds, resulting in seedling establishment under tree canopies. The study also investigated the potential of an invasive alien tree to transform vegetation by quantifying the relative abilities of *S. molle* and dominant native trees *Acacia tortilis* and *Rhus lancea* to compete for light when growing in association. Using canopy symmetry as an index of ability to compete for light, I showed that the alien *S. molle* consistently out-competes the dominant native tree species. The study also demonstrated that the performance of two dominant native trees is depressed by *S. molle* which is now often found growing in association with them. The ability of *Schinus molle* to compete strongly for light, and the fact that such competition drives changes in vegetation composition, is an ominous portent of the large-scale transformation of large areas

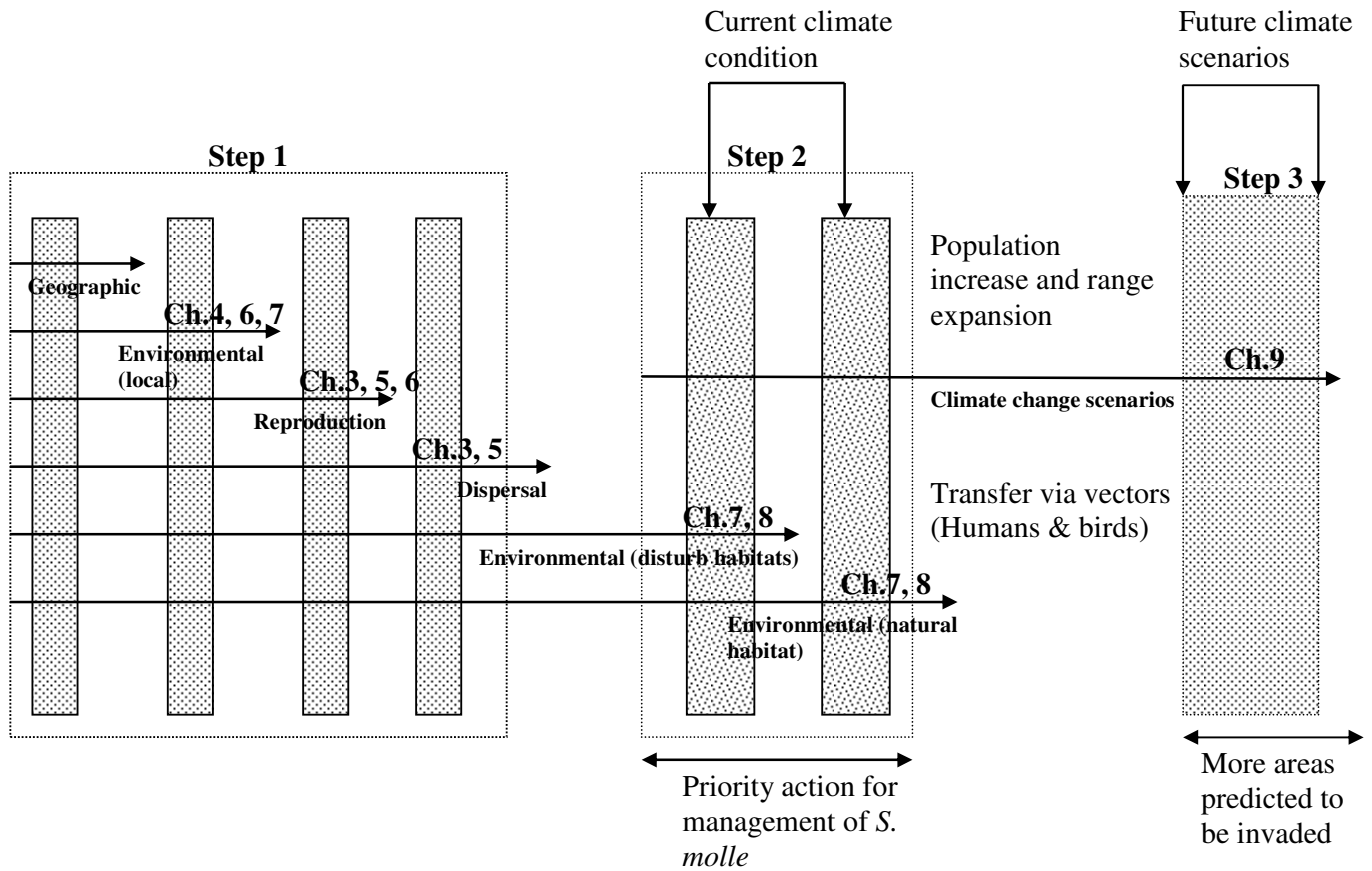
from grassy open savanna with scattered *Acacia*, to less grassy woodland dominated by *S. molle* that is likely if measures are not taken to curb the spread of this invasive species (chapter 8).

