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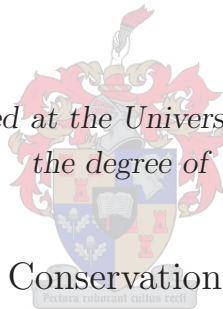
# Modelling Seed Dispersal in Restoration and Invasions

by

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*Dissertation presented at the University of Stellenbosch for  
the degree of*

PhD in Conservation Ecology



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# Declaration

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# Abstract

## Modelling Seed Dispersal in Restoration and Invasions

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Dispersal plays an essential role in determining the distribution of populations of species, especially species expanding their ranges. Two disciplines are concerned with gaining understanding of spread of species, namely restoration ecology and invasion biology. Conceptual understanding of dispersal, its mechanisms and its management is essential to both disciplines. Nevertheless, the disciplines have quite opposite objectives: in restoration ecology, spread of indigenous species into transformed landscapes is promoted, while invasion biology aims to prevent the (further) spread of alien species into pristine or restored habitats. Despite these two opposite objectives of facilitating spread and preventing spread of their respective target species, these disciplines have essentially the same requirements in terms of information needed for restoration. In this thesis, I will present two modelling studies—one looking at the impact of two different seed-feeding alien control agents on the spread of *Hakea sericea*, the other investigating the recolonisation by *Dicerothamnus rhinocerotis* of an old field dominated by *Cynodon dactylon*. Based on these studies, I will draw conclusions for the management in each case. In a second step, I will compare these two seemingly-different studies and draw conclusions on how these two disciplines can learn from each other, and how conclusions drawn and management recommendations developed for the one discipline can be translated for the other. The invasion biology study concluded that seed-feeding biocontrol agents do have a considerable impact on the velocity of the spread of the target species. In addition, management recommendations included the possibility of substituting seed-feeding biocontrol agents with an increased fire frequency where the negative impact on natural vegetation, on the site invaded by the target species, is acceptable. The restoration study concluded that the main impact on the velocity of spread, and the speed of the return of the shrub species onto the old fields, is the availability of micro-sites. A sensitivity analysis showed the even a slight change from 1% to 2% increases the velocity and pattern of spread dramatically. The other parameters playing an important role are the mean rate of establishment and the time span between

episodic germination events of the shrub species, which work in opposite directions. These similarities in the information needed by restoration ecology and invasion biology, and the transfer from management strategies in the one for usage in the other, offers the possibility of designing dispersal studies which yield results interpretable, and interpreted, for direct application in both disciplines. This is because management strategies that cover both objectives at the same time are much more time- and cost-effective than a two-stage process, in which alien plants are cleared first, leaving a highly disturbed landscape behind, which is then restored to a natural state in a second step.

# Uittreksel

## Modelling Seed Dispersal in Restoration and Invasions

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Dispersie speel 'n wesenlike rol in die bepaling van die verspreiding van spesies, veral by spesies wat hul meetgebied uitbrei. Restourasie-ekologie en indringerbiologie is twee dissiplines wat veral belang het om 'n beter begrip van 'n spesie se verspreiding te verkry.

Beide het 'n noodsaaklike behoefte om dispersie, die meganismes daar agter, en die bestuur daarvan, te verstaan.

Tog, het beide dissiplines heeltemal verskillende doelwitte: Met restourasie-ekologie word die verspreiding van inheemse spesies in 'n getransformeerde landskap bevorder, waar indringerbiologie dit ten doel het om die (verdere) verspreiding van indringerspesies na natuurlike of getransformeerde habitate te verhoed. Afgesien van hierdie verskillende doelwitte vir die fasilitering en bekamping van onderskeie teikenspesies, het hierdie dissiplines basies dieselfde behoeftes in terme van informasie wat benodig word vir restourasie. In hierdie tesis, wil ek twee modelle-studies voorlê. Een ondersoek die impak van twee verskillende indringerbeheermiddels deur saadvoeding op die verspreiding van *Hakea sericea*. Die ander studie ondersoek die rekolonisasie van *Dicerothamnus rhinocerotis* via natuurlike dispersie vanaf 'n aangrensende saadbron na 'n ou weiveld wat met *Cynodon dactylon* oorgroei is. Vervolgt, stel ek bestuursriglyne voor vir beide gevalle. In 'n verdere stap, vergelyk ek ook die oënskynlike verskillende studies en maak gevolgtrekkings oor hoe die twee dissiplines van mekaar kan leer. Gevolgtrekkings en bestuursriglyne ontwikkel vir die een dissipline, kan ook toepaslik wees vir die ander.

Die indringerbiologie-studie het getoon dat bio-kontrole-middels d.m.v. saadvoeding 'n aansienlike impak het op die tempo van die verspreiding van teikenspesies. Bestuursriglyne sluit boonop die moontlikheid in om bio-kontrole-middels d.m.v. saadvoeding, te vervang met 'n verhoogde frekwensie van brande, sodat die negatiewe impak op die natuurlike plantegroei in 'n gebied, wat ingedring is met 'n teikenspesie, aanvaarbaar is. Die restourasie-studie het getoon dat die hoof-impak op die snelheid van saadverspreiding en die terugkeer van struikspesies na die ou velde, die beskikbaarheid van mikro-terreine is.

Selfs 'n geringe verhoging van 1% na 2% verhoog die snelheid dramaties. Ander parameters wat 'n belangrike rol speel is die gemiddelde tempo van vestiging en die tydspanne tussen episodiese ontkiemingsgeleenthede vir struikspesies. Hierdie ooreenkomste in informasie wat benodig word vir beide restourasie-ekologie en indringerbiologie, en die oordrag van bestuursstrategieë van die een vir toepassing in die ander, skep die moontlikheid vir die ontwerp van studies op dispersie. Die resultate verkry kan interpreteer word vir direkte toepassing in beide dissiplines. Bestuursstrategieë kan terselfdertyd beide doelwitte dek en meer koste-effektief wees as die tweevoudige proses, waar indringerplante eers verwyder word en 'n erg versteurde landskap agterlaat, en dit dan vervolgens herstel word tot die natuurlike toestand.



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# Dedications

Dedicated to my grandfather, Dr. Otto Krug.



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# List of Abbreviations and Symbols

**2DT** 2DT Distribution

$\alpha$  Scale Parameter

$\beta$  angle

$\gamma$  Shape Parameter

**ADK** Area Source Seed Dispersal Kernel

**AIC** Akaike's Information Criterion

**COMP** Competitiveness a plant experiences

**CompEst<sub>0</sub>** Probability of establishment when the competition experienced by seedling is zero

**cs** *Cynodon dactylon* survival

**D** Distance from seed source

**EstMax** Maximum Establishment Rate

**FON** Field of Influence

**gi** Germination Interval of *Dicerothamnus rhinocerotis*

**HakSim** Model used for simulation of spread if *Hakea sericea* from a point source

**HakSimSpread** Model used for simulation of spread if *Hakea sericea* from an area source

**IP** Inverse Power Law

**IP\_NE** Mixed distribution of Inverse Power Law and Negative Exponential Distribution

**LNM** Log-Normal Distribution

**me** Mean Establishment Rate

**MFF** Mature Follicle Feeder

**MLE** Maximum Likelihood Estimator

**N** Number of individual plants

- $N_{\text{ADD}}$**  Number of seeds dispersed in a 1m wide transect, originating from the edge of the area source
- NE** Negative Exponential Distribution
- NM** Normal Distribution for  $x \geq 0$
- $p(\mathbf{D})$**  Probability density function (pdf) of distance  $\mathbf{D}$
- pdf** Probability Density Function
- PDK** Point Source Seed Dispersal Kernel
- $Q_x$**  Seed Count at Distance  $D_r$  Distance from point seed source
- $R_0$**  Net Reproductive Rate
- RelZof** Relative ZOI
- RenPatch** Model used to simulate spread of *Dicerotheramnus rhinocerotis* in an old field colonised by *Cynodon dactylon*
- rz** relative ZOI radius
- $S_N$**  Number of Seeds deposited at distance  $\mathbf{D}$
- $S_N(\mathbf{D})$**  Total number of seeds deposited at distance  $\mathbf{D}$
- $S_{\text{sqm}}$**  Expected Seed Rain per square meter
- $T_A$**  Total Number of seeds dispersed out of an Area Source
- $T_{\text{sqm}}$**  Seed Production per square meter
- $V$**  Velocity of spread
- $V^-$**  Minimum Velocity  $V$  expected
- $V^*$**  Equilibrium velocity  $V$
- $V^+$**  Maximum Velocity  $V$  expected
- WB** Weibull Distribution
- WB\_NE** Mixed distribution of Weibull and Negative Exponential Distribution
- YFF** Young Follicle Feeder
- ZOI** Zone of Influence
- $ZOI_{\text{rel}}$**  Relative ZOI



## **Part I.**

# **General Introduction**



# 1. General Introduction

## 1.1. Rationale

Habitat requirements of plant species, and environmental and climatic conditions play an important role in the distribution of species. Nevertheless, species distribution pattern can not simply be predicted by using these habitat requirements, and resulting environmental envelopes (as done e. g. by [Midgley et al., 2002, 2003](#)). Without propagules arriving in the potential sites, the species will not be able to grow there (see e.g. [Mueller-Dombois and Ellenberg, 1974](#); [Schupp, 1995](#)), establishing viable populations. Hence, dispersal plays an essential role in the life history of all plants as it determines, as [Harper \(1977\)](#) terms it, the “*potential* population”. If this “*potential* population” is non-existent, the actual population will be absent as well ([Harper, 1977](#)). Whether these arriving propagules, in most cases seeds, establish, depends on their habitat requirements and the environmental and climatic conditions at the sites. This is especially true when considering a species which is colonising new habitat, as movement of the species, sometimes over long distances, is a prerequisite ([Bonn and Poschlod, 1998](#)).

Apart from an academic interest in the understanding of the dispersal process, an understanding of the dispersal potential of a species has direct implications for management in situations where a manipulation of the spread of a species is desired. Two disciplines which deal directly with the spread of species are restoration ecology and invasion biology.

The spread of a species is, among other things, determined by its dispersal ability. Both restoration ecology and invasion biology are concerned with the spread of species. However, they have very different objectives. To quote [Bakker et al. \(1996\)](#), “Restoration ecology deals with the scientific and ecological background of nature management practises aiming at the re-establishment of plant species which have disappeared.”, while the Society for Ecology Restoration ([2004](#)) defines ecological restoration as “the process of assisting the recovery of an ecosystem that has been damaged, degraded or destroyed.”. One of the first steps in a restoration process is to determine which species would naturally occur on a site, and to investigate the potential of these species to disperse and establish at the site naturally. Very often, however, the re-establishment of the species depends on human intervention. Ecological restoration thus desires species to disperse into the sites to be restored, and using the understanding of dispersal processes and spread pattern to maximise the effectiveness of their restoration strategies—good dispersal of the target species is regarded as a desirable property.

The aim of invasion biology, by contrast, is to understand the processes and properties of

species and ecosystems leading to an alien species becoming naturalised and invasive (for a definition of the terms “alien”, “naturalised” and “invasive” see [Richardson et al., 2000](#)). Dispersal is one of the initial phases of an invasion, and alien species have to overcome the “local / regional dispersal barrier” ([Richardson et al., 2000](#); [Richardson, 2001](#)) in order to become invasive. As [Richardson et al. \(2000\)](#) states: “The shift from ‘naturalised, non-invasive to ‘invasive’ [...] represents the point at which the presence of an alien species may start to have detectable ecological or economic consequences.” Restricting further dispersal of the species is thus the first line of defence to prevent further spread of a species that is already present in a region. As the aim of invasive species management is the containment, or removal, of the alien species from a system, the understanding of dispersal and spread pattern is important to understand which management intervention is the most effective to fight alien species—good dispersal is facilitating spread and is therefore regarded as a undesirable property.

In this thesis, an ecological simulation model will be used to investigate the role of seed dispersal in regard to observed seed dispersal and spread pattern in both restoration and invasion. For restoration, the role of seed dispersal of a wind-dispersed asteraceous shrub from the Fynbos Biome in South Africa, *Dicerothamnus rhinocerotis* (renosterbos) on the recolonisation pattern on an old field covered with *Cynodon dactylon* (bermuda or quick grass) is determined and the simulated pattern and the pattern observed in the field are compared. In invasion, the impact of different seed dispersal kernels and two biocontrol agents on the spread of *Hakea sericea*, an alien invasive species in South Africa originating from Western Australia, is investigated.

## 1.2. Aim and Objectives

The aim of this study is to provide a synthesis of the role of seed dispersal and spread pattern in restoration and in invasion biology, using an ecological simulation model. Results from this study should inform both disciplines to use dispersal studies to assist in their respective efforts, namely, to either assist in the return of the desired species or avoid the spread of undesired species.

The objectives are therefore:

1. To create an individual-based spatio-temporal multi-species model which enables us to simulate seed dispersal and the spread of a species with minor modifications for simulating restoration and spread of invasive species scenarios;
2. For the restoration study: to use the developed model to simulate the return of *Dicerothamnus rhinocerotis* onto old lands covered with *Cynodon dactylon*;
3. For the alien invasive study: to use the developed model to analyse the impact of different dispersal kernels and two different biocontrol agents on the spread of *Hakea sericea*;

4. To compare the results of these two case studies to synthesise them into a coherent picture concerning the role of seed dispersal in the spread pattern of a species;
5. To outline aspects in dispersal in which restoration and invasive species ecology can supplement each other to avoid duplication of work.

### 1.3. Structure of Thesis

Part **I** is a general introduction, introducing the topic of the thesis, its objective and structure. It comprises two chapters, the first (Chapter **1**) providing the rationale behind the study, its aims, objectives and key questions and an overview of the structure of the thesis. The second chapter (Chapter **2**) gives an introduction of the topic, putting it into context of the literature.

Part **II** investigates the impact of seed-destroying biocontrol agents and fire frequency on the spread of *Hakea sericea*, an highly-invasive species in the Fynbos Biome, by using a stochastic spatio-temporal individual-based simulation model. It comprises two chapters where both chapters address the impact of two biocontrol agents on the spread of *H. sericea*. Chapter **3** discusses the spread of *H. sericea* from a single plant (a point source) in the centre of the simulated  $1000 \times 1000\text{m}$  landscape. Chapter **4** builds on Chapter **3** and analyses the spread from an area source at the short side of a simulated  $50 \times 10000\text{m}$  landscape and discusses the differences between these two scenarios. In addition, Chapter **4** includes a discussion of the impact of different fire frequencies.

Part **III** focuses on the role of seed dispersal in restoration. It comprises three chapters. The first chapter (Chapter **5**) introduces the reader to the study system, Renosterveld, using “historical ecology” (Swetnam et al., 1999) to determine the likely pattern and processes in this vegetation type. The second chapter (Chapter **6**) describes how the seed dispersal kernel of *Dicerotheramnus rhinocerotis* (renosterbos) was determined, based on a field study conducted by Shiponeni (2003). The obtained seed dispersal kernel forms the basis for the simulations in Chapter **7**. The third chapter (Chapter **7**) analyses the dynamics of *D. rhinocerotis* and *Cynodon dactylon* and includes a detailed description of the individual-based spatio-temporal stochastic simulation model RenPatch. The model RenPatch is used to analyse properties of *D. rhinocerotis* and *C. dactylon* and their impact on the pattern of the return of *D. rhinocerotis* recolonising a  $25 \times 25\text{m}$  large simulated old land covered in *C. dactylon* from an adjacent area source.

Part **IV**, the final section of the thesis, is comprised of one chapter (Chapter **8**) which discusses the commonalities and differences between Part **II** and Part **III** and analyses how the different approaches can inform each other.

There are five appendices. These include two published papers (appendix **A** and appendix **B**) directly related to the topic, and additional modelling outputs detailed in graphs and tables. Appendix **C** refers to Chapter **4**; appendix **D** and appendix **E** to Chapter **7**.

References follow the convention of Ecological Modelling. Numbers after the references refer to pages where references are cited. It was decided to include the references at the end of each part rather than the end of the thesis, as the literature pool between parts, especially Part II and Part III, is quite distinct.

#### 1.4. Attribution of effort in multi-authored chapters

There are two multi-authored chapters in this thesis, namely Chapter 3 and Chapter 5. The circumstances leading to the co-authorships and my contribution to the multiauthored chapters are as follows. Chapter 3 was initiated as the outcome of a workshop convened to understand the effects of seed predation on dispersal of an alien invasive plant. The workshop was convened by Dr D. le Maitre of the CSIR. I participated as the modeller, and subsequently developed a dispersal model with the data provided by other researchers. In addition to developing the model and running simulations and analysing the results, I wrote those parts of the chapter relating to the methods, results and interpretation of the model and analysis. The second chapter on invasion modelling, Chapter 4, uses the same data set as Chapter 3, but was conceptualised and authored only by myself. Chapter 5 is also a published, multiauthored paper. The data were provided by the co-authors and were combined by myself to a coherent picture of Renosterveld processes and pattern.

## 2. Role of Seed Dispersal in Restoration and Spread of Alien Species

### 2.1. Restoration

Restoration Ecology is the science of “ecological restoration” (Jordan et al., 1987), which is defined by the Society for Ecological Restoration International Science & Policy Working Group (2004) as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed.” This definition includes two terms which need further clarification, namely “assisting in recovery” and “degraded, damaged or destroyed”.

“Assisting in recovery” implies that ecological restoration needs to assist the recovery of the degraded system, as wholly-natural recovery is not possible or will take a long time.

To assist an ecosystem in its recovery, which often includes clearing of alien vegetation, it is important to understand the basic concepts which control the natural recovery. These concepts are succession, assembly rules of communities and ecosystems, and the role of disturbances. As discussed in Hobbs et al. (2007), these processes are closely interlinked, and influence each other, and each plays an important role in understanding the natural dynamics of the system.

Furthermore, “assisted recovery” implies a change of the current system toward a particular, desired, state. Therefore restoration must be seen as goal oriented (Hobbs, 2007) and as ecosystems are not static, this envisaged state of the restored system cannot be a static constant state (Hobbs and Harris, 2001), but will be dynamic and adaptable. In addition to structural pattern, the description of the goal state of restoration should also contain processes, as only a system with functional processes is able to survive over time (see Hobbs and Harris (2001) for further discussion). This setting of goals has to incorporate ecological, historical as well as socio-economic aspects. Swetnam et al. (1999) discusses the use of “historical ecology”, i. e. historical knowledge related to the ecology of a system, to guide ecosystems management or to set restoration goals for the structure and composition of the desired system. One example they discuss in detail is the montane grassland restoration project in northern New Mexico which was "justified and guided" by historical ecology. They used aerial photography ranging from 1935 to 1981 to show that tree invasions reduced the open grasslands in that time period by 55%. Despite earlier studies, which showed an encroachment of trees into the grasslands, the extent and speed of this spread was not known. The aerial photos were able to supply this valuable information. In addition, spatial pattern of this encroachment indicated that anthropogenic actions accelerated this change. As a consequence of this information, a restoration pro-

gram was initiated to counteract this encroachment. Another example they discussed is the reconstruction of fire history based on fire scars within the boles in surviving trees. Fire scars can provide information on the year of the fires and even the season. Despite the problems and shortcomings of this method (records only available when no logging occurred; decreasing completeness with increasing time since fire; records are point data), these fire scars can be used to determine fire pattern (frequency, season and spatial extent). This knowledge has been used to justify the reintroduction of surface fires and can ultimately be used to develop fire management strategies on temporal and spatial scales and consequently enable restoration of areas to a more natural state.

Another example of using historical data to reconstruct processes in an ecosystem can be found in Krug et al. (2004b) (Chapter 5), Krug and Krug (2007) (Appendix B) and also in Newton and Knight (2005); Newton (2006). Here, historic and prehistoric information obtained from archaeological records, historical sources such as Jan van Riebeck's travel journals, were used to reconstruct the ecosystem processes in West Coast Renosterveld and the transformation processes leading to today's highly-fragmented state (von Hase et al., 2003). These historical information sources were subsequently used to identify potential problems (e. g. change of soil properties due to changed grazing pattern), determine goals and derive methods for restoration of West Coast Renosterveld (Krug et al. (2004a), Appendix A and Krug and Krug (2007), Appendix B).

Even though the understanding of the processes governing the system and its pattern in the past and present are really important to derive restoration goals, it is not possible to only use past processes and pattern as goals themselves. To quote Hobbs and Harris (2001):

... most ecosystems are dynamic and hence restoration goals cannot be based on static attributes. Setting clear and achievable goals is essential, and these focus on the desired characteristics for the system in the future, rather than in relation to what these were in the past.

In addition to such historical information, other factors must also be considered to derive restoration goals to obtain a sustainable system. These factors include expected changes in the future (e. g. climate change (Harris et al., 2006; Halle, 2007b; Hobbs, 2007)), socio-economic factors (Hobbs, 2007) and the current status of the system to be restored (Halle, 2007a; Hobbs, 2007).

Two aspects should be highlighted: the role of disturbances and the necessity to assess the actual state of the system. Hobbs et al. (2007) discusses the importance of disturbances in restoration as well as in the causes for the degradation. He points out that, in many cases, a change in disturbance regime can be seen as the cause for the initial degradation of the system, but that disturbances can also be applied as management tools to change the trajectories of succession and therefore be used to guide the system towards a state closer to the final goal set for the restoration. This goes far beyond the idea of restoring or recreating a disturbance regime which is essential to maintain the envisaged system—it



includes disturbances as management tools or the creation of disturbance regimes to finally reach the goal which can then be maintained by a different disturbance regime.

Hobbs et al. (2007) also points out that the goal of the restoration effort depends on the status of the restored system. This reiterates the importance of actually identifying the degradation state of the system, which is not a trivial task. As Halle (2007b) states:

To classify a system as evidently degraded is in most cases straightforward, but this is not enough to develop a strategy for its restoration. For this task, it is precarious and misleading to rely on casual and aesthetical features alone; rather it is necessary to identify the system in depth, because what is left with respect to species composition, trophic interactions, and ecosystem functions are the basis from which any transition process to a more desirable state has to develop.

As it is not possible to do a full analysis of the degraded system for all sites that need to be restored, he emphasises the need to develop rules and pattern which can be applied to similar systems to make the process more efficient.

A somehow more limited definition of restoration ecology is given by Bakker et al. (1996), stating that restoration ecology deals with the re-establishment of plant species / natural vegetation which previously occurred but disappeared due to diverse causes. This definition nevertheless highlights the main concern of restoring a degraded site: to re-establish species that were previously present in the degraded site. The re-establishment of these species can be inhibited by two factors, i.e. the return can be seed limited (Holmes and Richardson, 1999; Donath et al., 2003; Foster and Tilman, 2003; Makana and Thomas, 2004; Bischoff et al., 2006; Rosenthal, 2006) or recruitment limited (Clark et al., 1998, 1999; Midoko-Iponga et al., 2005), or both (Bakker and Berendse, 1999; Poschlod and Biewer, 2005).