Through large-scale sampling the study also examined correlates of distribution for planted versus naturalized individuals of *S. molle* over large parts of South Africa (chapter 9). The aim was to produce accurate profiles of environmental conditions (both biophysical and those related to human activities) that characterize the two types of ranges of this species in its adventive range: namely planted trees (mostly along roads) and naturalized (self-established) individuals. The climatic envelope was used to predict the potential distribution of the species under future climate change scenarios, which were then used in an ecological simulation model to predict range of expansion of naturalized individuals of *S. molle* under different management scenarios. The study demonstrated that: not all arid parts of South Africa are likely to be invaded by *S. molle*, but, besides the arid savanna, some parts of the Fynbos, Succulent Karoo and Nama-Karoo biomes are susceptible to invasion. The study predicted that Nama-karoo; Succulent karoo and Albany Thicket must be considered to be at high risk of invasion by *S. molle*. Despite its widespread occurrence especially in semi-arid savanna under current climate conditions, models predicted that spread of *S. molle* in the Northern Cape (around Kimberley) and the central Karoo (Touwsriver) in the future will be limited by habitat suitability; this pattern was observed for all management scenarios.

### **Conceptual model for predicting the population dynamics, distribution, and spread of *Schinus molle* (and other fleshy-fruited alien species)**

The model I have used to synthesise my findings is based on the conceptualization of the naturalization and invasion of alien plants and their transformation of adopted ecosystems that was proposed by Richardson *et al.*, (2000); see chapter 2). This model describes a series of barriers or filters, through which species needs to pass over time from a pool of potential invaders. As species overcome barriers, their status changes from introduced, through naturalized and invasive, to that of ecological transformers. In the case of *S. molle*, several barriers have been weakened or removed by human

activities, including deliberate introductions or the establishment of new dispersal routes such as planting along roads and in gardens. On the basis of evidence presented in this thesis, *S. molle* has clearly overcome stage 1 in the model and is at stage 2 (invasive stage) in South African ecosystems. The study shows that it has a high potential to increase its range under current and future climate-change scenarios (chapter 9) - step 3 in the diagram - (Figure 10) and to become a transformer of habitats and ecological processes.



**Figure 10:** Conceptual diagram of barriers limiting the invasion process of introduced plants (adapted from concepts proposed by Richardson *et al.*, 2000). In the case of *Schinus molle*, the species has already overcome step 1, meaning that the species has surmounted the geographic (through human introduction) and environmental barriers (through biotic and abiotic factors), as demonstrated in chapter 4, 6 and 7, reproduction barriers (by high seed production, seedling germination and establishment, chapter 3, 5, 6), local and regional dispersal barriers (through dissemination by humans by planting along roads, and dispersal by birds). *S. molle* is now naturalized in disturbed areas (human modified or alien dominated vegetation) and natural habitat (step 2) (environmental barriers, chapter 7 and 8). The species is predicted to sample more areas under current and future climate-change scenarios (step 3, chapter 9). The arrows indicate the paths followed by *S. molle* in reaching different stages from introduced to invasive in natural vegetation.