Under either limitation, the species will not be able to re-establish as either the seeds do not reach the site to be restored or the the seeds cannot germinate or establish in situ. But for both cases, a successful dispersal of the species is the beginning of the reestablishment and a breakdown of the seed dispersal will lead to no successful regeneration even if the species was previously recruitment-limited. Even if some seeds reach the site through “natural” seed dispersal, supplemental broadcasting of seeds or planting of seedlings is recommended, and practised in restoration, to facilitate a speedy recovery of the site to be restored (Holmes and Richardson, 1999; Robinson and Handel, 2000; Makana and Thomas, 2004; Hooper et al., 2005). While this approach of supplemental broadcasting and replanting guarantees enough seeds, it is also the most costly, especially if larger areas need to be restored. In addition, the seeds broadcast should be from the same species, subspecies and ecotype to avoid the mix of two different ecotypes of the same species (Holmes and Richardson, 1999). This mixing proves to be another obstacle for supplemented broadcasting.

To avoid the complications of choosing the right ecotype of a species and at the same

time to lower the costs of the restoration, it is often necessary (and advisable) to rely on natural seed sources in the vicinity of the site to be restored (Holmes and Richardson, 1999; Rosenthal, 2006). These natural seed sources are often only small remnants of natural vegetation and in most cases they are not directly adjacent to the site to be restored. As most of the seeds are only dispersed relatively short distances (Bischoff, 2002; Donath et al., 2003; Rosenthal, 2006), it becomes essential to understand the seed dispersal process in more detail than when actively broadcasting the seeds. An understanding of the phenology of the seeds, seed dispersal vector (primary and secondary and probably even more) and expected seed dispersal distances is therefore essential to be able to employ this strategy successfully.

Methodologies to understand seed dispersal include seed trapping (Clark et al., 1998; Bullock and Clarke, 2000; Shiponeni, 2003; Skarpaas et al., 2004; Saura-Mas and Lloret, 2005), seed release (Tackenberg et al., 2003; Skarpaas et al., 2004; Soons et al., 2004), wind tunnel experiments (Jongejans and Schippers, 1999), determination of the seed dispersal vector through the phenology of the seeds (Willson and Traveset, 1992; Bonn and Poschlod, 1998; Bonn et al., 2000) or sampling of the soil seed bank (Holzel and Otte, 2003; Shiponeni, 2003; Devlaeminck et al., 2005), and phenomenological modelling (Greene and Johnson, 1996; Greene et al., 2004; Skarpaas et al., 2004, 2005) or methodological modelling (Nathan and Muller-Landau, 2000; Tackenberg et al., 2003). As outlined by Bullock et al. (2006), these methods can work together to provide better knowledge of seed dispersal of a given species and in general. This knowledge can be used, during restoration planning, to determine feasibility of relying upon an external seed source and expected dispersal into the restoration site.. If the seed dispersal is not sufficient to guarantee an adequate seed supply for the whole site, additional seeds can either be broadcast or used to establish “islands” or “nuclei” on the site (such islands or nuclei then act as seed sources for the whole site). However, it is often out of the scope of a restoration exercise to do a full dispersal study as this is very time-consuming. Therefore, it becomes essential to be able to draw conclusions from other studies, which focus on dispersal, for questions concerning restoration.

A number of studies have highlighted the importance of seed dispersal for restoration of altered habitats (alluvial meadows (Donath et al., 2003), central European grasslands (Bischoff, 2002), tropical rainforest (Holl, 1999) and low production vegetation types after top soil removal (Verhagen et al., 2001)) or isolated forest fragments (Jacquemyn et al., 2003). All authors concluded that the main reason of the poor recovery of these habitats are poor dispersal ability and limited (long-distance) dispersal of the target species.

Despite these findings, most of the seed dispersal models are not developed for applicability in restoration, rather for increasing the general understanding of seed dispersal and specifically of long-distance dispersal. Without doubt, these results are useful contributions for restoration ecology (e.g. Chambers and MacMahon, 1994), but actual evaluations of specific management strategies cannot be done with general seed dispersal models.

## 2.2. Invasion Biology

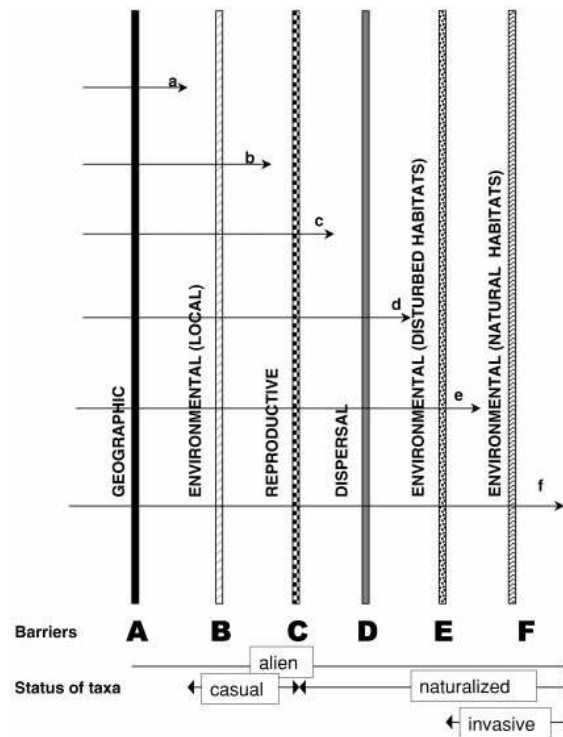
Alien invasive species are seen as one of the major threats to biodiversity (Global Invasive Species Programm, 2007; Richardson et al., 2004; Richardson and van Wilgen, 2004; Rouget et al., 2003) and the functioning of ecosystems (Holmes and Cowling, 1997; Wilcove et al., 1998; Mack et al., 2000; Ehrenfeld, 2003; Le Maitre et al., 2004; Richardson and van Wilgen, 2004; Samways and Taylor, 2004; Musil et al., 2005a; Arim et al., 2006; White et al., 2006). Apart from impacts on the ecosystems, invasive species also have socio-economic impacts and impacts on essential resources like water availability (see for example the Working for Water program in South Africa). Based on this importance of understanding the processes leading to invasions, the properties which make a species a successful invader and the properties which make an ecosystem susceptible to invasions, the field of invasion biology<sup>1</sup> has experienced a rapid growth in the recent years (Pyšek et al., 2004, 2006), which made a clear definition of the terms used necessary (Richardson et al., 2000; Pyšek et al., 2004). To clarify the classifications of invasive species, Richardson et al. (2000) developed a barrier model which describes the different barriers a species has to overcome before it can be considered an invasive species (Figure 2.1) and uses it to classify the species into “casual”, “naturalised” and “invasive”, depending on how many barriers they can cross. Richardson et al. (2000) and Richardson (2001) introduce six barriers limiting the spread of introduced plants (see Figure 2.1). If a species manages to overcome all these barriers, it is considered invasive. The barrier model can also be used to identify “fronts” on which a (potentially-) invasive species can be stopped or controlled. In both definitions (Richardson et al., 2000; Pyšek et al., 2004), the initial introduction of the species has to be based on human activities, intended or unintended. This means that natural range expansion is excluded from the definitions provided in both papers. In contrast to this, Vermeij (1996) argues for an integration of invasion biology, evolution and ecology and defines invasions consequently as “the geographical expansion of a species into an area not previously occupied by that species”, i. e. the expansion is independent from human activities. Petit (2004) even suggests defining alien invasions as introductions of alien genotypes or alleles. Following this definition, hybrids between alien and indigenous species have to be regarded as alien species (Vermeij, 1996). In this thesis, I will use, unless noted otherwise, the definitions by Richardson et al. (2000) and Pyšek et al. (2004).

The identification of potentially-invasive alien species, before they become invasive, became an important aspect of the field of invasion biology (Rejmánek, 2000), as a species which is invasive in one habitat is often invasive in another, (Kolar and Lodge, 2001;

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<sup>1</sup>The DST-NRF Centre of Excellence for Invasion Biology (2007) defines Invasive Biology as:

“... the study of both the species that become invasive in a system and their impacts on the system they have invaded, as well as the remediation of such invasions. Through studies in invasion biology scientists and practitioners hope to better understand, manage and mitigate the impacts of invasive species, and to prevent further invasions from occurring. This research helps scientists, conservation managers, and government agencies to understand and manage the impacts of invasive species.”



**Figure 2.1.:** A schematic representation of major barriers limiting the spread of introduced plants. Barriers can be separated in spatial barriers (A and D) which need to be overcome through dispersal and environmental / physiological barriers (B, C, E and F). Barrier A is usually overcome through intentional or unintentional human activities. For further details see [Richardson et al. \(2000\)](#). Figure reproduced with permission from [Richardson et al. \(2000\)](#)

[Richardson, 2004](#)), and thus lists of invaders are extremely useful to predict the invasiveness of alien species. An example is the one compiled by [Weber \(2003\)](#) (as reviewed by [Pyšek \(2004\)](#)) and the database BioFlor ([Kuhn et al., 2004](#)), which can be used to check if a species is already invasive elsewhere and also to identify new pattern and to predict invasiveness of a species. The investigation of the relationship between species characteristics and likelihood of invasiveness is promising, and [Kolar and Lodge \(2001\)](#) have shown a consistent pattern and relationships between species characteristics and likelihood of invasiveness. In addition, they also showed this relationship between certain properties of release events and the likelihood of invasiveness.

In addition to simply correlating invasiveness with plant properties, [Richardson and Rejmánek \(2004\)](#) show the importance of taxonomy by analysing invasive conifers which show a distinct bias towards the family Pinaceae and particularly the genus *pinus* having the majority of invasive species. [Richardson \(2006\)](#) highlights the importance of this “natural experiment”, started by the dissemination of 111 species of pines (genus *pinus*, family *Pinaceae*): “No other speciose genus of plants has yielded important insights on so many facets of invasion ecology.” Analysis of the invasiveness of these species and correlation with life history traits identified three traits which set the invasive species apart from the non-invasive species, namely potential of long-distance dispersal, high degree

of competitiveness and being able to survive and proliferate under different disturbance regimes.

A characteristic highlighted by several studies is an invader's ability to disperse over long distances (Richardson et al., 1987; Rejmánek, 1996; Saura-Mas and Lloret, 2005; Deckers et al., 2005). In their study, Deckers et al. (2005) highlight the importance of dispersal, which in their case (*Prunus serotina*) consists of short-range dispersal consistent with classic seed shadow models and long-range bird-mediated dispersal, which leads to establishment away from the seed source. This long-range dispersal is directed and therefore highly dependent upon the landscape structure. In another study, Buckley et al. (2005) show the importance of long-distance dispersal, juvenile survival and seedling establishment by using a modelling approach. They also show that, despite incomplete data, useful results can be obtained for management.

In addition to investigating the invasive species, it is important to understand the invasability of an ecosystem by invaders (Prieur-Richard and Lavorel, 2000). They argue that in addition to being able to identify characteristics of invadable ecosystems, an understanding of the mechanisms underlying the impact of the ecosystem's species diversity on the invasability is required, as this understanding would help in the control and prevention of invasions.

The understanding of what makes a species a successful invader is transferable to the control of already-invasive species (Richardson et al., 2004). This control can address the spread at different life stages of the invader i.e. seed production (Hoffmann et al., 2002; Impson et al., 2004), dispersal (Donnelly and Hoffmann, 2004; Impson et al., 2004; Gosper et al., 2005), establishment (Buckley et al., 2005), or survival of adult plants (Hoffmann et al., 2002; Ding et al., 2006). Different alien control measures can be employed at the different life history stages, e.g. manual clearing (Cione et al., 2002; Midoko-Iponga et al., 2005; Musil et al., 2005b) or chemical clearing (Cione et al., 2002; Midoko-Iponga et al., 2005; Musil et al., 2005b; Ogden and Rejmanek, 2005), burning (DiTomaso et al., 2006) or biocontrol agents (Lesica and Hanna, 2004; Center et al., 2006), or a combination of various approaches (Paynter and Flanagan, 2004). In general, it can be more cost-effective to avoid the spread than to clear the established plants. It is therefore important to target the seed for destruction through e.g. biological control agents (Donnelly and Hoffmann, 2004; Impson et al., 2004), before germination and successful establishment.

As in the case of restoration, models can play an important role in assessing if the management action will have the planned impact on the spread of the invasive species. As discussed above, seed dispersal (barrier D in Richardson et al. (2000)) is one of the main determinants of spread and should be incorporated into these models. Nehrbass et al. (2007) uses an individual-based model, which is based upon aerial photographs, to analyse the spread of *Heracleum mantegazzianum*, which showed that the small fraction of seeds being dispersed over long distances has a over-proportional effect on the spread. But in addition to the seed dispersal itself, seed production is also an important factor which determines the spread of a species: Dauer et al. (2007) use an empirical model and show

that a high infestation, which is equivalent to a high seed production per area, increases the dispersal distances dramatically. Depending on the dispersal vector, another factor becomes important: [Deckers et al. \(2005\)](#) show that spread of bird-dispersed seeds of black cherry (*Prunus serotina*) is influenced by landscape structure because of directional long-distance dispersal by birds. These examples demonstrate that many different factors, and therefore parameters, influence the dispersal of seeds. But [Buckley et al. \(2005\)](#) make an important point in their paper: that despite uncertainty in certain parameters, robust predictions can be made about the impact of factors and parameters on the spread of a species. Based on these predicted impacts, management plans can be developed and their impacts tested in the model.

### 2.3. Commonalities and Differences — how one can inform the other

A number of authors emphasise that a closer cooperation between invasion biology and plant ecology ([Davis et al., 2005](#)), community ecology ([Shea and Chesson, 2002](#)) and even biological control ([Ehler, 1998](#)) would be advantageous for each discipline, as this would result in improved understanding and avoidance of duplication of studies. [Davis et al. \(2005\)](#) even state that the missing cross-referencing between the disciplines of invasion biology and plant ecology is detrimental for both disciplines.

It is possible to make the same case for invasion biology and restoration ecology. Nevertheless, only a few papers deal with the integration of the two and the possibilities of cross-referencing. One of the few papers linking invasion biology with restoration ecology discusses cases where the removal of alien invasive species would threaten indigenous species or where it is useful to consider aliens as a part of the restoration plan. However, they only consider the possibility of including alien species in the restoration plan instead of removing them immediately.

[D’Antonio and Meyerson \(2002\)](#) suggest building “a framework for the consideration of invasive species in ecological restoration”, which is a step in the right direction, but does not include cross-referencing between these fields of study and their respective theories. To illustrate the possibility of cross-referencing between these two disciplines, one can use the spread of species as an example. Both disciplines deal with spread as they want either to prevent (invasion biology) or facilitate (restoration ecology) the spread of their respective target species. Both disciplines are in need of dispersal data to be able to accomplish their goals. The type of information they need is quite similar, i. e. information about dispersal distances, shape of the dispersal kernel, resulting spread pattern and the dependence of the spread pattern on processes ranging from dispersal to establishment and seed production.

The opposite aims are no obstacle in using information from the other discipline to supplement their own expertise. Nevertheless, no study has investigated the suitability of linking alien invasive studies investigating dispersal and spread to restoration and vice versa. This is surprising when considering that the academic goal of both invasion ecology



and restoration ecology is to understand population processes. The ultimate management goal of invasion and restoration ecologists is to restore self-maintaining, resilient biotic communities. In this regard, the goals are very similar, even though the aims concerning their respective target species are different.

How the results and understanding in seed dispersal obtained in one field can be applied to the other depend on the type of information gathered and required. If a basic understanding of seed dispersal in the context of restoration ecology or invasion biology is needed, the conversion of results from one discipline to the other is relatively straight forward as they are governed by the same principles. If, on the other hand, more problem-oriented information is needed, or available from the other discipline, the results need to be translated from one discipline to be applicable to the other. Depending on the context of the kind of information needed and the type of information available, this can include translation of the framework and conditions under which the study was conducted, transfer from one species to another or interpretation of the external processes influencing the observed dynamics (e.g. management interventions). Consequently, the complexity of the translation process depends on the information collected, its context and the system to which it should be applied, yet, as will be shown in this thesis (Part IV), important and useful information can be obtained in each direction for the two disciplines.

An important aspect of these two disciplines is urgency: both are faced with the need for fast action and cannot afford to lose too many resources, or too much time and money in research instead of tackling the actual problem. Cabin (2007) discusses this problem in detail for restoration ecology and suggests that in the interest of actual restoration of degraded ecosystems, fewer resources should be allocated for traditional research into restoration and rather used in actual restoration measures. This view is disputed by Giardina et al. (2007), who justify traditional research approaches in restoration ecology as they assist in the planning and implementation of the actual management plan. Nevertheless, if restoration or invasion control can save resources, these resources can be allocated for the actual management implementation. One aspect, the cross-fertilisation between invasion biology and restoration ecology, is already outlined above. A second aspect is the use of ecological models. Modelling, especially in this context, has several advantages, ranging from identifying critical processes (Buckley et al., 2005), to optimising research design (Skarpaas et al., 2005), to estimating parameters (Gilioli and Pasquali, 2007) and, last but not least, to increasing understanding of the system and the processes involved. Looking at seed dispersal and spread modelling, one can identify essentially two types of seed dispersal models: mechanistic models, which try to predict the dispersal distances based on properties of the seed and their dispersal vectors, and phenomenological models which simply describe the seed dispersal kernel by using statistical functions whose parameters are fitted to the observed seed rain. Both of these have their advantages and disadvantages, which relate to their data requirements and their ability to predict the seed rain outside the observed distance range (for a more detailed discussion of these two types see Chapter 6).

A range of different models, from diffusion-type models (Almeida et al., 2006), integrodifference equations (Kot et al., 1996) to individual-based models which simulate the flight of individual seeds and take turbulences into account (Tackenberg, 2003; Tackenberg et al., 2003) have been used in dispersal and spread modelling. It is impossible to say which models are better suited for invasion and restoration as it depends on the availability of data, the dispersal syndromes and, last but not least, the question asked.

It is important to note that most of the publications which address questions concerning dispersal, are more general papers about dispersal (for example (Clark, 1998; Nathan et al., 2002; Higgins et al., 2003; Skarpaas et al., 2004; Nathan and Katul, 2005; Skarpaas et al., 2005; Nathan, 2006, and others)). These studies provide invaluable insight into the process of dispersal and spread, which can be used in restoration ecology and invasion biology. Nevertheless, specific questions can only be answered with specific models—models which are build to address a certain question. An example is Higgins et al. (1996), who developed a model to address the question of the impact of plant and environmental attributes on the spread of alien pine trees. They were able to quantify the impact of juvenile periods, fecundity and dispersal distances on the velocity of invasion. In addition, they compared two different model types, a reaction-diffusion model and a spatially-explicit, individual-based simulation model, and were able to compare the results. This design of a model which combines a specific situation, here the spread of pines in Fynbos, with generality, provides an approach which will be able to address management questions but also obtain results which are important for other disciplines.

In this study, I introduce a seed dispersal model that, with slight modifications, is being applied to address questions in invasion biology and restoration ecology. In invasion biology (Part II), the model will be used to assess the effects of two biocontrol agents on the spread of *Hakea sericea*, an invader of pristine Fynbos. In the context of restoration ecology (Part III), the model is used to investigate the conditions required for the shrub *Dicerothamnus rhinocerotis* to successfully spread onto an old field covered by a creeping grass species, *Cynodon dactylon*. For both models, outcomes and conclusions are explored and management recommendations, based on the results, are drawn. Both models highlight the importance of seed availability and long-distance dispersal for the velocity of spread. In Part IV, commonalities and differences between these two applications are explored and potential cross-fertilisations are examined.



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## **Part II.**

# **Dispersal Modelling for Invasion Control**



### **3. *Hakea sericea*: development of a model of the impacts of biocontrol on population dynamics and dispersal**

*The question of whether the biocontrol agents have an impact on the spread of *Hakea sericea* and if it is possible to quantify these, was raised by David le Maitre (CSIR). The availability of data was discussed at a workshop, attended by the other co-authors. The dispersal kernel estimates were provided by experts (Dr Brian van Wilgen, CSIR, (BW), Dr David Le Maitre, CSIR (DM), Prof Dave Richardson, CIB SUN, (DR), Prof John Hoffmann, UCT, (JH), Dr Anthony Gordon, ARC-PPRI, (TG)). Distribution functions were fitted using a maximum likelihood approach. The dispersal kernels and the other parameter values chosen were discussed and confirmed in a group workshop.*

*My contribution to this paper was the development of the dispersal model with the data provided by other researchers and interpretation of results together with Dr David Le Maitre. In addition to developing the model, running simulations and analysing the results, I wrote the parts relating to the methods of the model, contributed to the results section and provided input to the other sections.*

*This paper has been authored by David C. Le Maitre (CSIR), Rainer M. Krug (University of Stellenbosch), John H. Hoffmann (University of Cape Town), Anthony J. Gordon (Agricultural Research Council, Plant Protection Research Institute), Theresa N. Mgidi (CSIR). The senior author, Dr. David Le Maitre, agreed that this paper could be included in my PhD as a chapter. It has been accepted by Ecological Modelling. The title is “*Hakea sericea*: development of a model of the impacts of biocontrol on population dynamics and dispersal”. The chapter reflects the paper as accepted and only editorial changes were made in the text.*

#### **3.1. Abstract**

This paper reports on the development and testing of a simulation model to assess the impacts of two seed-feeding biological control agents on the dispersal of an invasive perennial tree, *Hakea sericea* (Proteaceae), which was introduced into South Africa from Australia during the 1850s. The agents are known to reduce seed banks at the individual plant level but the population-level effects are not well understood. The aim of the study was to estimate the extent to which the biological control has reduced the population growth and rate of spread of this species. *Hakea sericea* is a serotinous species which releases its

wind-dispersed seeds en masse when the parent plants are killed, usually by fire. Field data were used to develop functions describing the fecundity of the plants and the impacts of the biological control agents as well as seedling recruitment rates and density-dependent mortality. A group of “experts” provided estimates of the cumulative proportion of seeds that would disperse over distances from 50 to 1 000 m following a fire. The estimates were used to fit various long-range dispersal functions. Of these functions, the Weibull distribution gave the overall best fit and this was used to generate parameter sets from each expert’s estimates of dispersal. Simulations were then run using a reasonable range of fire intervals and dispersal parameters for the two experts whose estimates represented the minimum and maximum dispersal distances. Biological control agents have reduced the seed loads on *H. sericea* plants by more than 95%. This, in turn, reduced population growth rates, maximum seed dispersal distances and the formation of new invasion foci. Population growth rates and spread rates were positively correlated because greater dispersal distances resulted in lower densities and, thus, lower levels of density-dependent mortality. Numerous previous studies have found that biological control can limit population growth rates of invasive plants, but this is one of the few studies to have estimated the impacts on the invasion rates and to use an individual-based modelling approach to estimate population level effects.

**Keywords:** *Hakea sericea*; South Africa; biological control; population dynamics; seed dispersal; Weibull distribution; fire frequency; seed banks

## 3.2. Introduction

The effectiveness of seed-feeding biological control agents against invasive plant species has been questioned because excessively high levels of seed destruction are needed, supposedly, to reduce the density and overall abundance of the target weed (e.g. Myers and Risley, 2000). For many plant species, natural losses during the seed-seedling transition frequently exceed 95% (Salisbury, 1942; Harper, 1977). Therefore, plant populations are generally limited by factors other than seeds and seed-feeding insects may be achieving nothing more than destroying seeds that would be lost at a later stage anyway. Biological control agents may even have a detrimental impact if they increase the survival rates of seedlings by, for example, reducing post-establishment thinning due to intra-specific competition (Myers and Risley, 2000). Evidence from biological control programmes is equivocal. For example, a 99.7% reduction in seed production of *Sesbania punicea*, due to the combined damage caused by two species of biological-control agents, resulted in only a marginal decline in population densities of the host plant, despite it having relatively short-lived seed banks (Hoffmann, 1990; Hoffmann and Moran, 1998). Conversely, Rees and Paynter (1997) found that even a 75% reduction in seed production could have a significant impact on the overall abundance of *Cytisus scoparius*.

Moran et al. (2004) have countered these arguments by suggesting that biological control agents that limit viable seed production can be effective in other ways, such as when

combined with other control measures to deal with adult plants or during follow-up operations to deal with seedlings in previously-cleared areas. Lower seedling densities can make control operations less costly and more efficient by allowing less expensive or less manpower-intensive control methods to be used. Seed-feeding agents can also prevent conflicts of interests by enabling those who wish to use the plant to do so whilst minimising seed production in uncultivated populations (Dennill and Donelly, 1991). Limiting seed production may also reduce the dispersal of the weed species making it a less successful invader (Van Klinken et al., 2004), but the magnitude of this potential reduction has not yet been quantified.

One of the earliest biological control programmes to use agents that reduce seed production against a perennial alien plant invader was initiated against *Hakea sericea* Schrad. & J.C. Wendl. (Proteaceae) in South Africa in 1970. A key characteristic of *Hakea sericea* is its extreme serotinous habit: all of its seeds are retained in pairs in tough woody follicles which accumulate along the branches throughout the life of the plant. The wind-dispersed seeds are released en masse when the parent plant dies and the follicles dehisce, usually as a result of fires (Richardson et al., 1987b). The terminal velocity of the winged seeds has been measured at 1.03m/sec in calm air and plants seldom exceed 5m in height so most seeds will fall within tens of metres of the parent plants (Richardson et al., 1987b). However, some of the seeds may be blown for considerable distances (kilometres) by the prevailing south-easterly winds, which are unusually strong for a Mediterranean climatic region (Deacon et al., 1992) but are characteristic of the coastal regions of the Western Cape during the warm, dry summer months. Continuous spells with mean velocities of 25–32km/hr (6.9–8.9m/sec), with gusts reaching twice these speeds, are frequent and can last for periods of several days. In this region, *Pinus radiata*, which has seeds that are morphologically similar to *Hakea* species, commonly disperses more than 1km from source (Richardson and Brown, 1986). It is likely that long-distance dispersal models for pines, such as those developed by Ledgard (2001); Clark (1998); Clark et al. (1998); Nathan et al. (2001), are applicable to *Hakea* species as well. Such long-range dispersal allows the plant to rapidly invade new areas by establishing founder colonies or foci far from the parent stands (Moody and Mack, 1988), making it difficult to control.

*Hakea sericea* is considered one of the most aggressive invasive species of the Cape fynbos vegetation, where it thrives particularly on nutrient-poor, sandy soils in the Cape Mountains (Fugler, 1979; Richardson, 1984; Richardson et al., 1992). It is thought to have been introduced in 1858 to a botanical garden in Cape Town and was later planted in the mountain areas, often as a hedge around livestock enclosures (Neser and Fugler, 1983; Shaughnessy, 1986; Richardson et al., 1992). It spread very rapidly from these original plantings and by 1978 it had invaded almost 4800km<sup>2</sup> of land originally covered in “montane fynbos”, including remote areas where control operations would be prohibitively expensive (Neser and Fugler, 1983; Kluge and Richardson, 1983; Macdonald, 1984; Shaughnessy, 1986). Although *Hakea sericea* was promoted far less than other *Hakea* species, it has invaded by far the greatest area, emphasising its invasiveness (Richardson et al., 1992).

Although there was a considerable effort to control *Hakea* in most of the affected areas, it soon became evident that mechanical control programmes would not succeed on their own. As a result, 1970 saw the introduction of two seed-destroying biological control agents against *H. sericea* in South Africa: a weevil, *Erytenna consputa*, whose larvae develop in and destroy the immature fruits; and a carposinid moth, *Carposina autologa*, whose larvae destroy the ripe seeds in fully-formed follicles (Kluge and Naser, 1991). Both agents have become widespread and abundant and have been credited with having at least some success in reducing the status of *H. sericea* as a weed (Kluge and Naser, 1991; Gordon, 1999). However, extensive thickets of the weed persist in many areas (Te Roller, 2004) and *H. sericea* still accounted for 56% of the costs of controlling alien plants in the Western Cape during 2002/03 (Marais et al., 2004). These contrasting observations suggest that the biological control agents have curbed the invasiveness (i.e. the rate of spread) of *H. sericea* during the last four decades, but that they have not been able to reverse the invasion in already-affected areas.

It has proved to be practically impossible to determine empirically the effect of biological control agents on the rates of spread of invasive species and doing so remains an intractable problem (Van Klinken et al., 2004). An alternate way of gaining an understanding of the dynamics of these systems is to use simulation models. This paper describes the development, parameterisation and testing of a stochastic, individual-based spatio-temporal simulation model to compare population growth and spread rates of *H. sericea* over a series of generations (induced by fires), with and without the biological control agents. As the interest was mainly in the spread of *H. sericea*, the model was optimised for long-distance seed dispersal. Dynamics within stands were not modelled in detail except for density-dependent mortality of seedlings and young plants. Many studies have reported on the impacts of biological control on seed bank dynamics (e.g. Dennill and Donnelly, 1991; Rees and Paynter, 1997; Hoffmann and Moran, 1998; Shea, 2004; Paynter, 2005) but few have assessed the impacts on dispersal (e.g. Neubert and Parker, 2004; Shea, 2004) and, as far as we know, none have used an individual-based model to assess population level impacts, particularly the rate of spread.

### 3.3. Methods

#### 3.3.1. Field methods and available knowledge

##### Field sites and sampling methods

Six survey sites (Table 3.1) were selected opportunistically by finding *H. sericea* stands in which there had been a “natural” fire event within the previous year. The sites were first visited after the onset of rains following the fire, when all of the surviving *H. sericea* seeds had germinated and become small seedlings. Straight-line transects were laid at random intervals through portions of the burnt patches and metre square plots were set out at intervals of 5m along each transect, as used by Bond et al. (1984). During the first survey



at each site, the number of dead pre-fire adult (parent) plants within each metre square was recorded (the adult plants are killed by fire but remain standing for a number of years after the fire). The parent plant closest to each 5m interval point along a transect was located. Its basal stem diameter was measured and the number of dehiscent seed follicles was counted. These counts were used to determine the number of seeds/m<sup>2</sup> that had been shed by the parent plants. The number of seeds was estimated by doubling the average number of follicles per plant (to account for the two seeds per follicle) and multiplying the result by the average number of plants/m<sup>2</sup>.

Seedling recruitment levels were estimated from field surveys at each of the field sites by counting the number of seedlings within each sqm. The measure of seed density relative to seedling density was used to estimate overall post-dispersal seed mortality. Although some seeds would have been lost through long-range dispersal from the parent plants, this loss was assumed to have been balanced by immigration of seeds into the sample plots from other plants nearby. The sites were revisited annually, up to four times after the initial visits, to monitor the survival, growth and fecundity of the new generation of plants. The total number of plants within the sqm was recorded and the height of the plant closest to the transect point was measured to gauge growth rates of the plants. Counts were then made of fruits that had been produced by any of the young plants within the metre-square plots.

### Impact of biological control on fruit load

A number of seed-destroying insects were introduced to control *Hakea sericea*, two of which have been particularly successful (Kluge and Neser, 1991; Gordon, 1999). The weevil *Erytenna consputa* Pascoe lays its eggs on the young follicles and its larvae destroy a percentage of the current year's seed crop (its mnemonic is thus YFF). The percentage of follicles that are destroyed increases as the age of the *Hakea* population increases because the weevils are slow to colonize plants that are regenerating after fires (Gordon, 1999) (Table 3.2). The seed-feeding moth *Carposina autologa* Meyrick lays its eggs on the mature follicles of all ages, selecting only for its preferred (knobbly) form and ignoring whether or not the follicle has already been damaged (Gordon, 1993, 1999) (its mnemonic is thus MFF). The larvae tunnel into the follicle and destroy the seeds. The proportion of the destroyed mature follicles from a given year also increases with time because the MFF continues laying eggs on follicles of all ages (Table 3.2). The figures for the MFF are, therefore, the cumulative percentage of all the old follicles on the plant that would be destroyed. This is most easily understood with an example. The MFF arrives early in year 5 by which stage a mature *H. sericea* plant may have 100 mature follicles which have escaped destruction by the YFF. During year 5 the MFF will destroy 1% of those 100 leaving 99. In year 6 the plant adds 60 more mature follicles which escape the YFF making the new total 159. The MFF now destroys 2% of the 159, leaving about 154 mature follicles, and so on.

To estimate the impact of *Erytenna consputa* (YFF) on the fecundity of *H. sericea*,

**Table 3.1.:** Site information, dates of fire occurrences, dates of first and last visits, and transect details for *Hakea sericea* infestations monitored after fires between 1998 and 2000. Annual rainfall data supplied by R. Wentzel (AgroMet, Institute for Soil, Climate and Water, Stellenbosch; personal communication 2006). Rainfall season: s = summer, w = winter.

Site Names	Geographic location & vegetation type	Annual rainfall (mm) & season	Dates when fires occurred	Dates of first & last visit	No of transects	Transect lengths (m)
Slanghoek Western Cape	33 36.0° S 19 13.7° E Fynbos	1346 w	Jan 1998	Oct 1998 Jun 2002	2	250
Stettynskloof, Western Cape	33 52.0° S 19 21.2° E Fynbos	680 w	Feb 1999	Dec 1999 Jun 2002	2	250
Welwerdiend, Western Cape	33 39.9° S 19 12.5° E Fynbos	641 w	Feb 2000	Nov 2000 Jun 2002	2	125
Goudini, Western Cape	32 40.1° S 19 12.5° E Fynbos	616 w	Feb 2000	Nov 2000 Jun 2002	2	125
Grahamstown, Eastern Cape	33 19.9° S 26 34.8° E Grassy Fynbos	630 s	Nov 1999	Mar 2000 May 2003	4	50
Kareedouw, Eastern Cape	33 56.2° S 24 15.8° E Fynbos	698 s	Oct 1999	Mar 2000 Mar 2001	4	65

counts were made on follicle loads on plants at several sites. At least 20 plants were randomly selected at each of 29 sites in the Cape Province, including the six sites in Table 3.3. For each plant, the basal stem diameter was measured and the number of mature follicles on the plant was recorded. Basal stem diameters were converted to basal stem areas which were used to plot linear regressions of fruits against basal stem area for each plant. This relationship was compared with one from Australia (where *H. sericea* occurs naturally) and one from South Africa that was obtained from a population before biological control had been implemented (Fugler, 1979). Reductions in follicle (seed) production were calculated by comparing relationships between plant size and the number of follicles from the post-biological control counts with the pre-biological control counts.

The biological control agents are either killed (immature stages) or disperse (adults) during fires. Adults move back into the burnt areas when the plants reach a suitable stage of development to support the insects. This process can be hastened by making deliberate manual reintroductions of the insects but the values used in this study are based on the

**Table 3.2.:** Maximum percentage destruction of follicles by both agents based on surveys at a range of field sites (T Gordon and J Hoffmann unpublished data).

Years after fire	Young follicle feeder (% of new follicle production destroyed)	Mature follicle feeder (% of total number of follicles destroyed)
4	1	0
5	10	1
6	40	3
7	60	10
8	80	25
9	99	40
10	99	60
11	99	80
12 and older	99	80

assumption that the agents have recolonised by themselves and that there is minimal delay between the onset of fruit production and the arrival of the agent. The agents are assumed to spread rapidly throughout the simulated stand and to have a uniform impact on the *Hakea* plants.

## Fire

Studies of the regeneration requirements of the tall, seed-regenerating shrubs of the Proteaceae (Kruger and Bigalke, 1984; Van Wilgen et al., 1992; Le Maitre, 1999) indicate that fires occurred naturally in fynbos at intervals of about 10–20 years. Fires are necessary to rejuvenate fynbos ecosystems which would otherwise become moribund, with the exception of limited areas where forest vegetation can establish itself (Le Maitre and Midgley, 1992; Manders and Richardson, 1992). Most fires occur in summer and autumn, whether from natural causes or human action, with prescribed management fires occurring mainly after the first winter rains to minimise the risk of losing control of the fire (Van Wilgen et al., 1992; Richardson et al., 1994). The simulated fires were assumed to occur in autumn, which is the season when recruitment of the ecologically similar seed-regenerating indigenous Proteaceae shrubs is the most successful (Bond et al., 1984, 1995).

### 3.3.2. Model structure

The description of the HakSimSpread model follows the ODD protocol suggested by Grimm et al. (2006) where ODD is an acronym based on the major sections of the description, namely: Overview; Design Concepts; and Details. The aim of the protocol is to provide a framework which makes it easier to understand the model and covers all the relevant aspects required for a comprehensive description of an individual-based model. The standard sequence in which the different aspects are presented makes it easier to locate particular information.

**Table 3.3.:** Data for *Hakea sericea* stands and plants from selected populations which were sampled after fires. For more information on the study sites see Table 3.1.

Site	Density	Basal area	Fruits	Seeds		Seedlings	
	<i>plants/m<sup>2</sup></i>	<i>mm<sup>2</sup></i>	<i>1/plant</i>	<i>1/m<sup>2</sup></i>	<i>1/plant</i>	<i>1/m<sup>2</sup>year</i>	<i>1/seed</i>
Slanghoek	0.30	7.40	63.00	35.30	117.67	9.40	0.27
Stettynskloof	0.20	13.20	54.20	20.10	100.50	1.00	0.05
Grahamstown	0.40	10.70	48.80	39.00	97.50	5.40	0.14
Kareedouw	0.20	6.80	4.50	1.60	8.00	0.00	0.00
Goudini	0.80	11.80	86.60	135.10	168.88	1.96	0.01
Welverdiend	3.40	5.00	7.90	53.00	15.59	1.20	0.02

**Table 3.4.:** Parameter values for different processes. ZOI stands for Zone of Influence.

Process	Value
Parameter	
Species Parameter	
Relative ZOI radius	2.2
Competitiveness	1000
GERMINATION & ESTABLISHMENT	
Establishment probability	0.04
Maximum establishment up to competition of	0
Zero establishment at competition higher then	1
SEED PRODUCTION	
FIRE	
Fire interval	7, 9, 11, 20
SEED DISPERSAL	
Seed dispersal kernel	Weibull, parameter see Figure 4.3

## Overview

*Purpose:* The purpose of the model is to model the pattern of spread of *Hakea sericea* invasions under different scenarios. To keep the model tractable and to facilitate interpretation of the outputs, the environment in the model is assumed to be homogeneous with respect to seed dispersal and germination, seedling recruitment and seed production, and no interactions with other species occur.

*State Variables and Scales:* HAKSIMSPREAD is an individual-based spatiotemporally-explicit stochastic single-species simulation model which was developed in Delphi 7. It consists of three hierarchical levels, namely the individual plants, the species (a single one, in this case) and the simulated patch with a size of 1km×1km. A grid (cell size 1m×1m) is used to model the interactions between individuals, i.e. competition and seed dispersal. Individuals are characterised by their location on the grid (x and y coordinates). Species-specific parameters characterise the life history and competitiveness (Table 3.4). The simulated patch is considered to be spatially homogeneous, i.e. conditions are the same across the patch and do not change in space or time. Seeds dispersing out of the simulated landscape are lost from the simulated domain and plants occurring outside the

simulated landscape have no competitive effects on plants within the simulated landscape.

*Process Overview and Scheduling:* The simulation model consists of four processes, namely GERMINATION & ESTABLISHMENT, SEED PRODUCTION (including the impact of the biocontrol agents), FIRE (releasing seeds from the plant) and SEED DISPERSAL, which are executed in that order. Processes act on either the individual plant or on the seeds. The Competition Grid links the species and brokers the interaction between plants. The parameters and their initial values are shown in Table 3.4.

One time-step represents one generation, namely from seed germination to adult plant death during a fire. Therefore, it is equivalent to the fire recurrence interval.

Plants exert a certain amount of competition into their neighbourhood. The degree of competition experienced in a cell is caused by all other plants on the grid and is stored in the Competition Grid. The degree of competition experienced by an individual plant is indifferent to the individual causing the competition. The GERMINATION & ESTABLISHMENT process is influenced by the competition to which the seedling is exposed and, in return, these processes update the Competition Grid. As all plants die during the process FIRE, the Competition Grid is reset to zero.

## Design Concepts

*Emergence:* The life cycles of the individual plants are modelled using empirical rules and probabilities from which the spatial pattern of the simulated patch emerges.

*Sensing:* It is assumed that individual plants are affected by the relative competitiveness to which they are exposed. In addition, it is assumed that seedlings experience the competition in the location in which they have germinated.

*Interaction:* Interaction among individuals is modelled through competition following the FON approach (Field of Neighbourhood) described by Berger and Hildenbrandt (2000). Each plant experiences a certain amount of competition, depending on its species, in its neighbourhood. This is called the Zone of Influence (ZOI) (Czárán, 1998; Berger and Hildenbrandt, 2000). The size of the ZOI is determined by the size of the plant itself and a constant factor specific to the species,  $ZOI_{rel}$  the “relative ZOI radius”. The strength of the competition within this ZOI, the FON, is not constant, but is dependant on the distance  $r_p$  from the location of the plant following:

$$FON(r_p) = \begin{cases} r_p \leq r & \text{Comp} \\ r < r_p < r \cdot ZOI_{rel} & \text{Comp} - (r_p - r) \frac{\text{Comp}}{r(ZOI_{rel} - 1)} \\ r_p \geq r \cdot ZOI_{rel} & 0 \end{cases} \quad (3.1)$$

Where  $r$  is the radius of the cover of the plant and  $\text{Comp}$  is the maximum competitiveness of the species. As we are dealing with a one-species system, and the absolute value of  $\text{Comp}$  is only important in multi-species system in which it describes the relative competitiveness from one species to the other,  $\text{Comp}$  is arbitrarily set to 1000. The FONs of all plants are

superimposed to obtain the competition at each given point  $(x, y)$  in space:

$$F(x, y) = \sum_N \text{FON}_n(x, y) \quad (3.2)$$

and finally  $F(x, y)$  is stored in a grid which is updated by the processes FIRE and GERMINATION & ESTABLISHMENT.

*Stochasticity:* HAKSIMSPREAD is a stochastic simulation model — the processes SEED DISPERSAL and GERMINATION & ESTABLISHMENT are stochastic, while SEED PRODUCTION is deterministic to reduce the complexity of the model. SEED DISPERSAL is modelled based on probability density functions for the distance and directions in which the seeds disperse. GERMINATION & ESTABLISHMENT are founded on probabilities of germination and establishment, however, the establishment probabilities are modified according to the competition to which the seedling is exposed. The order in which the individuals are evaluated in the different modules follows the order in which they were created during the simulation (in most cases this coincides with the age of the plants).

*Observation:* After completion of each time step, the location of each individual is saved and is later analysed.

## Details

*Initialisation:* The simulation is initialised with empty cells except for one individual established plant in the centre cell. This individual forms the initial seed source for the spread.

*Input:* The inputs in the model are the selected fire frequencies. As one time-step in the model represents one fire cycle, the fire cycle only impacts the number of seeds produced per time-step. The longer the cycle, the more seeds are produced. In addition, the number of seeds produced also depends on the biocontrol agents present (see section 3.3.1).

## Sub-models of HakSimSpread

**Germination & Establishment:** The process GERMINATION & ESTABLISHMENT includes two separate sub-processes: germination and establishment. Germination takes place every time-step and, as the species has no dormancy (Richardson et al., 1987b), it is assumed that all seeds germinate immediately after the first substantial rainfall event that follows dispersal. Germination is characterised by a vector which relates the probability of germination to the age of the seed so that older seeds have poorer germination.

Density-dependent thinning occurs during the second phase of the process, establishment. The probability of establishment is based on a maximum probability of establishment when no competition is experienced. The impact of competition on the maximum establishment is characterised by two parameters. One parameter specifies the level of competition at which there is no effect on a seedling in a cell and a second parameter specifies the level of competition which results in the death of the seedling, reducing the

probability of establishment to zero. The probability of establishment decreases linearly between these two values.

**Seed Production:** Seed production was assumed to be deterministic and only dependent on the age of the plant. Seed production per generation, therefore, depends on two factors: the simulated fire frequency and the biocontrol regime to which *H. sericea* is exposed. The longer the interval between two fires, the more seeds are produced and accumulated on the plant (Figure 3.1). The field data described above were used to define the relationship between seed production and accumulation and post-fire age, giving the number of seed produced per plant for a given fire frequency.

The biocontrol agents destroy a certain proportion of the seeds produced as described earlier. The model allows us to assess the impacts of: no biocontrol; Young Follicle Feeder (YFF); and Mature Follicle Feeder (MFF); and calculate the number of seeds per plant under different biocontrol treatments (Figure 3.1).

**Fire:** Fire kills all the existing *H. sericea* plants. The seeds are released from the seed bank on the plant as the dead plants dry out. The viability of the seeds is not reduced by the fire in accordance with the findings of Richardson et al. (1987b). By combining the four fire frequencies (7, 9, 11 and 20 years) with the four possible biocontrol treatments (YFF, MFF, YFF & MFF, NONE), we can get 16 different sizes of the seed bank at the time of the fire (Figure 3.1).

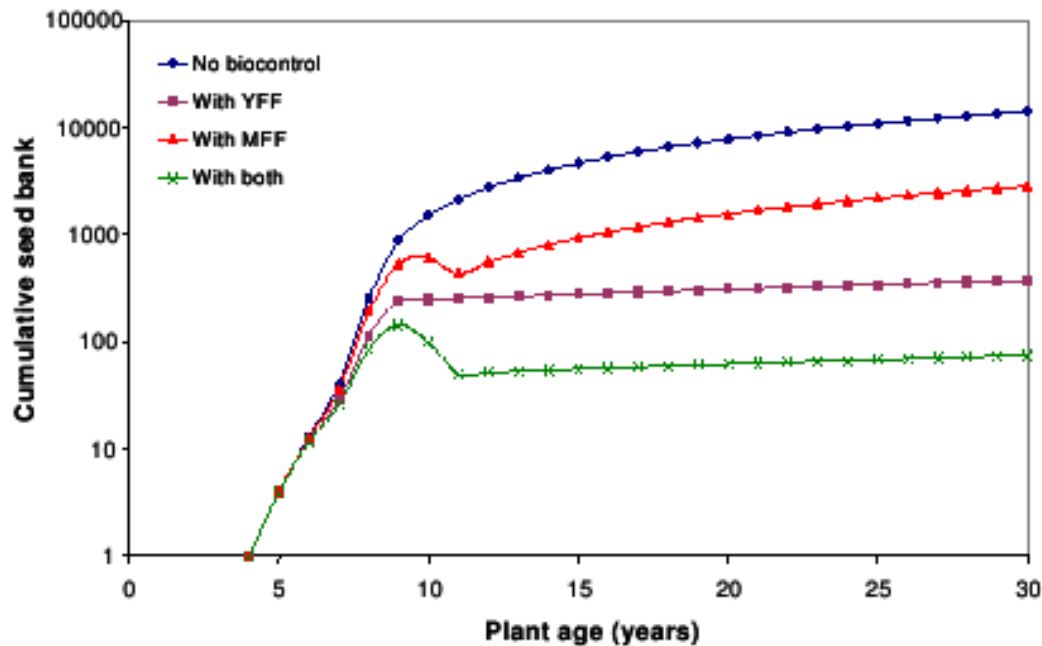
**Seed Dispersal:** Seed dispersal is modelled stochastically using the probability distribution specified in the seed dispersal kernel for an individual plant. Six Weibull kernels were chosen based on expert estimates. Five parameter sets are based on individual expert estimates, while the sixth represents the average of these estimates.