## General conclusions

This work comprised a series of studies that set out to provide an understanding of the vulnerability of each stage in the life of *Schinus molle* to physical and biotic factors which may promote or prevent spread of this species in its adopted range in South Africa. Each case study (from seed bank to reproductive stage at different scales) involved a field experiment where a particular life stage of *S. molle* was studied. My research showed that *S. molle* is now highly invasive in arid and semi-arid areas of the Northern Cape and especially around Kimberley, but also in the Eastern Cape and in the arid part of the Western Cape. The bioclimatic envelope developed shows that the species has considerable potential to invade more areas in the northern and Eastern Cape as well as the arid zone of the Western Cape.

My experience with *S. molle* in semi-arid savanna of South Africa, suggests that if abiotic conditions are appropriate for this species to establish, it is likely to become invasive; regardless of the biota factors (such as endophagous insects) already present. Invasion failures in some areas may best be attributed to failure to adapt to abiotic conditions rather than to biotic resistance of the recipient community mostly in the woodland of the semi-arid savanna. Field experiments demonstrated that physical factors (probably frost) damaged seedlings in the open, whereas biotic factors (probably herbivory) damaged seedlings beneath canopies. Under the current climate and vegetation in the arid zone of South Africa, no recruitment of *S. molle* is likely to occur in open areas in semi-arid savannas at altitudes of 1000 m or more above sea level. The possibility of *S. molle* plants being facilitated by tree canopies in semi-arid savanna has to be considered when assessing the potential for further invasion. In other words, microsite structure plays an important role for *S. molle* seed germination and seedling growth.

I also consider that invasion of southern African arid savanna by *Prosopis* sp. (mesquite) may have a negative effect on the rate of invasion of this ecosystem by *S. molle*. However, where mesquite trees are invading grasslands where few other perches are available to birds, the alien host would provide microsite conditions that would advance the invasion of *S. molle*. I have demonstrated through field experiments how success at each life-history stage influences potential for invasion by *S. molle* in semi-arid savanna and shown that regeneration and spread of this species

depends on continuous seed production and dispersal rather than a persistent seed bank.

## **Management implications and recommendations**

The knowledge gained by investigating those traits of an alien plant that affect its invasive potential should improve our ability to make reliable predictions about the invasiveness of *Schinus molle* at the scale of landscapes, regions, and the whole country thereby informing management strategies. The problems arising from invasive ornamental plants sometimes lead to conflicts of interest between horticulturists, landowners, municipalities and conservationists (e.g. Foxcroft *et al.*, 2008). Although, various initiatives in different part of the world aim to reduce the use of known invasive species in horticulture, *S. molle* is still widely used in South Africa as a shade tree and especially along roads by municipalities. Invasion can definitely be reduced by promoting the use of locally indigenous species as alternatives for alien species.

Several attempts have been made to prioritize alien species based on their invasive potential in different parts of the world (e.g. Robertson *et al.*, 2003). However, less systematic attention has been directed at classifying invasive alien plant species which are already in a region to help formulate regional or national plans for managing invasions (Nel *et al.*, 2004). Studies in South Africa have sought to prioritize alien plant species on the basis of their potential invasiveness, spatial characteristics, and potential impacts have defined categories for different alien species. Those studies generally apply expert knowledge to score criteria of invasiveness and impact for classification of alien plants species (Nel *et al.*, 2004).

Classification is a necessary means of prioritizing a species at the national level, because it avoids the problem of prioritization across multiples spatial scales (Nel *et al.*, 2004). In South Africa, the Conservation of Agricultural Resources Act (CARA) (Act 43 of 1983) regulates various activities that may have an impact on agricultural resources including water sources and deals directly with the combating of invasive alien plants (Henderson, 2001). These regulations provide legislation that lists different categories (three categories) of 199 weeds and invasive alien species, and



prescribes the actions which landowners are obliged to take control of these species. These categories are:

**Category 1 declared weeds;** these may not occur on any land or on any inland water surface throughout the Republic of South Africa. No person may:

- sell, agree to sell or offer advertise, keep exhibit, transmit, send, convey or deliver for sale, or exchange for anything or dispose of to any person in any manner for a consideration, any weed, or
- in any manner permit whatsoever disperse or cause or permit the dispersal of any weed from any place in the Republic to any place in the Republic

**Category 2 declared invaders** are generally species grown for commercial purposes or used for woodlots, shelter belts, building material, animal fodder, soil stabilization or other beneficial function that may determined. Their continued use is permitted in demarcated areas.