## 3.4. Results

### 3.4.1. Fecundity

Data on the relationship between plant age and fecundity are sparse but the limited data show that the number of seeds (follicles) per plant generally increases with increasing basal area (Table 3.3). The juvenile period of *Hakea sericea* is about three years (Table 3.5). Simulated seed production begins in year 3 and reaches an annual seed production of about 630 seeds/yr by eight years of age. This level is maintained up to an age of 30 years. The number of seeds stored in the follicles on the plant increases rapidly with increasing age (Figure 3.1). The high seed numbers are confirmed by field observations that old plants without biological control can have very large numbers of closed follicles and high seed loads (J. Hoffmann and T. Gordon, unpublished data). There is no evidence of a density-dependent reduction in the number of follicles (fruits) per plant except at the Welverdiend site where the densities were an order of magnitude greater than at the other sites (Table 3.3).





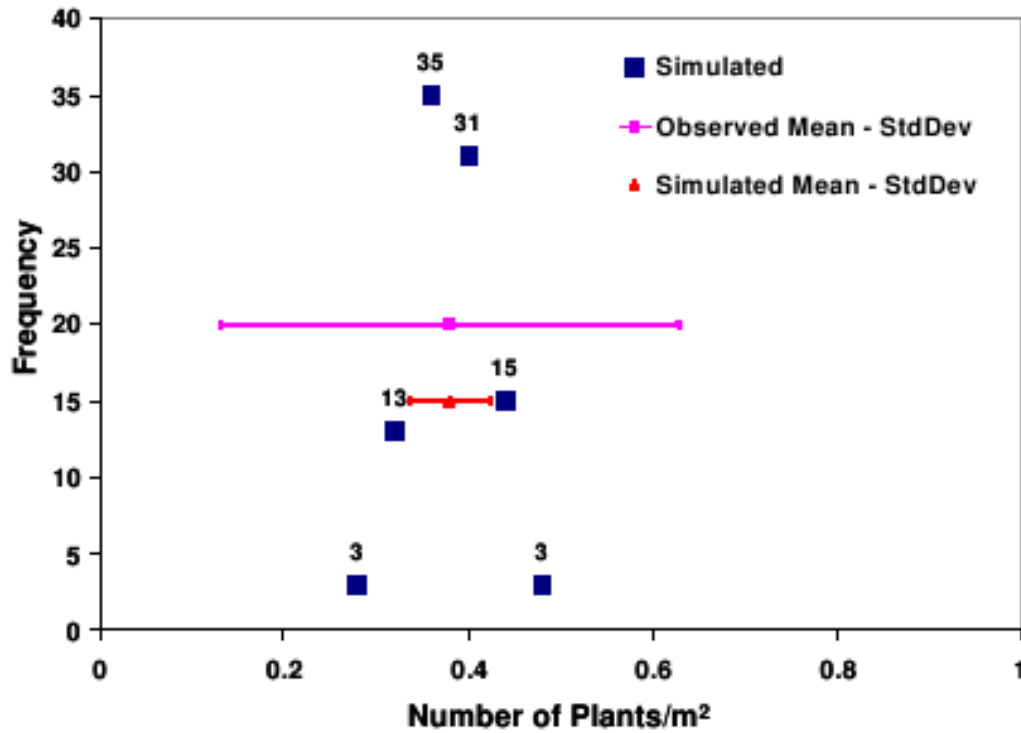
**Figure 3.1.:** Simulated seed banks of *Hakea sericea* with and without biocontrol (YFF = young follicle feeder; MFF = mature follicle feeder). Note the log scale for the seed bank data. The cumulative seed banks decline from age 9-11 because the MFFs effectiveness is still increasing so that it will destroy a proportion of the previously accumulated seed bank.

### 3.4.2. Dispersal kernels

The estimates of the cumulative proportions of the seeds, that travel different distances, differed between the experts (Table 3.6). The most conservative were those by JH and DR (see Table 3.6 for explanation of the mnemonics) who estimated that large proportion of the seeds dispersed less than 10 metres and 99% less than 100 m. The estimates by the other experts were less conservative with 5–10% of the seeds travelling more than 100 metres. The best overall fit to the expert's estimates was given by the Weibull distribution ( $-\ln(L) = 0.0006$ ) followed by the inverse power ( $-\ln(L) = 0.0038$ ) and the lognormal ( $-\ln(L) = 0.0145$ ) distributions (Figure 3.2). The Weibull distribution provided the best fit for all the different experts except JH, having a mean rank of 1.3 compared with 2.0 for the inverse power. The best fit for estimates provided by JH was the inverse power followed by the lognormal. The resulting seed-dispersal kernels can be seen in Figure 3.2. The Weibull function was chosen for the simulation model because it provided the best overall fit.

There is wide range in the values for the parameters of the fitted Weibull distributions between experts (Table 3.7). Alpha (the scale parameter) ranges from 5.1–25.3 and Gamma (the shape parameter) from 0.44–4.00. The extreme Gamma value is for the estimate by JH which differs markedly from the others (Table 3.6), but there is no systematic pattern to the values of the Alpha parameter. The final fitted relationships show that most of





**Figure 3.2.:** Observed and simulated seedling densities used in modelling density-dependent mortality of *Hakea sericea*.

**Table 3.5.:** Reproductive maturation of young *Hakea sericea* plants based on repeated surveys of populations in the field (for details of the study sites see Table 3.1).

Years after fire	Percentage of plants with fruits
1	0.00
2	0.00
3	4.02
4	39.30
5	81.03
6	89.80

the dispersal distributions are similar, the exception being the one for JH which has no seeds within a metre of the parent and almost all of the seeds within 100m (Figure 3.2). We used all the parameter sets from all experts and the Weibull distribution fitted to the average estimate for simulations but mainly describe the results of simulations using the estimates by BW and DR as these proved to be the extreme cases.

**Table 3.6.:** Cumulative proportions of seeds that travel different distances as estimated by five people with extensive field experience. BW = Brian van Wilgen, DM = David Le Maitre, DR = Dave Richardson, JH = John Hoffmann, TG = Tony Gordon.

Dispersal distance (m)	BW	DM	DR	JH	TG	Mean	Std Dev
10	0.50	0.50	0.75	0.95	0.50	0.64	0.2
50	0.65	0.85	0.95	0.98	0.85	0.856	0.13
100	0.95	0.95	0.99	0.99	0.90	0.956	0.04
500	0.99	0.9999	0.9999	0.99999	0.99	0.99596	0.01
5000	1.00	1.00	1.00	1.00	1.00	1.00	0.00

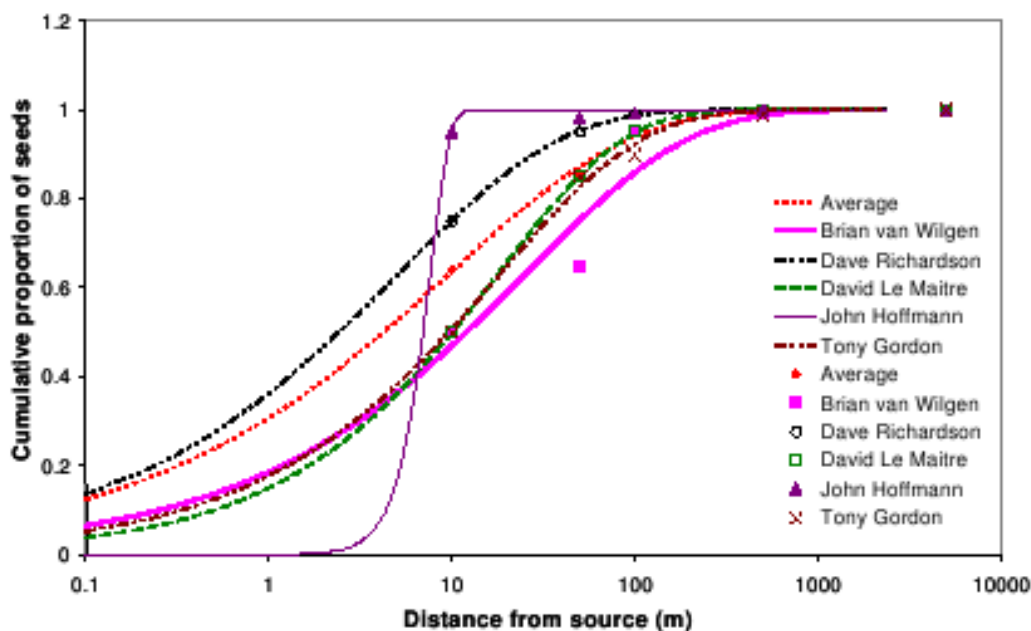
**Table 3.7.:** Parameter values and maximum likelihood estimates of the fit for the Weibull distribution to the estimates of seed dispersal provided by the experts (see Table 3.6 for the expert estimates and explanation of the mnemonics). The lower the value of the MLE the better the fit.

Expert	$\alpha$	$\gamma$	MLE
DM	17.9	0.63	0.00008
DR	5.1	0.49	0.000024
BW	25.3	0.49	0.019654
JH	7.6	4.00	0.000500
TG	18.5	0.56	0.001293
Mean	9.7	0.44	0.000573

### 3.4.3. Mortality & density dependence

The available field data give an estimated mean of 0.082 one-year old seedlings per seed (range 0 to 0.27) over all the sites (Table 3.3). The net recruitment includes both the mortality of seeds in the follicles during the fire, post-release predation and other losses until the seedlings reach an age of one year. For year 1 to 2, the mean mortality over four of the sites was 51%. Only one of the sites provided mortality data for years 2-3 and at that site it was 21%. The overall mortality at this site for years 1-3 was about 57% - only 43% of the seedlings from year 1 survived until year 3. The net survival from seeds through to young plants was, therefore, 3.49%, which was rounded to a maximum probability of establishment of 0.04 for the simulation model (EstMax).

Density-dependent mortality was adjusted by varying of  $ZOI_{rel}$  and comprised a reduction of the seedling densities (per  $m^2$ ) to the range observed in field surveys (Figure 3.3). The observed mean density at the six field sites was 0.38 plants/ $m^2$  (Table 3.3). A value of 0.25 for the parameter  $ZOI_{rel}$  gave a mean density of 0.25 plants/ $m^2$  (for 100 simulations) and  $ZOI_{rel} = 1.5$  gave 0.82 plants/ $m^2$ , again for 100 simulations. The final simulated mean of 0.3804 plants/ $m^2$  (given by  $ZOI_{rel} = 2.2$ ) is essentially identical to the observed, the main difference being that the standard deviation of the densities in the simulated data (0.04,  $n = 100$ ) is much lower than in the observed data (0.24,  $n = 6$ ), probably because of the larger sample size in the simulated data.

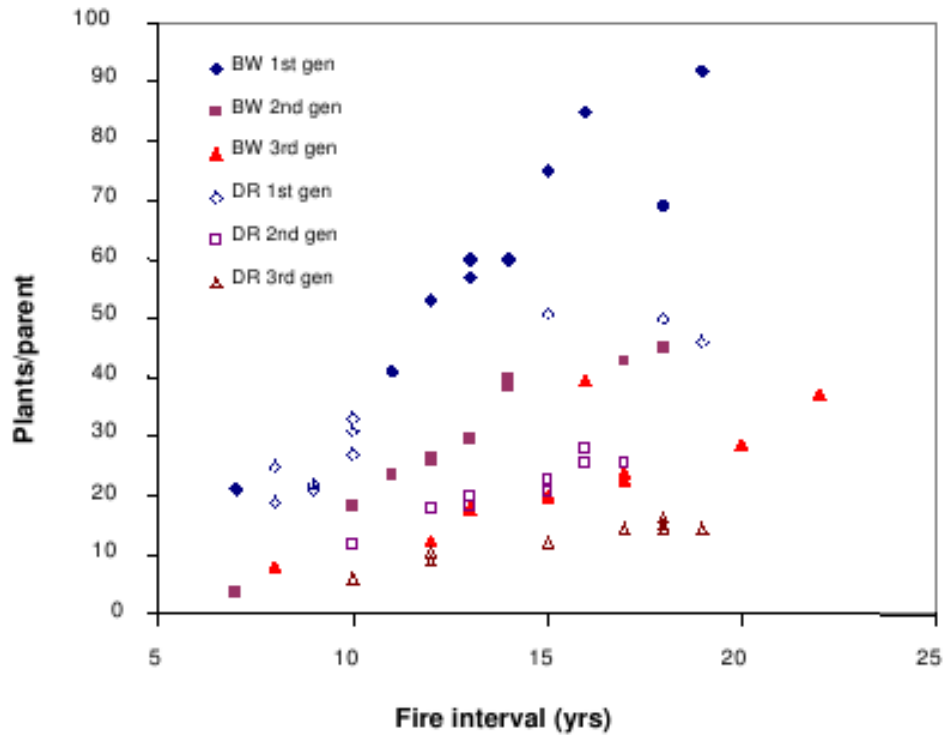


**Figure 3.3.:** Raw data (points) and fitted cumulative seed dispersal curves (lines) for each of the experts and the mean of the expert's estimated values. The Weibull dispersal kernel was used in each case.

#### 3.4.4. Densities in circles and net population growth rate

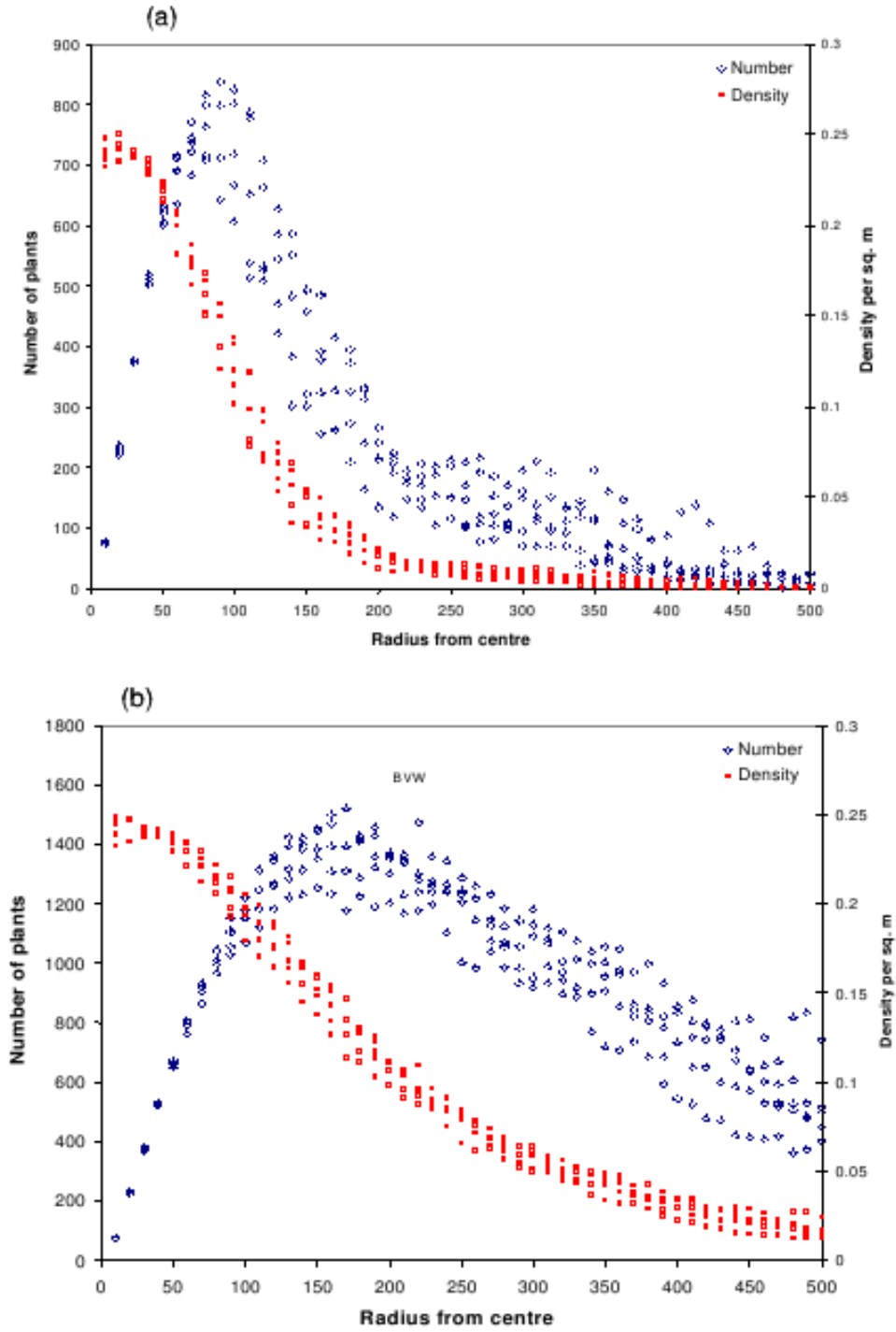
The net result of the dispersal and the self-thinning depends on which expert's dispersal estimates were used to derive the parameters for the Weibull dispersal kernel (Figure 3.5). The final densities, after three generations, decrease with increasing distance from the initial plant at different rates for the DR and BW dispersal parameters, with the DR densities declining from 20m and the BW only from about 50m. The actual number of plants in each 10m annulus from the initial plant increases up to about 10m; it then declines rapidly from about 800 plants to less than 50 between 490 and 500m from the initial plant. Using BW's parameter estimates, the numbers of plants per annulus increases up to about 170m from the initial plant and the decline from 200–500m is more gradual and roughly linear instead of exponential. The more conservative dispersal estimates (e.g. DR) result in relatively few seeds dispersing more than 100–200m from the initial plant and a reduction in population growth rates because of the high density-dependent mortality rates of the seedlings. Mean populations after three generations ranged from 41 000 plants for BW to 12 400 for DR, with the other experts falling between these extremes.

The net recruitment per generation also was markedly affected by the choice of dispersal parameters and intervals between fires (Figure 3.4). For BW's estimates, the number of plants increases rapidly with increasing fire intervals in the 1st generation (Table 3.8) but



**Figure 3.4.:** Relationship between the interval between fires (years) and the number of established young plants per parent for successive generations of *Hakea* plants. Ten runs with random fire intervals were done for each expert's seed dispersal estimates. For more information see the text. BW = Weibull seed dispersal kernel parameters based on estimates of cumulative seed dispersal by BW; DR = the same for DR.

increases more slowly in the 2<sup>nd</sup> and 3<sup>rd</sup> generations, respectively. The same pattern is evident when using DR's estimates but the highest population growth rate in this case (1<sup>st</sup> generation) is only equivalent to the 3<sup>rd</sup> generation for BW. The net rate of increase for each generation is substantially higher for BW's estimates, than for DR's. In both cases, the rate of increase is lower in the 2<sup>nd</sup> and 3<sup>rd</sup> generations because of the increase in density-dependent thinning due to the increase in the total number of plants in each successive generation. The net outcome of the differences in population growth rates is shown by the mean number of plants in each generation which is much higher for BW than for DR (Figure 3.4); the ratio of BW to DR is 1.89, 2.88 and 4.53 for generations 1, 2 and 3 respectively showing that the BW population is increasing at an ever-faster rate relative to the DR one.



**Figure 3.5.:** Distribution of the plants in concentric circles up to 500 m from the initial plant (which was at the centre of the circle) after 3 generations with a fire interval of 11 years. Note the different scales for the number of plants. The number of plants is for each successive 10 m annulus (e.g. 10-20 m, 20-30 m). Five separate runs per expert were done. Parameter values for the Weibull distribution derived from the estimates by: (a) DR and (b) by BW (see Tables 5 and 6).

**Table 3.8.:** Relationship between the number of seedlings per parent and the interval between fires for successive generations of *Hakea*. Two experts (BW and DR, see Table 3.6) estimates of the cumulative seed dispersal were used to derive the parameters for the Weibull seed dispersal kernel. An x-intercept of 3 was used throughout because that is the age of first seed production.

Expert	Generation Number	Linear regression of fire interval (years) and plants per parent (Y) in each generation	$r^2$	Mean Number of plants in each generation
BW	1	$Y = 4.30 \cdot \text{years} + 3$	0.83	61.3
	2	$Y = 2.15 \cdot \text{years} + 3$	0.75	1810.3
	3	$Y = 1.34 \cdot \text{years} + 3$	0.59	33049.4
DR	1	$Y = 1.34 \cdot \text{years} + 3$	0.84	32.5
	2	$Y = 1.28 \cdot \text{years} + 3$	0.77	627.9
	3	$Y = 0.63 \cdot \text{years} + 3$	0.80	7295.3

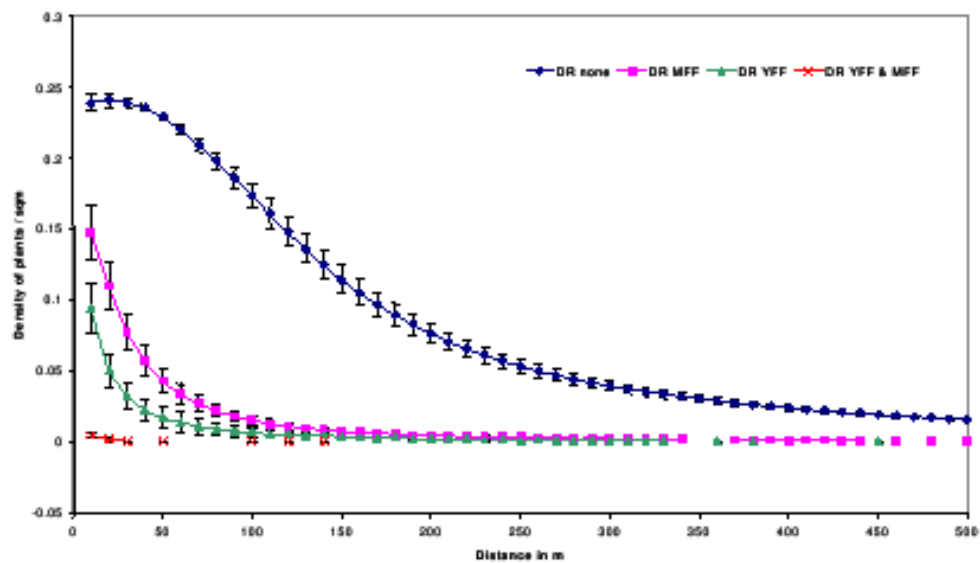
### 3.4.5. Impacts of biological control on seed dispersal

Although only the Weibull distribution was used in the later simulations, we did some initial sensitivity tests using all the kernels. In the sensitivity analysis, we looked at the maximum distance at which we can expect to find a seed with a given probability of 0.95, from now on referred to as “maximum dispersal distance of a seed”. If the negative exponential relationship (the “standard” seed dispersal curve in most studies) is used, then reductions in seed numbers per plant from 1 000 to 500 seeds have little effect on the maximum dispersal distance of a seed, changing it from 47 to 39m (Table 3.9). But a reduction from 100 to 50 seeds changes the distance from 14 to 9m, a much greater proportional impact. The most sensitive dispersal kernel is the Weibull distribution, which gave a greater probability of long-range dispersal than the others. A reduction from 1 000 to 500 seeds reduced the maximum distance from 86 to 56m, and from 100 to 50 seeds from 16 to 9m. The inverse power seems to be the next most sensitive to reductions in seed numbers per plant, especially for relatively high seed numbers, with the others being most sensitive when there were fewer seeds per plant. Overall, the distributions that resulted in greater maximum dispersal distances were the most sensitive to reductions when seed banks per plant were relatively large.

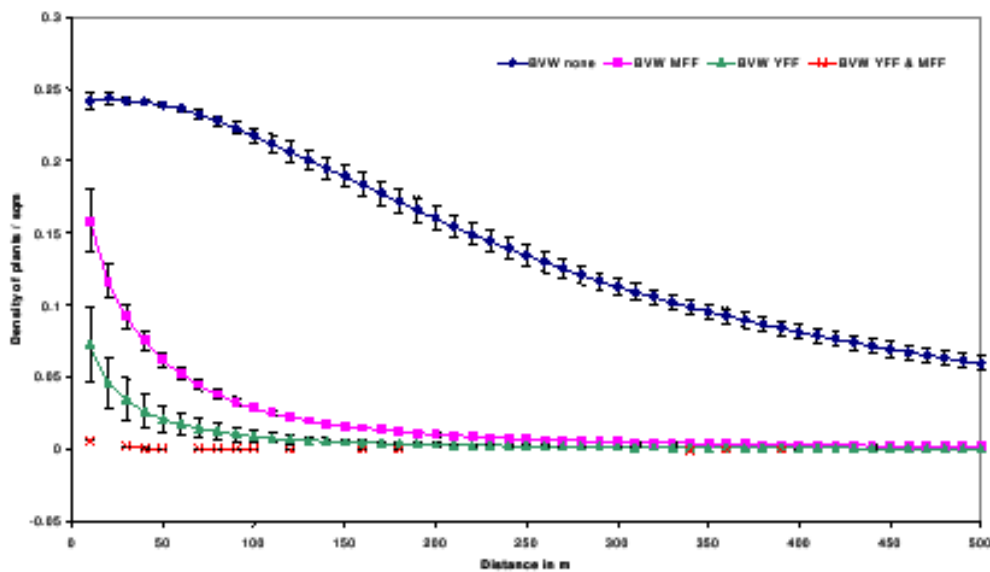
The impacts of the two agents, i.e. the proportions of follicles destroyed, initially increased as the stand ages but levelled off after 9 years for the YFF and 11 years for the MFF (Table 3.2). The impacts on the accumulated seed banks are quite marked, with the rate of seed bank accumulation being substantially reduced by both the YFF and MFF (Figure 3.1). When just the YFF is present, the annual seed production peaks in year 9 and then declines substantially. The impact of the MFF is evident through the net decline in the accumulated seed bank between the age of 9 and 11 years. If the decline is not simply an artifact of the data and how it is captured in the model itself, it implies that there is a period, roughly between 7 and 11 years after the last fire, when control operations may result in greater seedling recruitment than those in younger or slightly older stands.

**Table 3.9.:** Effects of a reduction in the seed bank of a single plant on the maximum distance (m) reached by a seed using the different seed distribution kernels. The parameter values for the distributions were derived from the mean of the expert's estimates of cumulative seed dispersal (see Table 3.6).

Distribution	Changes in maximum distance (m) given a reduction in numbers of seeds per plant from			
	100 $\rightarrow$ 50	250 $\rightarrow$ 100	500 $\rightarrow$ 250	1000 $\rightarrow$ 500
Inverse power	14 $\rightarrow$ 9	22 $\rightarrow$ 14	44 $\rightarrow$ 22	71 $\rightarrow$ 44
Negative exponential	23 $\rightarrow$ 16	33 $\rightarrow$ 23	39 $\rightarrow$ 33	47 $\rightarrow$ 39
Half-normal	25 $\rightarrow$ 17	33 $\rightarrow$ 25	37 $\rightarrow$ 33	42 $\rightarrow$ 37
Log normal	13 $\rightarrow$ 9	23 $\rightarrow$ 13	35 $\rightarrow$ 23	50 $\rightarrow$ 35
Weibull	16 $\rightarrow$ 9	34 $\rightarrow$ 16	56 $\rightarrow$ 34	86 $\rightarrow$ 56



**Figure 3.6.:** Mean density of seedlings in each 10 m annulus from the initial parent plant by the third generation. Four iterations were used with the cumulative seed dispersal estimates from DR, the Weibull dispersal kernel and an interval of 11 years between fires.



**Figure 3.7.:** Mean density of seedlings in each 10 m annulus from the initial parent plant by the third generation. Four iterations were used with the cumulative seed dispersal estimates from BW, the Weibull dispersal kernel and an interval of 11 years between fires.

The log scale used for clarity in Figure 3.1 somewhat obscures the impacts. By the age of 20 years, the accumulated seed bank per plant is 7777 seeds with no biological control compared with 1555, 308 and 62 for the MFF, YFF and both agents, respectively. All of these are very substantial reductions of 81, 96 and 99.3%, respectively.

### 3.4.6. Impacts of biological control on population growth and dispersal

The analyses of the outcomes of using the Weibull dispersal kernel parameters derived from the different experts' seed dispersal estimates (Table 3.6) found that those based on DR's estimates had the most limited dispersal and those of BW resulted in the most extensive dispersal (see Figure 3.5). The reduction of seed banks due to biological control has a marked impact on the distances seeds travel. Using DR's parameter values, the reductions in plant densities are greatest between 40 and 70m for the MFF, with the YFF having a greater impact than the MFF (Figure 3.6), as would be expected from their impacts on seed banks. The greatest differences for the YFF and for both agents are in the 0–30m range. Both agents together have a major impact, with no seeds reaching beyond 140m and very low densities throughout. Using BW's estimates, the reductions are less marked for the YFF and MFF on their own (Figure 3.7), but for both together, the density reduction is similar to DR's parameter estimates. The greatest differences between no agents and MFF are from 40–90m and 0–20m for the YFF and for both agents. The reduction in the maximum distance travelled by seeds is much less for both agents, with a few seeds still reaching 330–350m and one plant to 380m, well beyond the distances reached using DR's



parameter estimates. This extra distance would be important for establishing new foci and would be very important for increasing spread rates in subsequent generations.

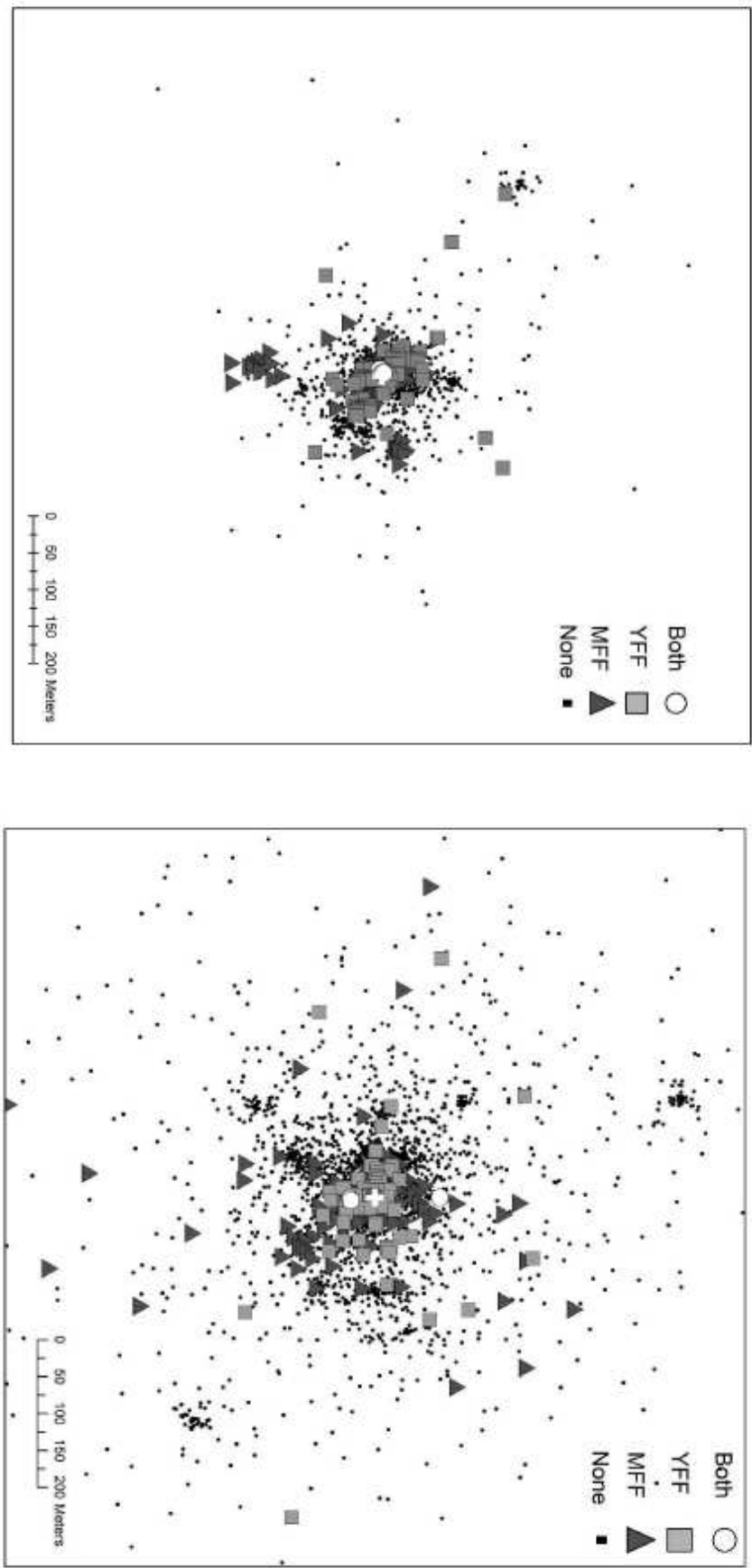
### 3.4.7. Spatial pattern

The formation of new foci and the clustering effect this has on seedlings can be clearly seen in the distribution of seedling around the parent plants. Using DR's parameter estimates, only one plant becomes established more than 150m away (Figure 3.8). This then forms the nucleus for the 2<sup>nd</sup> generation plants which clump around it. Using BW's parameter estimates, six plants occur beyond 150m, one of them more than 400m away (Figure 3.9). These long-range dispersers then become the nuclei for the 2<sup>nd</sup> generation which is far more evenly spread over the model domain than is the case using DR's parameter estimates. The model was not setup to track seeds which dispersed outside the modelling domain, but it is reasonable to deduce that few 2<sup>nd</sup> generation seeds will have dispersed beyond the borders for DR's parameter estimates compared with those of BW.

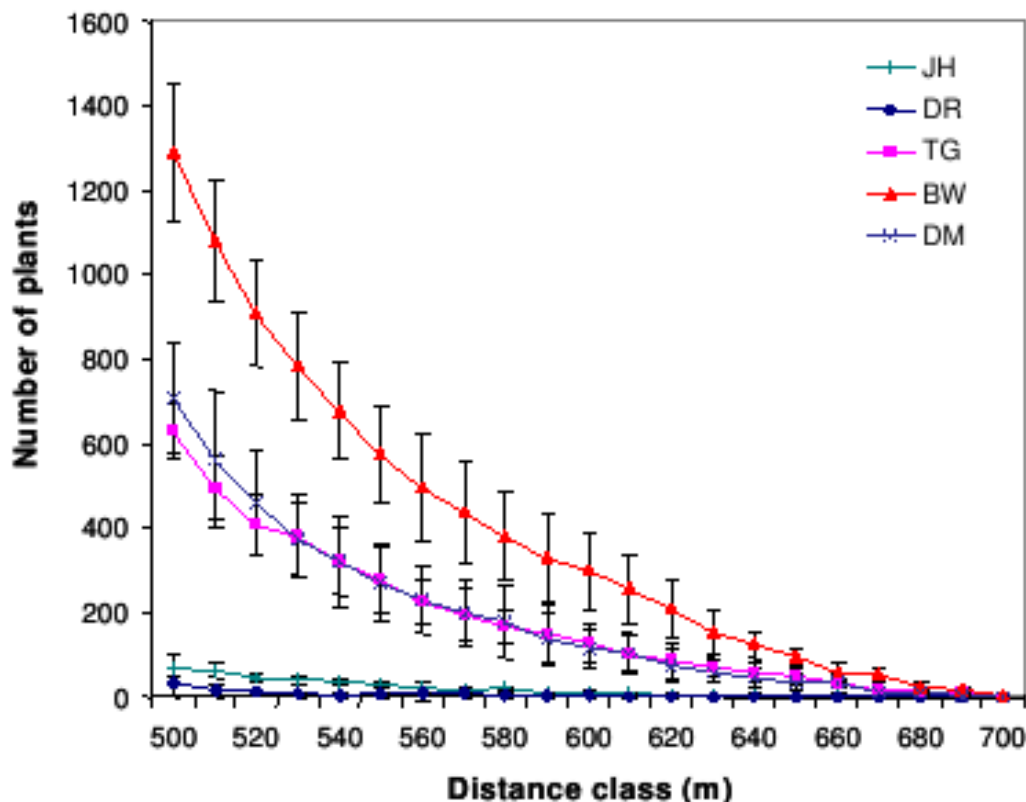
An indirect estimate can be obtained from seeds which dispersed diagonally into the corners and thus could disperse more than 500m without being lost. It is not directly possible to compare different distance classes with each other, but nevertheless it is possible to compare the same distance class between different dispersal kernels and treatments. The number of seeds (plants) which were between 500 and 510m ranges from about 1350 for BW to 30 for DR (Figure 3.9), with the others falling between these two expert estimates. The numbers decline steeply, partly because the area of the 1000 × 1000m square model domain that remains decreases rapidly after a radial distance of 500m from the parent (only the corners are left). Only one seed was dispersed as far as 680–690m in five model iterations using DR's parameters, with 600m being the furthest that seeds consistently reached. Using BW's parameters, 1–3 seeds consistently reached 700m (Figure 3.9). The percentage of the total population that was dispersed more than 500m from the parent plant was highest for BW and lowest for DR with the other experts in between (Figure 3.10). This same pattern holds for the actual number of plants dispersed for more than 500m.

## 3.5. Discussion

The outputs from the simulation model provide compelling evidence that biological control can play a role in limiting the rate of invasion of a given area and in decreasing the population growth rates and, thus, the densities of the resulting stands relative to those without biological control. *Hakea sericea* is capable of producing and accumulating large numbers of seeds (Richardson et al., 1987b) and maintaining a positive trend in the numbers of follicles (and thus seeds) per plant up to a very high density of 5.5 plants per m<sup>2</sup> in a mature stand (Bond et al., 1995; WJ Bond pers. comm. 2005). Its high fecundity, combined with heat-resistant, woody follicles (fruit) and well-dispersed seeds, made it the most successful of the four *Hakea* species which invade fynbos (Richardson et al., 1987b). The interaction between dispersal distance and net population growth rates, due to high density-dependent

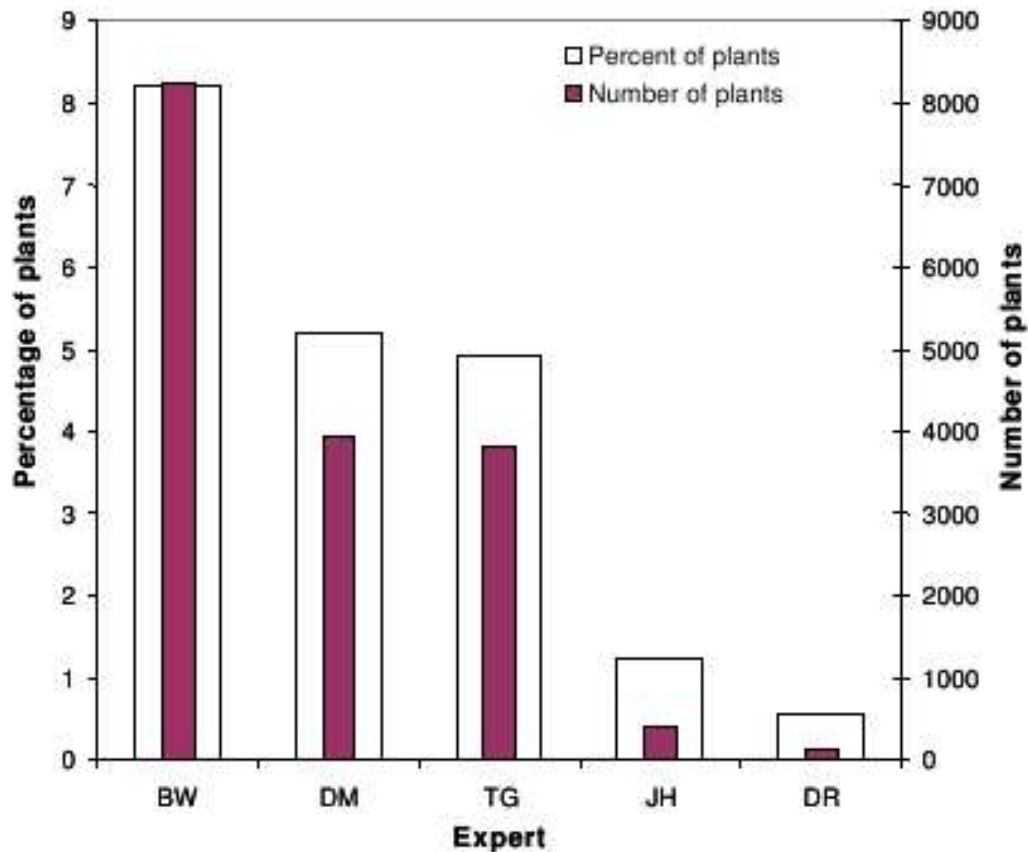


**Figure 3.8:** Diagram showing the location of the parent plant and the established young plants of the 2nd generation with the four different combinations of biocontrol: None, YFF, MFF and Both derived using the Weibull dispersal kernel. The left graph is using parameter estimates from DR, the right one parameter estimates from BWV.



**Figure 3.9.:** Number of seedlings per 10 m annulus that were dispersed more than 500 m from the parent plant. Weibull dispersal kernel parameters based on each expert's estimate of the cumulative seed dispersal curve and a fire interval of 11 years.

mortality in the dense stands that formed when dispersal distances were relatively short, was to be expected (Auld and Coote, 1980; Moody and Mack, 1988), but the magnitude of the reduction in population growth was greater than expected. Using DR's dispersal parameter estimates, the population after three generations was only 30% of the one using BW's estimates. The simulation model was kept simple by deliberately excluding spatial and temporal variations in the simulated environment, plant growth and fecundity, seed predation and seedling and adult mortality, although these are important factors (Bergelson et al., 1993; Hastings et al., 2004; With, 2004). This was done deliberately to reduce the amount of data required, and the complexity of the model outputs, and to focus on the main factors of interest to this analysis: seed dispersal patterns, overall fecundity versus the interval between fires, population growth rates and density dependent-mortality. Therefore, the results of this study are believed to have captured the major patterns in the outcomes and provide a reasonable reflection of the actual impacts on invasions by *Hakea sericea*. One aspect that was not assessed was spatial and temporal variability in the effectiveness of the biological control agents which can be an important determinant of the overall level of control achieved (Fagan et al., 2002), but field observations in *H. sericea* stands show that the agents are almost uniformly present by the time the plants are flowering and producing fruits (AJ Gordon, unpublished data), so this should not be



**Figure 3.10.:** Percentage of the total number of plants and the total number of plants that were dispersed more than 500 m from the parent plant after three generations. Weibull dispersal kernel parameters based on each expert's estimate of the cumulative seed dispersal curve and a fire interval of 11 years.

a significant issue for the simulated area of  $1\text{km}^2$ .

Although there have been many studies of the impacts of biological control on plant seed banks and population dynamics such as growth rates (e.g. [Dennill and Donelly, 1991](#); [Rees and Paynter, 1997](#); [Hoffmann and Moran, 1998](#); [Hoffmann et al., 1998a,b](#); [Shea and Kelly, 2004](#); [Paynter, 2005](#)), and a few have assessed the potential impacts on dispersal rates ([Neubert and Parker, 2004](#); [Shea, 2004](#)), this study is the first to use an individual-based model to quantify the impacts on seed-dispersal patterns and, thus, on invasion rates. The reductions in *H. sericea* seedbanks due to biological control have a significant impact on both its ability to disperse for long distances and on its net population growth rates, especially when the parameters used in the dispersal kernel favour relatively short-distance dispersal. The same effects were observed when the interval between fires was varied and similar impacts could be expected from any other factors which reduced the number of seeds per plant. High fecundity (i.e. propagule pressure) and high seedling recruitment rates have been recognised as key attributes of successful invaders for a long time ([Salisbury, 1961](#); Baker 1965 in [Baker, 1968](#)); for a recent review see [Rejmanek et al.](#)

(2005). One of the earliest attempts to model the dispersal of an invading species made this link explicit by relating the population diffusion rate to the population per capita growth rate (Skellam, 1951) and this approach has recently been revitalised by linking it to matrix and diffusion models (Neubert and Caswell, 2000; Neubert and Parker, 2004; Shea, 2004). Thus, if fecundity plays a key role in the success of a particular invader, as seems to be the case in *H. sericea* (Richardson et al., 1987b), then reductions in seed production which lead to reduced spread rates, like those found in this study, are to be expected. A detailed simulation model of pine invasion rates also found that rates of spread were particularly sensitive to dispersal parameters and that seedling establishment and juvenile survival also interacted significantly with mortality of recruits (Buckley et al., 2005). Neubert and Parker (2004) found similar interactions in a detailed model for *Cytisus scoparius* which incorporated biological control. These results all suggest that variation in mortality, whether density-dependent or density-independent, is a critical factor as well.