**Category 3 declared invaders.** These plants usually used as ornamentals, are invaders that are permitted to grow where they already exist, as long as all reasonable steps are taken to prevent the spreading there of, except within the flood line of watercourses and wetlands. However, no new planting or trade or propagating of these plants is permitted.

Nel *et al.*, (2004) in their prioritization of invasive alien plants, grouped *S. molle* under the category of “major invaders”. However, the legal status of this species in the CARA legislation is “proposed Category 1 weed”). This category includes those species that were proposed for listing under the Conservation of Agriculture Research Act, but require further investigation before they can be included (Henderson, 2001; Nel *et al.*, 2004).

The results presented in this thesis clearly show that *S. molle* has the traits required to be invasive over large parts of South Africa. It is already spreading in some areas, and clearly has great potential for further invasion, particularly along rivers in arid areas. Although a more proactive and integrated approach is needed for assessing the risk of habitats susceptible to invasion, *S. molle* definitely deserves to be upgraded to a higher category of invasiveness (Category 1). All appropriate measures need to be taken to reduce the extent and density of current invasive populations, and to reduce the likelihood of further invasions. The species needs to be declared a

noxious weed in parts of the country, especially in the Eastern Cape, Northern Cape, and Western Cape provinces.

The implications of the work reported in this thesis for on-the-ground management of the species in areas where invasions are already at an advanced stage are that it is important to control further plantings and to clear existing plantings and self-sown stands. Results presented here suggest that, once the species has been cleared from an area, re-establishment will be slow provided that resprouting is prevented. In areas where invasions are not yet widespread, but which have been identified as being at risk of invasion, I recommended that management should follow an integrated approach as set out below:

- No planting of the species should be allowed in habitats of high conservation value, such as savanna woodland, where the species may spread quickly.
- Trees planted along roadsides should be removed and replaced by locally indigenous tree species, particularly where roads are close to rivers.
- Low-density stands of self-sown *S. molle* should be removed before further recruitment, densification, and increased levels of impacts are realized.
- No planting of the species should be allowed in the Eastern Cape, Northern Cape, and Western Cape provinces.
- No planting of this species should be allowed around highly disturbed habitat such as mine dumps, and the species should not be used for rehabilitation/restoration projects.
- Biological control options need to be fully investigated, starting with a thorough examination of the impacts of seed predation by *Megastigmus transvaalensis* (Hussey) (Hymenoptera: Torymidae) and its potential to reduce reproduction.
- Results from this study need to be brought to the attention of the horticulture industry, and appropriate measures need to be taken to limit the sale and planting of this species in South Africa.

Further studies of invasion patterns of *S. molle*, spanning several spatial and temporal scales, are required to infer process from pattern to gain additional understanding of the invasion process and spread of this species. Although the combination of habitat-

suitability models and spread simulation models (chapter 9) has generated interesting predictions for the future of *S. molle* in South Africa, additional, novel modelling approaches are needed to explore in more detail the dimensions of potential future spread and impact at a timer scale. Such approaches need to examine interactions between species dynamics and land use and should also capture the spatial structure of landscape. The work reported in this thesis has produced a sound basis for such work, and indeed *S. molle* has proved a good model system to explore many aspects of invasion dynamics. More work is also needed to determine the genetic structure of *S. molle* populations in different parts of its range in South Africa. All the work reported here has assumed that *S. molle* is genetically uniform in South Africa, and this may not be the case.

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## **APPENDICES**