Modelling of seed dispersal, particularly long-range or long-tailed seed dispersal, is a rapidly growing field as shown by the larger number of papers published in this field in recent years (e.g. Clark, 1998; Clark et al., 1998; Higgins and Richardson, 1999; Ledgard, 2001; Nathan et al., 2001, 2002; Higgins et al., 2003; Nathan et al., 2003; Levin et al., 2003; Tackenberg et al., 2003a; Katul et al., 2005; Trakhtenbrot et al., 2005). These papers have found that the rates and patterns of spread of species with long-distance dispersal are very sensitive to a range of factors, including the form of the function used in the model (Clark, 1998; Greene et al., 2004), life-history of the organism, and inherent uncertainties in data used to set up the models (Clark et al., 2003). Some authors have suggested mixed dispersal models should be used rather than single functions, either because different processes dominate for short versus for long-distance dispersal (e.g. laminar flow versus turbulence or updrafts) or because long-distance dispersal is seen as unusual rather than simply a rare event (Greene and Johnson, 1995; Higgins and Richardson, 1999; Horn et al., 2001; Nathan et al., 2002; Higgins et al., 2003; Soons et al., 2004). Others have argued that thermal updrafts are more important than shear induced turbulence (Nathan et al., 2002; Tackenberg, 2003; Tackenberg et al., 2003b). Detailed mechanistic modelling suggests that the small fraction of the seeds lifted above a pine forest canopy may be dispersed for kilometres (Williams et al., 2006). Greene (2005) found that high intensity but short-period wind velocities are needed to abscise *Taraxacum* seeds, so that seeds which require lifting out of their receptacle in the fruit, like *Hakea*, are mainly dispersed during turbulent wind conditions which facilitate their spread.

The possibility of using an analytical mechanistic model rather than a phenomenological model was considered but not attempted in this study largely because of the difficulties in collecting the data needed to test and properly parameterise these models (see Nathan et al. (2003) for a discussion of this issue). Two-phase models, as discussed above, were also considered but also would be difficult to set up given the very limited available information, leaving relatively simple functions as the most parsimonious option. Given that the parameterisation of the dispersal was based solely on expert opinion, some corroboratory

evidence was needed to test whether the simulated dispersal patterns were representative of the actual patterns in the field. Katul et al. (2005) provided a simplified and apparently robust model for independently estimating dispersal but this still requires estimates of the vertical wind velocities which were not available. However, Tackenberg et al. (2003a) have developed an approach which is based on their standard weather conditions and only requires data on the release heights and the terminal velocity of the seeds. If those weather conditions are accepted as suitably representative or conservative — their wind speeds were lower than those reported by Deacon et al. (1992) — and a terminal velocity of 1.0m/sec (Richardson et al., 1987b), the Wind Dispersal Potential (WDP) for a reference distance of 100m ranges from 4 for a 1.0m seed release height, to 6 for a seed release height of 5m (Figure 4 in Tackenberg (2003)). A  $WDP_{100}$  of 4 is equivalent to a between 1.6 and 3.2% of the seeds reaching more than 100m from the source and a  $WDP_{100}$  of 6 to 6.4–12.8% (Table 3 in Tackenberg (2003)). In this study, the expert estimates of the proportion of the seeds reaching 100m from the parent ranged from 0.10–0.01 (Table 3.6) which is rather more conservative. In addition, the simulations used by Tackenberg et al. (2003a) were for grassland environments which generally have smoother canopies and less turbulent near-ground conditions than shrublands or forests (Jarvis, 1985), leading to lower WDPs. The close correspondence with the independent estimate provided by Tackenberg et al. (2003a) suggests that the dispersal parameters used were conservative and, thus, that the dispersal patterns simulated in the model may even underestimate actual values in invaded areas. Genetic analysis has indicated that seed dispersal distances in *Banksia hookeriana* — which has a similar growth form and wind-dispersed seeds with a higher terminal velocity and thus lower WDP than *Hakea sericea* — may exceed 1.6km (He et al., 2004). Some of the *Banksia* seeds may have been transported similar distances by parakeets but, given this proviso, the *Banksia* data support the argument that our simulations may be conservative.

This analysis used a Weibull function for the dispersal kernel, primarily because this function gave the best overall fit to the estimates of the cumulative proportion of the seed dispersed versus distance from source. Greene et al. (2004) have argued that the lognormal function is the best one to use for plants because it can be interpreted mechanistically, provides a better fit to actual field data (it does not require highest seed densities at source), and may allow for greater long-range dispersal than other functions. We did not have field data to compare but, given the low release height for *Hakea* (<5m) compared with taller plant species, it is likely that the greatest seed densities might be around the plant source so the lognormal would not necessarily give the best fit. Our analysis also found that the maximum distance reached by a seed was most sensitive to changes in the number of seeds at the source (for more than 50 seeds) when a Weibull function was used. The lognormal function was less sensitive in these situations. Our findings also do not support the note by Richardson et al. (1987b) that a 20% increase in seeds would increase dispersal distances by 80% which was based on the use of a negative exponential function. This can only be the case when the seed numbers at the source are < 50. Neubert and



Parker (2004) found that more than 95% of seeds of the ant-dispersed seeds of *Cytisus scoparius* needed to be destroyed to stop invasions but their study only examined short-distance dispersal mechanisms (metres) and not the long-distance dispersal used in this study.

A key feature of the simulated dispersal patterns is the formation of new invasion foci around individual plants which dispersed far from their parent (Figures 3.8). The number of foci formed in the 2<sup>nd</sup> generation is far greater when the dispersal parameters allow for greater long-range dispersal (Figure 3.8, right side) than for less long-range dispersal (Figure 3.8, left side). These patterns interact with the impacts of biological control on the number of seeds to determine both the number of foci and the distance at which they establish. The clustered patterns output in this simulation confirm the importance of nascent foci in accelerating the spread of an invading species (Auld and Coote, 1980; Auld et al., 1983; Mack, 1985; Moody and Mack, 1988; Clark et al., 1998), especially given that density-dependent thinning is low in new foci but increases rapidly as the density in the vicinity of the foci increases with each succeeding generation of plants. The ability to establish distant foci was severely limited by reductions in the seed banks as well. If the agents are also able to rapidly colonise these founder populations then they can have a significant impact on the rate of spread and, ultimately, on the overall costs of control operations.

Although there are questions about the degree of seed destruction needed for effective biological control using a seed-feeding agent, it is likely that the reduction in seedling densities following biological control, and the resulting reductions in rates of spread, may still make this a cost-effective option (Moran et al., 2004; Van Klinken et al., 2004). This study has shown that both population growth and spread rates of *Hakea sericea* are reduced by the biological control agents. Initial clearing of dense *Hakea* stands (75–100% canopy cover) costs about R500/ha compared with sparse stands (1–5%) at about R50/ha, and the relationship between cover and cost is roughly linear (Marais et al., 2004). Using BW's dispersal parameters and fire intervals of 11 years to get a high population growth rate, the 4<sup>th</sup> generation has a population of about 210 000 plants in 100ha (1 000×1 000m) or 2 100 plants per ha, a dense stand. Using the same conditions and DR's dispersal parameters would result in about 72 500 plants. With both biological control agents, the populations would be 5 and 7 plants, respectively. Assuming the plants are evenly distributed, even if the number of plants after biological control was 100-fold greater than the model predicts, the densities would still be so low that the cost saving would be of the order of 50–90% of the pre-biological-control cost. The saving would decline to about 25–50% if there were 1 000-fold more plants after biological control. The results of this modelling exercise show that biological control using seed feeders can be a cost-effective method, as argued by Moran et al. (2004), even when the reductions in seed banks are lower than seems to be the case for *Hakea sericea*.

### 3.6. Acknowledgements

This research was funded by the Working for Water Programme as part of its biocontrol research programme. We thank Drs Brian van Wilgen and Dave Richardson for their estimates of seed dispersal ranges and comments and Dr Cliff Moran for advice on the design of the study. We also thank the two anonymous reviewers whose comments have significantly improved the paper.



## 4. Impact of Seed Destroying Biocontrol Agents and Fire Frequency on the Spread of *Hakea sericea*

### 4.1. Introduction

In Chapter 3, we explored whether seed-destroying biocontrol agents impact negatively on the spread of an invasive species, *Hakea sericea*. Although we were able to conclude that they have a considerable impact, we were not able to quantify the impact due to the initial conditions chosen for the model. One measure to characterise the spread of a species is to consider the velocity of the spread, i.e. the speed with which the species colonises new habitat. In order to quantify the impact the biocontrol agents have on the velocity of the spread of *H. sericea*, a different approach to the one used in Chapter 3 was required. Instead of simulating the spread from a single point source, we simulated the spread originating from an area source, over four generations, and determined the resulting velocity using the same underlying datasets. As both biocontrol and fire frequency determine the number of viable seeds produced by the individual plant, following the submodel described in Chapter 4.2.3, we did not separate these two effects, i.e. we analysed the impact of the overall seed production on the velocity of the spread. In the discussion, we will interpret the latter in the framework of biocontrol and fire frequency-determined seed production.

As discussed earlier, there is no consensus whether seed-destroying biocontrol agents have an impact on the dynamics of an invasive species. Hoffmann (1990) and Hoffmann and Moran (1998) observed only a marginal decline in population density of *Sesbania punica* after a destruction of 99.7% of all seeds. This would indicate that other processes and factors are limiting the density, like availability of micro-sites for germination or other environmental conditions, hence the conclusion that seed-destroying biocontrol agents are not effective. On the other hand, Rees and Paynter (1997) found that a 75% reduction in seeds had a significant impact on the abundance of *Cytisus scoparius*. As we showed in Chapter 3, seed-destroying biocontrol agents do have an impact on the spread of *Hakea sericea*, but there has been no quantification of the impact of the reduction of the seed production on the dispersal distances and the velocity of the spread. This quantification would add to the understanding of the effectiveness of these biocontrol agents by enabling us to make predictions on their impact and also provide insight into the suitability of these under different management scenarios.

A widely-used approach to determine the velocity of the spread of an expanding species

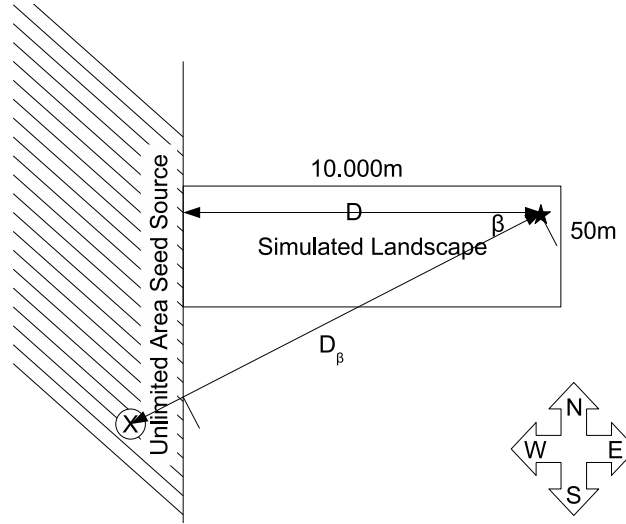
is to determine and to analyse the locations of the furthest-dispersed remote individuals (Clark et al., 2001; Cannas et al., 2003). As this measure is based on identifying the single furthest dispersed plant, it is quite sensitive to being able to find this individual. Especially in cases where the dispersal kernel is not exponentially bound, these individuals can be relatively far from the nearest plants. A measure which would not depend only on this single extreme disperser would be more robust and potentially easier to determine. Therefore we tested 8 different measures which did not include only the furthest plant, but also the next closer plants, to determine the velocity, and compared the measures' predictions.

Clark et al. (2001) describe a method for calculating the expected velocity of the spread of a species based on extreme dispersal events, i.e. the furthest dispersal distance in one generation. Based on this methodology, they calculate a minimum expected velocity based on dispersal from one plant ( $V^- = E[C; 1]$ ) and a maximum expected velocity based on a stand of plants ( $V^+ = E[C; \infty]$ ). As a whole, the methodology is one-dimensional (the spread is considered in only one direction), a stand is characterised by individual plants at distance  $h$  from each other, citing the spread in a linear riparian system as an example. This represents a special case, which is not directly applicable to situations of many alien invasive species, who are not limited to a linear habitat.

Although these results of the one-dimensional framework give an interesting insight into the expected velocity of the spread of a species, especially the upper limit of the spread,  $V^+$ , they are not applicable for the situation confronted with *H. sericea*. Here, the spread originates from an area source, and seed dispersal is not uni-directional. To accommodate this case, we introduced an additional upper boundary, using the dispersal from a single point source with the dispersal kernel for an area source and the corresponding number of seeds expected to be dispersed into the simulated landscape. We will refer to this expected upper bound of the area source as  $V_{ADK}^+$ .

In this paper, we will address the following questions:

1. How do the different seed dispersal kernels of the individual plant, based on the expert estimates, influence the velocity of the spread of the species in a simulated landscape?
2. To what extent does the velocity of the species' spread depend on the seed production?
3. Do different measures used to calculate the velocity of the spread yield different velocities? If yes, what are the implications?
4. Do the velocities measured in the simulation model coincide with predictions based on the methodology developed by Clark et al. (2001)?
5. Does the inclusion of  $V_{ADK}^+$  yield any additional information?



**Figure 4.1.:** Setup of the simulated landscape including the seed source and relevant parameter discussed in the text.

## 4.2. Methods

The description of the models follows the standard protocol suggested by Grimm et al. (2006), the ODD protocol, for the description of individual-based models. ODD stands for the sections in the protocol, i.e. Overview (Chapter 4.2.1), Design Concepts (Chapter 4.2.2) and Details (Chapter 4.2.3). The philosophy of the protocol is to provide a framework which makes it easier to understand the model, as the protocol covers all relevant aspects for the understanding of individual-based models. In addition, due to the standardised order in which the different aspects of the model are presented, relevant information is more easily accessible.

### 4.2.1. Overview HakSimSpread

#### Purpose

The purpose of the model HakSimSpread is to model the spread of *Hakea sericea* under different scenarios. It is assumed that the environment is homogeneous and no interactions with other species occur.

#### State Variables and Scales

HakSimSpread is an individual-based, spatio-temporally explicit, stochastic single-species simulation model which was developed in Delphi 7. It consists of three hierarchical levels, namely the individual plants, the species and the simulated patch with a size of  $10,000 \times 50\text{m}$  (see Figure 4.1). A grid (cell size  $1 \times 1\text{m}$ ) is used to model the interactions between individuals, i.e. competition, and seed dispersal. Individuals are characterised by their location on the grid ( $x$  and  $y$  coordinates). Species-specific parameters characterise the life history and competitiveness. The simulated patch is considered as being spatially

**Table 4.1.:** Parameter values for different processes. ZOI stands for Zone of Influence.

Process	Value
Parameter	
Species Parameter	
Relative ZOI radius	2.2
Competitiveness	1000
GERMINATION & ESTABLISHMENT	
Establishment probability	0.04
Maximum establishment up to competition of	0
Zero establishment at competition higher then	1
SEED PRODUCTION	
	see Figure 4.2
FIRE	
none	n/a
SEED DISPERSAL	
Seed dispersal kernel	Weibull, parameter see Figure 4.3

homogeneous, i.e. conditions are the same across the patch and do not change in space or time. To account for the fact that the same processes which occur in the simulated landscape also occur north and south of the simulated landscape, periodic boundary conditions for seed dispersal were assumed for the north and south boundary, i.e. seeds dispersing out of the simulated landscape in northerly direction enter the simulated landscape again from the south and vice versa. As different conditions occur to the east and the west of the simulated landscape, absorbing boundary conditions were assumed for these, i.e. seeds dispersing out of the simulated landscape in these directions are lost for the simulation. In regard to competition, all boundaries were considered as absorbing, i.e. plants outside the simulated landscape have no competitive impact on plants inside the simulated landscape.

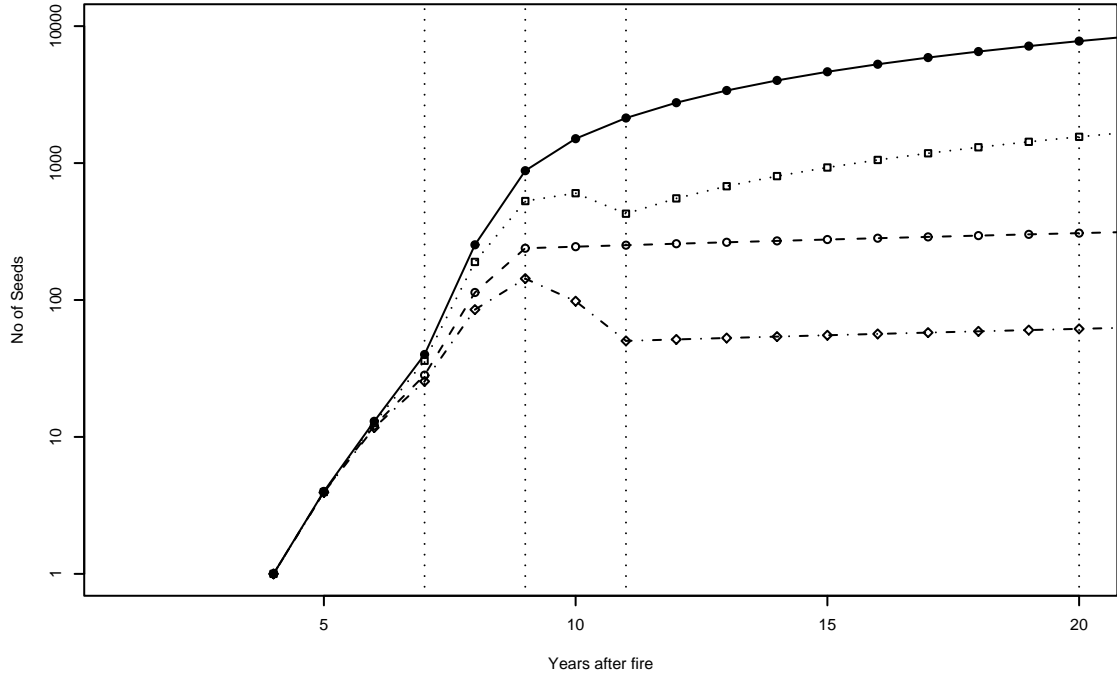
One time-step in the model reflects one fire interval.

### Process Overview and Scheduling

The simulation model consists of four processes, namely GERMINATION & ESTABLISHMENT, SEED PRODUCTION (including the impact of the biocontrol agents), FIRE (releasing the seeds from the plant) and SEED DISPERSAL, which are executed in that order. Processes act on either the individual plant or on the seeds. The Competition Grid links the species and brokers the interaction between plants. The parameters and their initial values are shown in Table 4.1.

One time-step represents one generation, i.e. from germination of the seed to death of the adult plant through fire. Therefore, it is also equivalent to a fire cycle.

Plants exert a certain amount of competition into their neighbourhood. This competition experienced in a cell, caused by all other plants on the grid, is stored in the Competition Grid. The competition experienced by an individual is indifferent to the individual causing the competition. The process GERMINATION & ESTABLISHMENT is influenced by the competition to which the seedling is exposed and in return these processes update the



**Figure 4.2.:** Seeds accumulated on *H. sericea* plant under different biocontrol exposures at years after the last fire. The x-axis can also be interpreted as the fire interval in the system. Solid line with filled circles: NONE, dotted line with open squares: MFF, dashed line with empty circles: YFF, dot-dashed line with open diamonds: YFF & MFF. Vertical dotted lines indicate fire intervals chosen as scenarios.

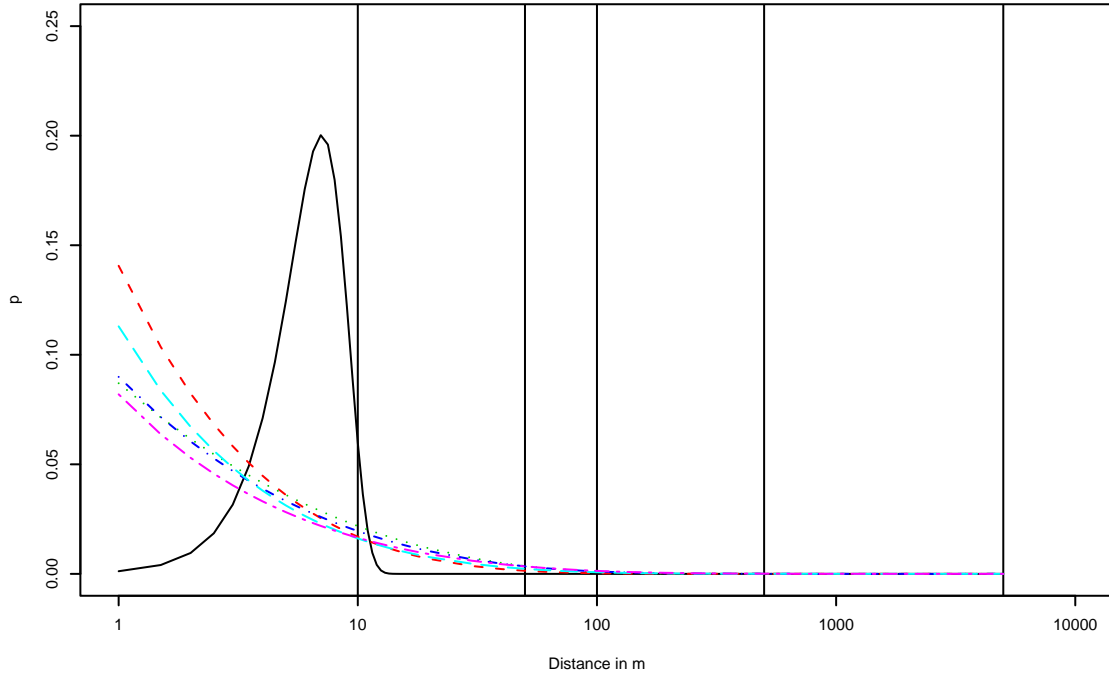
Competition Grid. As all plants die during the process FIRE, the Competition Grid is reset to zero.

#### 4.2.2. Design Concepts HakSimSpread

*Emergence:* The life cycles of the individual plants are modelled by using empirical rules and probabilities from which the spatial pattern of the simulated patch emerge.

*Sensing:* It is assumed that individual plants are aware of the relative competitiveness to which they are exposed. In addition, it is assumed that seedlings “know” the competition in the location in which they germinated.

*Interaction:* Interaction among individuals is modelled through competition following the FON approach (Field of Neighbourhood) described by Berger and Hildenbrandt (2000). Each plant exhibits a certain amount of competition, depending on its species, in its neighbourhood. This is called the Zone of Influence (ZOI) (Czárán, 1998; Berger and Hildenbrandt, 2000). The size of the ZOI is determined by the size of the plant itself and a constant factor specific to the species,  $ZOI_{rel}$  the “relative ZOI radius”. The strength of the competition within this ZOI, the FON, is not constant, but is dependant on the



**Figure 4.3.:** Seed Dispersal kernels used for HakSimSpread Based on expert estimates of cumulative seed dispersal kernels (see Chapter 3 for details). All are Weibull distributions where  $\alpha$ : scale parameter and  $\gamma$ : shape parameter. JH ( $\alpha = 7.6$ ,  $\gamma = 4.00$ ): solid black, DR ( $\alpha = 5.1$ ,  $\gamma = 0.49$ ): dashed red, DM ( $\alpha = 17.9$ ,  $\gamma = 0.63$ ): dotted green, TG ( $\alpha = 18.5$ ,  $\gamma = 0.56$ ): dot-dash blue, Mean ( $\alpha = 9.7$ ,  $\gamma = 0.44$ ): long-dash cyan and BW ( $\alpha = 25.3$ ,  $\gamma = 0.49$ ): two-dash magenta. Vertical lines indicate distances of which experts estimated the cumulative dispersal kernel.

distance  $r_p$  from the location of the plant following

$$\text{FON}(r_p) = \begin{cases} r_p \leq r & \text{Comp} \\ r < r_p < r \cdot \text{ZOI}_{rel} & \text{Comp} - (r_p - r) \frac{\text{Comp}}{r(\text{ZOI}_{rel} - 1)} \\ r_p \geq r \cdot \text{ZOI}_{rel} & 0 \end{cases} \quad (4.1)$$

where  $r$  is the radius of the cover of the plant and Comp is the maximum competitiveness of the species. As we are dealing with a one-species system, Comp is an arbitrarily-chosen value. The FONs of all plants are superimposed to obtain the competition at each given point  $(x, y)$  in space

$$F(x, y) = \sum_N \text{FON}_n(x, y) \quad (4.2)$$

and finally  $F(x, y)$  is stored in a grid which is updated by the processes FIRE and GERMINATION & ESTABLISHMENT.

*Stochasticity:* HakSimSpread is a stochastic simulation model—the processes SEED DISPERSAL and GERMINATION & ESTABLISHMENT are stochastic, while SEED PRODUCTION is, to limit the complexity of the model, deterministic. SEED DISPERSAL is modelled based on probability density functions for the distance and directions in which the seeds disperse. GERMINATION & ESTABLISHMENT are founded on probabilities of germination

and establishment, however, the establishment probabilities are modified according the competition to which the seedling is exposed. The order in which the individuals are evaluated in the different modules follows the order in which they were created during the simulation (in most cases this coincides with the age of the plants).

*Observation:* After completion of each time step, the location of each individual is saved and is analysed following the procedure outlined in Chapter 4.2.6.

### 4.2.3. Details of HakSimSpread

#### Initialisation

The simulation is initialised with an empty patch. We assume an unlimited seed source, i.e. an area seed source which stretches in x-direction (west – east) from  $-\infty$  to zero (the left edge of the simulated landscape) and in y direction (north – south) from  $+\infty$  to  $-\infty$  (see Figure 4.1). Seeds are dispersed at each time step, from the western side of the simulated landscape following a area source dispersal kernel (ADK) based on the point source dispersal kernel (PDK) of the expert used in the simulation (see Chapter 4.2.4 and Chapter 4.2.5 for details).

#### Input

The input in the model is the fire frequency. As one time-step in the model represents one fire cycle, the fire cycle only impacts the number of seeds produced per time-step. The longer the cycle, the more seeds are produced. In addition, the number of seeds produced also depends on the biocontrol agents present. See the discussion about the SEED PRODUCTION below for details.

#### Sub-models of HakSimSpread

**Germination & Establishment** The process GERMINATION & ESTABLISHMENT includes two separate sub-processes, i.e. germination and establishment. Germination takes place every time-step and, as the species has no dormancy (Richardson et al., 1987a), it is assumed that all seeds germinate immediately after the first rainfall event that follows dispersal. Density-dependant thinning occurs during the second phase of the process, establishment.

After germination of the seeds, establishment of the seedlings takes place. The probability of establishment is based on a maximum probability of establishment when no competition is experienced. The impact of competition on the maximum establishment is characterised by two parameters. One parameter specifies the maximum level of competition in a cell at which the seedling is not affected by the competition to which it is exposed, and a second, higher value specifies the amount of competition which results in the death of the seedling, reducing the probability of establishment to zero. Between these two competition values, the probability of establishment is extrapolated linearly. GERMI-

NATION is characterised by a vector providing the probability of germination of a seed of certain age.

**Seed Production** To simplify the model, we assumed seed production to be deterministic and only dependent on the age of the plant. Therefore, seed production per generation is dependent on two factors: the simulated fire frequency and the biocontrol regime to which *H. sericea* is exposed. The longer the interval between two fires, the more seeds are produced and accumulated on the plant (see Figure 4.2). Field data give some indication of the seed production (Chapter 3) and we can therefore calculate the number of seeds produced per generation under a certain fire frequency.

The biocontrol agents destroy a certain proportion of the seeds produced on the plant. Two different biocontrol agents are used and are included in the model: Young Follicle Feeders (YFF) and Mature Follicle Feeders (MFF). As the name suggests, YFF feed only on the new follicles produced in the current year, while MFF feed on all follicles present in the seed bank on the plant. Using the probabilities of the destruction of seeds by the different biocontrol agents, which are also dependent on the time after the last fire, we can calculate the number of seeds accumulating on the plant under different biocontrol treatments (YFF, MFF, YFF & MFF, NONE) for each year since the last fire (see Figure 4.2).

**Fire** FIRE kills all existing *H. sericea* plants. The seeds are released from the seed bank on the plant as the dead plants dry out. The viability of the seeds is not affected by the fire. In years without fire, the seeds produced are accumulated on the plant. As seed production only starts in year 3, fire return times of less than four years result in no seeds accumulating on the plants and as there is no dormancy, there is also no soil-stored seed bank. Combining the four fire frequencies analysed in Chapter 3 with the four possible biocontrol treatments, we obtain 16 different seed production values. i.e. 25, 28, 36, 40, 50, 62, 143, 239, 251, 308, 427, 528, 880, 1555, 2134 and 7777. It was decided to analyse the following subset in this paper: 25, 143, 308, 880, 2134 and 7777; as they cover the whole range of seed production relatively evenly.

**Seed Dispersal** SEED DISPERSAL is modelled stochastically based on a probability distribution specifying the seed dispersal kernel for the seed dispersed from an individual plant. Six Weibull kernels were chosen based on expert estimates (for details see Chapter 3). Five parameter sets are based on individual expert estimates, while the sixth represents the average of these estimates (see Figure 4.3).

#### 4.2.4. Derivation of Area Source Kernel (ADK) from Point Source Kernel (PDK)

The PDK used for the simulations are derived as described in Chapter 3, i.e. Weibull distributions with the scale and shape parameters determined by using a maximum likeli-



hood approach based on the estimates of five experts (BW, DM, DR, JH, TG) as well as the average estimate (Mean)

$$\text{PDK}(D) = \frac{\gamma}{\alpha} \left( \frac{D}{\alpha} \right)^{\gamma-1} \exp \left( - \left( \frac{D}{\alpha} \right)^{\gamma} \right) \quad (4.3)$$

where  $\alpha$  is the scale parameter and  $\gamma$  is the shape parameter. If we multiply  $\text{PDK}(D)$  with  $T_a$ , the number of seeds dispersed from the point source, we obtain the predicted seed rain  $S_N(D)$  from the point source at distance  $D$ :

$$S_N(D) = T_A \text{PDK}(D) \quad (4.4)$$

The values for  $\alpha$  and  $\gamma$  for the different experts are listed in Table 4.2.

For a seed originating from the area source in the west, the direction it disperses from to a given distance  $D$  on the simulated landscape ranges between, but excludes, north  $(-\frac{\pi}{2})$  and south  $(+\frac{\pi}{2})$ . We call this direction  $\beta$ . The potential dispersal distance of a seed depends on direction  $\beta$  and is between  $D_\beta$ , the distance from the location of the seed after dispersal to the edge of the area source in direction  $\beta$ , to infinity (see Figure 4.1). Therefore, we can describe the probability that a seed is dispersed to a distance  $D$  on the simulated landscape from the area source in the west, i.e.  $\text{ADK}$  with

$$\text{ADK}(D) = a \int_{-\frac{\pi}{2}}^{+\frac{\pi}{2}} \left( \int_{D_\beta}^{\infty} \text{PDK}(x) dx \right) d\beta \quad (4.5)$$

where  $a$  is a standardisation factor to guarantee that

$$\int_0^{\infty} \text{ADK}(D) dD = 1 \quad (4.6)$$

so that  $\text{ADK}(D)$  is a PDF (Probability Density Function). With

$$D_\beta = \frac{D}{\sin(\beta)} \quad (4.7)$$

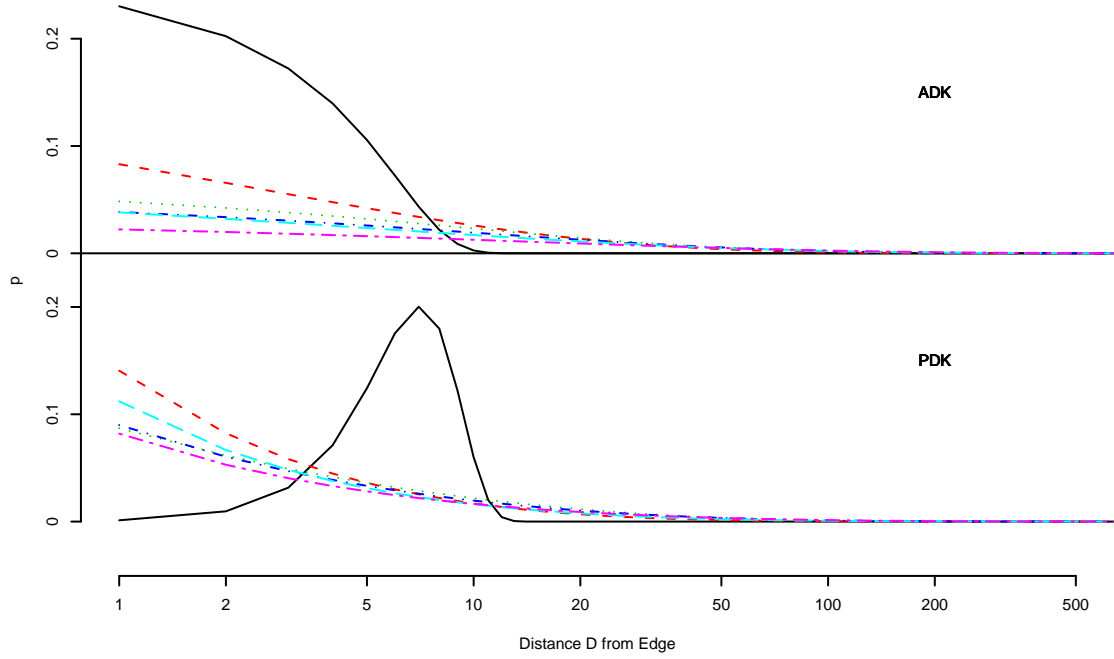
follows

$$\text{ADK}(D) = a \int_{-\frac{\pi}{2}}^{+\frac{\pi}{2}} \left( \int_{\frac{D}{\sin(\beta)}}^{\infty} \text{PDK}(x) dx \right) d\beta \quad (4.8)$$

As Equation 4.8 cannot be solved analytically in the case of  $\text{PDK}(D)$  being a Weibull distribution, it was solved numerically by using R (R Development Core Team, 2005).

#### 4.2.5. Derivation of Number of Seeds Dispersed from the Area Source into the Simulated Landscape

As shown in the previous Chapter, we can derive the  $\text{ADK}$  from the  $\text{PDK}$ . In addition to the shape of the kernel, Equation 4.8 also provides information on the number of seeds expected on a transect eastwards from the edge of the area source. This information



**Figure 4.4.:** Dispersal kernels from an area source (ADK), upper graph, and from the point source (PDK), lower graph. The colours and pattern indicate the different seed dispersal kernels based on the expert estimates: JH: solid black, DR: dashed red, DM dotted green, TG dot-dash blue, Mean long-dash cyan and BW two-dash magenta

is represented in the factor  $a$ , which standardises  $ADK(D)$  (Equation 4.8) to one. If we multiply  $PDK(D)$  with the seed production per sqm ( $T_{sqm}$ ), we obtain the seed rain which can be expected at any given distance from the edge:

$$S_{sqm}A(D) = a \int_{-\frac{\pi}{2}}^{+\frac{\pi}{2}} \left( \int_{\frac{D}{\sin(\beta)}}^{\infty} T_{sqm} \cdot PDK(x) dx \right) d\beta \quad (4.9)$$

$$= T_{sqm} \cdot a \int_{-\frac{\pi}{2}}^{+\frac{\pi}{2}} \left( \int_{\frac{D}{\sin(\beta)}}^{\infty} PDK(x) dx \right) d\beta \quad (4.10)$$

$$= T_{sqm} \cdot ADK(D) \quad (4.11)$$

We obtain  $S_{sqm}A(D)$ , representing the expected seed rain per sqm at distance  $D$  from the edge on the simulated landscape originating from the unlimited area source in the west,

**Table 4.2.:** Scale parameter  $\alpha$  and shape parameter  $\gamma$  for the five different dispersal scenarios based on the expert estimates. For further discussions, the sorting order of the experts is kept the same.

Expert	Parameter		$a^{-1}$
	Scale $\alpha$	Shape $\gamma$	
JH	7.6	4.00	13.777
DR	5.1	0.49	21.190
DM	17.9	0.63	50.697
TG	18.5	0.56	61.292
Mean	9.7	0.44	50.721
BW	25.3	0.49	105.119

by multiplying  $ADK(D)$  with  $T_{sqm}$  (Equation 4.11). Consequently,

$$N_{ADD}(0, \infty) = \int_0^{\infty} S_{sqm} A(D) dD \quad (4.12)$$

$$= \int_0^{\infty} T_{sqm} \cdot ADK(D) dD \quad (4.13)$$

$$= T_{sqm} \int_0^{\infty} ADK(D) dD \quad (4.14)$$

$$= \frac{T_{sqm}}{a} a \int_0^{\infty} ADK(D) dD \quad (4.15)$$

$$= a^{-1} T_{sqm} \quad (4.16)$$

represents the number of seeds dispersed in a 1 m-wide transect, originating from the edge of the area source in the west, to the east.  $N_{ADD}(0, 10.000)$  is the number of seeds dispersed along the transect in the simulated area (see Table 4.2 for the resulting  $a^{-1}$  values for the different experts). If  $N_{ADD}(0, 10.000)$  is multiplied with the north – south extent of the simulated landscape, i.e. 50 m, we obtain the number of additional seeds dispersed onto the simulated landscape originating from the unlimited area source (see Figure 4.4 for the resulting seed rain for the different dispersal kernels based on the expert estimates).

#### 4.2.6. Analysis

The spread of *H. sericea* was simulated using HakSimSpread over 4 generations, which is equivalent to a time frame between 28 years (in the case of a fire interval of seven years) and 80 years (fire interval of 20 years). The seed production used in the simulations were 25, 143, 308, 880, 2134 and 7777 seeds per generation. Combined with the seed dispersal kernels based on the estimates of the five experts and the mean of these estimates, we simulated 36 scenarios. Due to the stochastic nature of the model, these simulations were repeated 5 times and were assumed to be independent replicates of the current scenario.

To characterise the spread of *H. sericea*, we used 8 different measures. A “measure” in this context is defined as a characteristic distance in units of m of the dispersed plants from the seed source. Therefore “velocity of the measure” is the distance by which the

“measure” increases per timestep, in our context, one generation. These measures are calculated as follows: The individual plants in the simulated landscape were sorted according to their distance from the seed source in descending order, i.e.  $N_i^{dist}$  refers to the  $i^{th}$  furthest individual which is located at distance  $dist$  and individual  $i = 1$  is the individual furthest away from the initial seed area source. The measures which we used were the distance of the  $i^{th}$  individual with  $i$  equal one (x0001), five (x0005), ten (x0010), 50 (x0050), 100 (x0100), 500 (x0500), 1000 (x1000) and 5000 (x5000) respectively. The measure x0001 is equivalent to the one used by [Clark et al. \(2001\)](#) and [Cannas et al. \(2003\)](#) which is the distance to the furthest spread individual, measured from the western edge of the simulated landscape.

Based on these measures, we calculated the velocity of the spread of *H. sericea* per generation using linear regression. The five simulations of a scenario were combined and used as data points for the linear regressions, resulting in four generations  $\times$  five simulations equalling a maximum of 20 data points for the linear regressions and resulting in a total of 288 linear regressions (six experts  $\times$  eight measures  $\times$  six seed production values). The resulting velocities, i.e. the slopes of the linear regressions, will be referred as  $V_{x0001}$  for the measure x0001 for one specific expert and seed production, and respectively for the other measures. It is important to note that these velocities represent the spread per generation (or fire interval) and not the spread per year.

To determine whether these measures produce significantly different velocities, the velocities  $V_{x0001}$  to  $V_{x5000}$  of each expert and seed production were compared by investigating whether the confidence intervals overlapped. The p values were calculated using Bonferroni correction.

The  $V_{x0001}$  of all scenarios were compared with the predictions based on the methodology presented by [Clark et al. \(2001\)](#) (they refer to  $E$  as the expected velocity of the spread). This methodology calculates the expected one-dimensional velocity  $E$  based on expected extreme dispersal events from a seed source which consists of one individual point source at location 0 (determining the minimal expected dispersal velocity  $V^-$ ) and infinite point sources evenly spread at locations smaller than zero, determining the maximum expected velocity  $V^+$ .  $R_0$ , the net reproductive rate, was the seed production multiplied by the maximum germination rate in our case.

To identify the impact of the number of individual plants  $N$  as a seed source, we calculated  $V^-(N)$  and  $V^+(N)$  for  $N = (0, 1, 2, 4, 8, 16, 32, 64, 128, 256, 1024, 2048)$  for all expert estimates for a seed production of 7777 seeds, which corresponds to no biocontrol and a fire interval of 20 years.

Extending [Clark et al.’s \(2001\)](#) method, we calculated the upper 95% confidence limit  $V_{0.95}^+$  for the upper bound of the velocity  $V^+$  and a lower confidence limit of 95% for the lower bound  $V_{0.05}^-$  of the velocity  $V^-$ . To calculate these, we used the cumulative extreme disperser probability density function ( $P(x; N)$  in [Clark et al. \(2001\)](#)) and determined the velocity at which  $P(x; 1) = 0.05$  for the lower confidence limit  $V_{0.05}^-$  and  $P(x; \infty = 0.95)$  for the upper confidence limit  $V_{0.95}^+$  of  $V^+$ .

To analyse the impact of the seed production on the velocity  $V$ , a linear regression was used in which the seed production was log-transformed. Each linear regression had a maximum of 6 data points, i. e. one for each seed production, resulting in 48 separate linear regressions (six experts  $\times$  eight measures). To determine whether the slopes based on the different measures for one expert differed significantly, the same methodology as for  $V$  was used.

### 4.3. Results

When scenarios based on different expert estimates are presented, the experts are sorted according to  $V^-$  in ascending order.

In accordance with Cannas et al. (2003) and Clark et al. (2001) we found that all measures used to describe the front showed a linear relationship to number of generations

$$xn \sim t \cdot V_{xn} \quad (4.17)$$

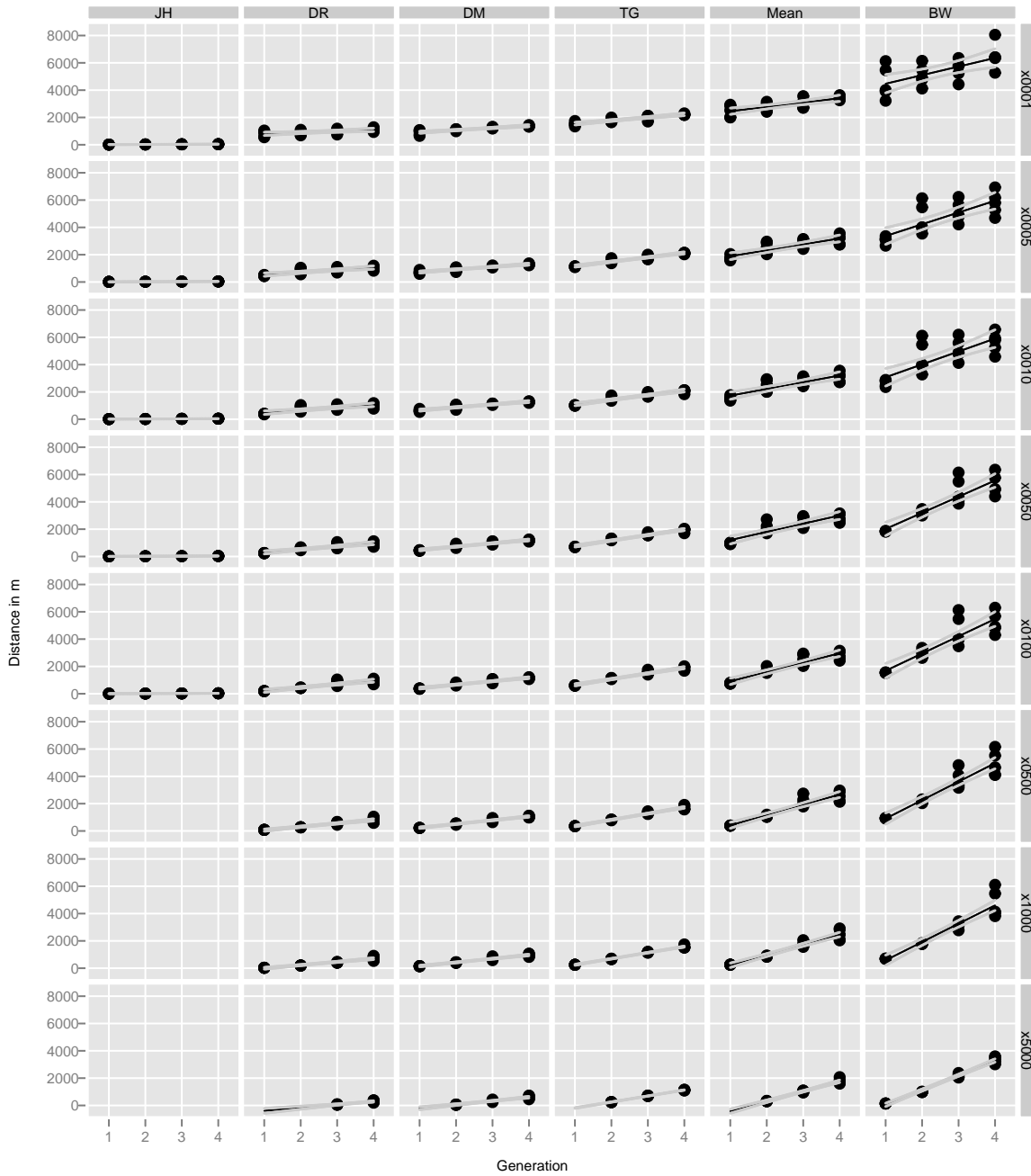
where

$$\begin{aligned} xn &= x0001, \dots, x5000 \\ t &= \text{generation} \\ V_{xn} &= \text{velocitybased} \end{aligned}$$

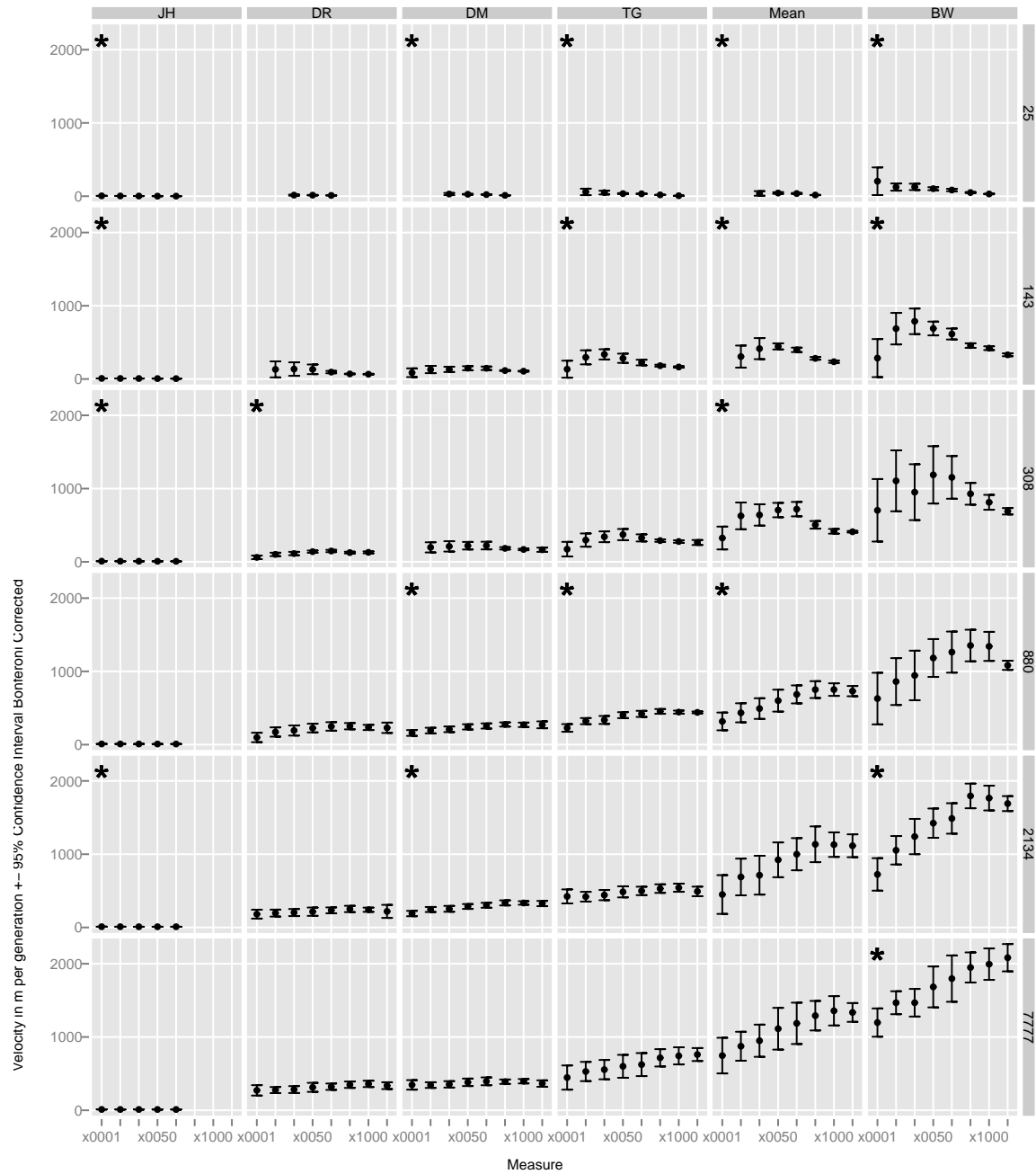
as shown in Figure 4.5 for a seed production of 528 seeds. Figures for the spread for all scenarios are provided in Appendix C. Most of the velocities determined by linear regression were significantly different from zero (see Appendix D for detailed linear regression results). Keeping expert and measure the same, the velocities increased with increasing seed production. Additionally, the velocity increased for the experts in the following order: JH, DR, DM, TG, Mean and BW, where JH had the slowest velocity and BW the largest.

Comparing the velocities based on the eight different measures in the same scenario, we found that, in 19 out of the 36 scenarios, the measures resulted in significantly different velocities with Bonferroni correction applied (Figure 4.6). Generally,  $V_{x0001}$  was the smallest velocity. The velocity increased in some cases up to  $V_{x0010}$  and decreased afterwards (e.g. expert TG with a seed production of 143 seeds) or showed a continuous increase (e.g. expert Mean with a seed production of 880).

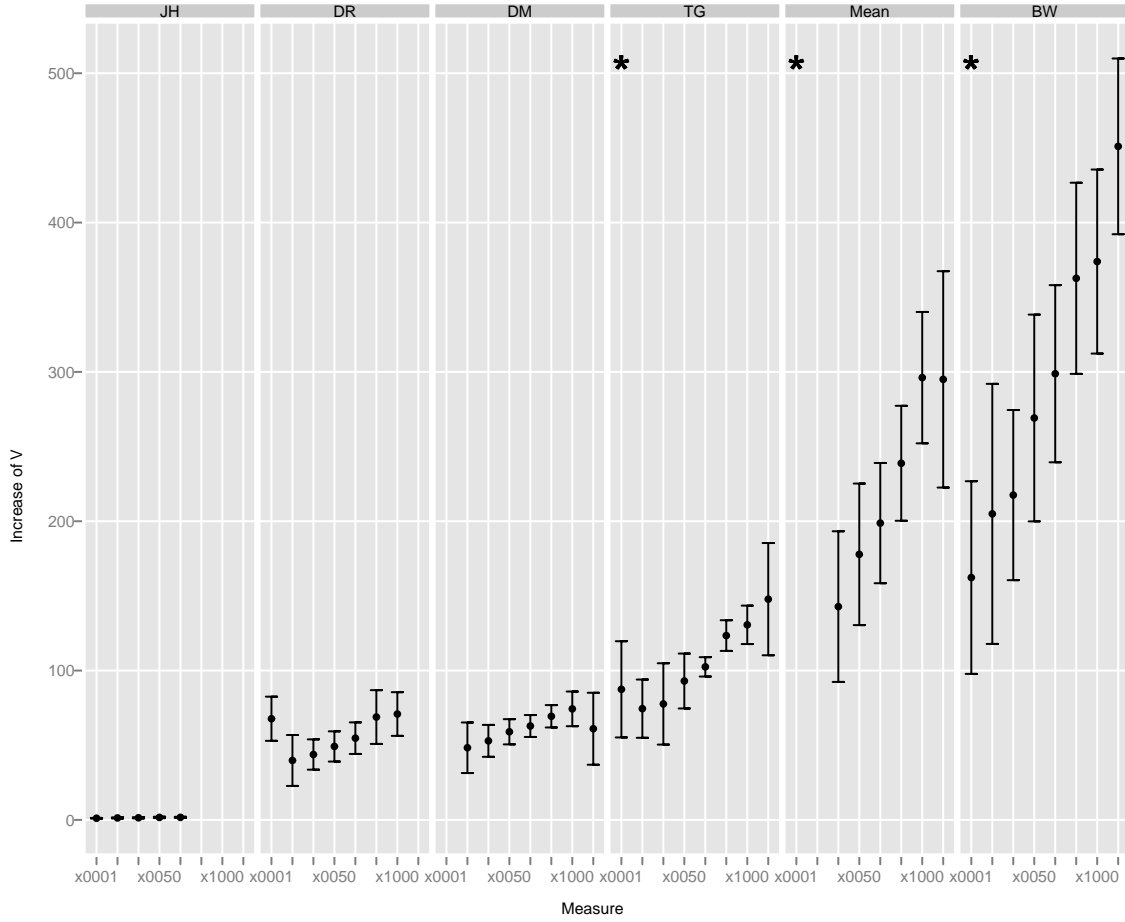
Seed production and velocity of spread showed a linear relationship between the velocity  $V$  and  $\ln(\text{SeedProduction})$  of the form  $V = m \cdot \ln(\text{SeedProduction}) + b$ , where  $m$  = intercept and  $b$  = slope (linear regressions and detailed results are provided in Figure D.1 and Table D.1). 34 out of 37 linear regressions had a slope significantly different from zero and  $R^2$  values of all but one were larger than 0.84 (one had a  $R^2$  value of 0.719). Those slopes significantly different from zero are shown, including their 95% confidence intervals, in Figure 4.7. For TG, Mean and BW, the slopes based on the different measures were



**Figure 4.5.:** Spread of the population over 4 generations with a seed production of 880 seeds per plant. The slope of the linear regression line represents the velocity of the spread of the different measures ( $V_{x0001}$  to  $V_{x5000}$ ). Each point represents a single simulation.



**Figure 4.6.:** Velocity against measures. Error bars indicate 95% confidence intervals. Scenarios for which the velocities based on the different measures are significantly different (using Bonferroni correction), are marked with an star in the upper left hand corner.

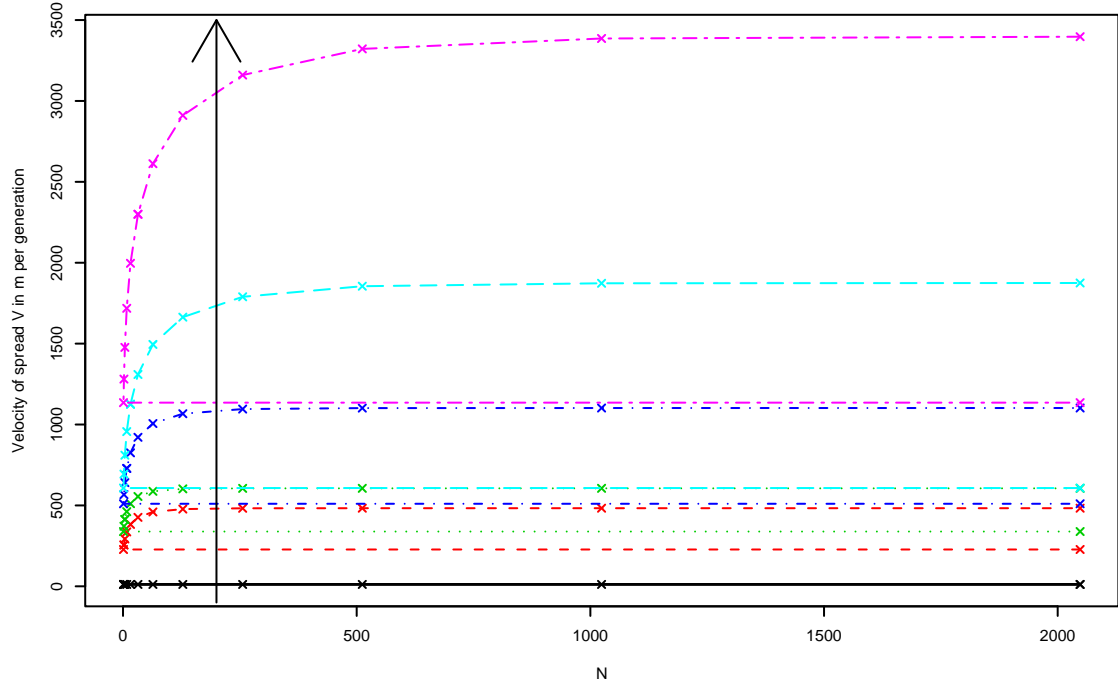


**Figure 4.7.:** Slope of dependence of Velocity  $V$  on  $\ln(\text{SeedProduction})$ . Error bars indicate 95% confidence intervals. Only slopes significantly different from zero are shown. Stars indicate significant differences (Bonferroni correction used) between the slopes based on different measures of one expert. Raw data can be seen in the Appendix, Figure D.1 and Table D.1.

significantly different (using Bonferroni correction), with the measures based on the larger numbers being larger than those ones based on the smaller values. The slopes based on the estimates from the experts DR and DM are in the same range and show the same pattern as TG, Mean and BW, namely an increase from the smaller measures (e.g. x0001) to the larger measures (x5000). Notable is DR, where the slope based on x0001 is considerably larger than the slope based on the measure of x0005. If only the slope based on x0005 is compared between the experts, the slope shows an increase from JH to BW. It is notable that for JH, the slopes are more than one order of magnitude smaller than the next steeper slope (namely x0005 of DR).

To be able to use the method presented by [Clark et al. \(2001\)](#), we first had to determine a number of  $N$  to be used to calculate  $V^+$ . We increased  $N$  from  $2^0$  to  $2^{11}$  and plotted  $V^+$  (Figure 4.8). To get an accurate estimate of  $V^+$ , a value of  $N$  larger than 512 should be used, but due to computational constraints (calculation times for the numerical calculations of the confidence limits of  $V^+$  in particular), we used  $N=200$  for the calculation of  $V^+$ . As shown in Figure 4.8, a larger estimate of  $V^+$  would not have changed the





**Figure 4.8.:** Dependence of  $V^+$  on the number of individual plants,  $N$ . The black arrow indicates the  $N$  value used for the calculation of  $V^+$ .

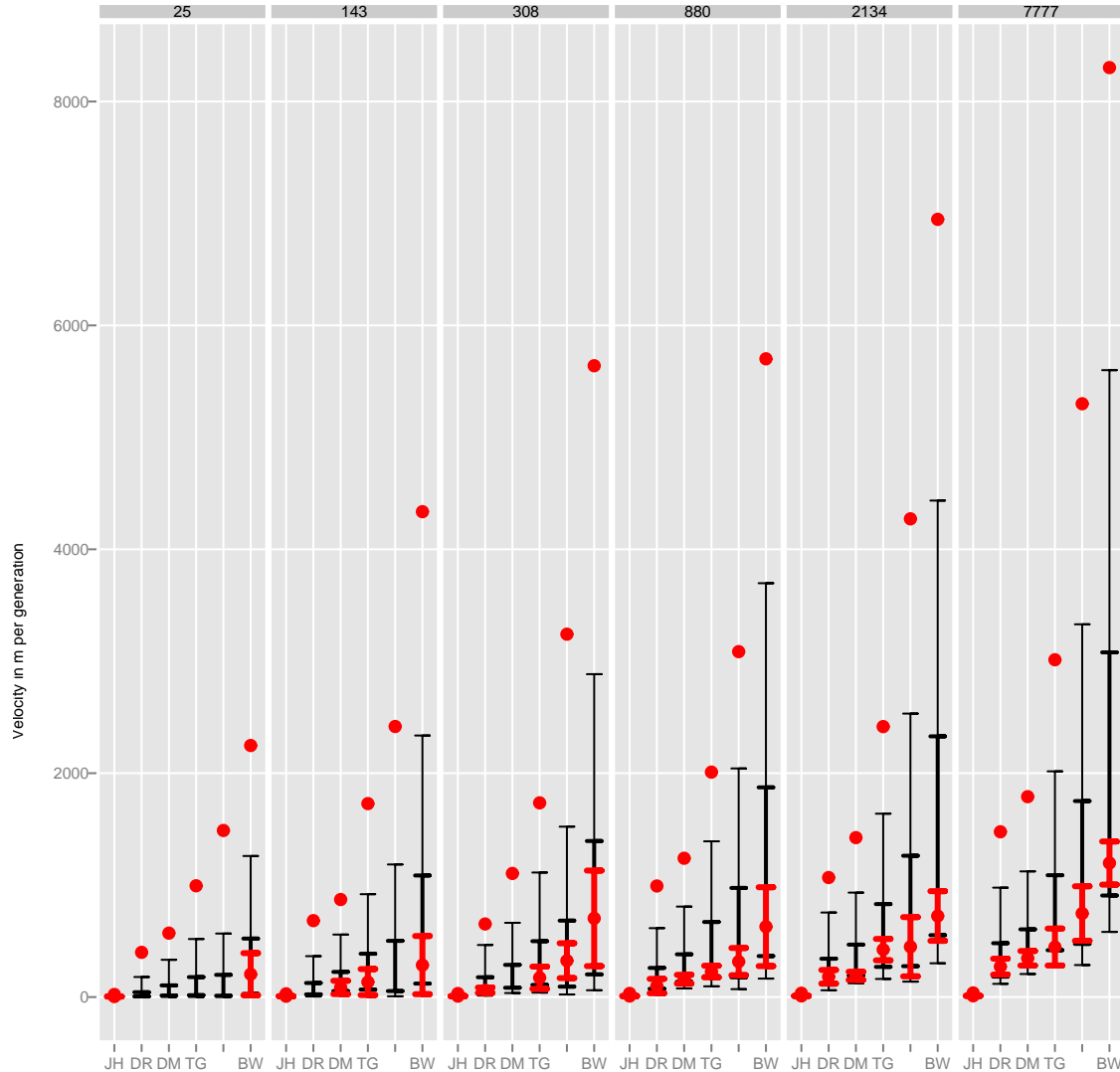
interpretation of the results.

Comparing  $V_{x0001}$ , including 95% confidence intervals, with the velocities  $V^+$  and  $V^-$  including their 95% confidence limits, we found that our simulated estimates were generally between  $V^+$  and  $V^-$  but much closer to  $V^-$  than to  $V^+$ . When including the confidence limits of the estimated velocities, no significant differences between experts were found when seed production was kept constant. Even when including varying seed production, only the more extreme scenarios were significantly different, i.e. their confidence intervals did not overlap. When including the 95% confidence limit of  $V^+$ , it is interesting to note that the maximum velocity limit is nearly twice as large as the expected value of  $V^+$ . Similarly, the 95% value for  $V^-$  is nearly half as big as the expected  $V^-$ .

## 4.4. Discussion

The velocity of spread is influenced by the shape of the seed dispersal kernel, i.e. the expert estimates, seed production, and the measure used to determine the velocity. As all measures (x0001, x0005, x0010, x0050, x0100, x0500, x1000 and x5000) used to describe the front are linearly related to the number of generations, a linear regression could be used to determine the velocity  $V_x$  which describes the velocity  $V$  based on the measure  $x$ . The comparison with  $V_{x0001}$  with the velocities based on Clark et al. (2001) confirmed that  $V^+ > V_{x0001} > V^-$ , as stated by Clark et al. (2001).

Including confidence limits for the  $V^+$  and  $V^-$  as an extension for the method presented by Clark et al. (2001) provides additional important insights into the expected velocities



**Figure 4.9.:** Comparison of velocities obtained from simulations with predictions based on Clark et al. (2001). Thick black bars denote the lower and upper estimates based on Clark et al. (2001) and the thin black bars their 95% confidence ranges. The red points represent the velocity obtained from the simulations, upper points from first generation, lower points from first to fourth generation. The thick red bars denote their 95% confidence intervals of the estimates based on generation two to four.

of spread. As  $V^+$  represents only the expected mean of the PDF representing the maximum velocity when assuming a large number of seed sources, it is important to know the confidence interval, especially the upper confidence limit. Knowledge of the maximal velocity of spread is especially important with regard to potential invasion of ecosystems by alien species. A basic understanding of the expected velocity of spread can be used to implement preventive measures, i. e. determining the minimum width of a cleared corridor to protect a nature reserve against invasion by alien plants in a patch nearby. Although  $V^+$  provides a good estimate, there is still a 50% chance that the actual velocity is higher than  $V^+$ . Knowing the 95% confidence interval of  $V^+$  adds further accuracy to the information on e.g. how wide this corridor has to be in order to prevent the spread of the species into the reserve with a 95% certainty. Knowledge of the confidence intervals in addition to the  $V^+$  also allows for sensitivity analysis of how vulnerable natural vegetation remnants might be to potential invasion by alien species occurring in the landscape. The 95% confidence of  $V^-$  does not provide such valuable information in the context of alien species, but it complements the picture when comparing the simulated or observed spread rates with the predictions of the method by [Clark et al. \(2001\)](#). The 95% confidence of  $V^-$  plays an important role when looking into restoration-related questions, e. g. how far natural habitats can be from to-be-restored sites so that natural dispersal still enables the return of the species.

The velocities obtained by linear regression, from the simulation approach and using the measure  $x0001$ , are well within the range of velocities predicted by [Clark et al. \(2001\)](#). However, when looking at the velocities in the first generation, i. e. the spread from the area source into the empty simulated landscape, the velocities are significantly higher than the predicted maximum velocities estimated by [Clark et al. \(2001\)](#) when including the upper confidence limit  $V_{0.95}^+$ . Their statement that  $V^+$  represents the upper limit of the velocity of the spread cannot be confirmed with our simulations. This discrepancy can be explained by taking the initial seed source of our simulation into consideration, i. e. an area source. [Clark et al. \(2001\)](#) argue that the maximum velocity of spread can be obtained by using a linear sequence of individual seed sources. This obviously applies to one-dimensional scenarios, where the habitat of the spreading species can be considered as one-dimensional, e. g. a riverine system. This assumption does not hold true if the system, and the seed source, is two-dimensional, i.e. an area. In our scenarios, the seed source is assumed to be two-dimensional, only limited by its east–west extent, i.e. limited to  $x$  coordinates smaller than zero. Consequently, seeds may not only originate from a one-dimensional line, but also from north and south of this line. This has been taken into consideration in the calculation of the ADK. As can be seen in Figure 4.4, the ADK provides for a thicker tail than the PDK resulting in a higher maximum velocity of the species' spread, than one based on the one-dimensional prediction from [Clark et al. \(2001\)](#).

The velocity  $V$  after the first generation is relatively constant, and no transient period, in which the velocity approaches a value independent of the initial condition, as described by [Cannas et al. \(2003\)](#), is observed. This difference is most likely due to different initial

conditions; Cannas et al. (2003) used a single area source that spread with an initial speed of  $V^-$ , while in our case, the spread originated from an area source. In the second year, more than one seed source is present, leading to  $V > V^-$ , and one would expect an asymptotic approach of  $V$  to velocity  $V^*$ . If the kernel is not exponentially bound,  $V^* = V^-$  (Clark et al., 2001).

As our initial conditions mimic an area source to the left of the simulated landscape, the initial velocity should be  $V_{\text{ADK}}^+$  and slowing down towards  $V^*$  which is expected to be close to  $V^-$ , as discussed in Clark et al. (2001). It is therefore interesting to note that, even after the first generation, the velocity drops dramatically (Figure 4.9) to a velocity not significantly different from  $V^-$ . We can therefore conclude that the spread of *H. sericea*, measured by using the measure x0001, is driven by isolated individuals resulting from extreme dispersal events as discussed in Clark et al. (2001). Additionally, the  $R^2$  values for the linear regression indicate that velocity does not change greatly between generations one to four, indicating that  $V^*$  has either been reached or that it is changing only slowly. The fact that the observed  $V$  is close to  $V^-$  clearly favours the hypothesis that  $V^*$  has been reached even after generation two.

Nevertheless, when considering the significantly different velocities based on the different measures (Figure 4.6), one can conclude that the shape of the front is changing. Interestingly,  $V$  is increasing with increasing measure, i.e. increasing number of individuals included in the analysis. This indicates that the distance between x0001 and the point at which the maximum density of the species is reached, is decreasing, i.e. more plants are coming closer to x0001. This would indicate that the velocity  $V$ , which is close to  $V^-$  for the first four generations, will increase in further generations. It is obvious that, over time, the velocities for the different measures have to adhere to

$$V_{x0001} \leq V_{x0005} \leq \dots \leq V_{x0500} \leq V_{x5000}$$

as the larger measures cannot “overtake” the smaller measures. It would be interesting to analyse this behaviour analytically, as it would give considerable insight in the dynamics of the spread.

An alternative explanation of these significant differences between the different velocities, based on the eight measures, is stochasticity in the simulations and the relatively low number of simulations per scenario. In the case of a seed production of 25 and 143 seeds per plant, more than 50% of the scenarios show significant differences in velocity (Figure 4.6). With these small seed productions, the stochasticity of the seed dispersal is much more visible than in cases with larger seed production. An example is the seed production of 7777 seeds, in which only one of six scenarios shows significant differences among the velocities based on the different measures. When excluding the scenarios using the expert JH, the number of significant differences between the velocities based on the different measures increases with increasing  $V^-$  from one, in the case of DR, to four, in the case of Mean and BW. A thicker tail of the seed dispersal kernel also increases the

stochasticity of the seed dispersal, especially when the number of seeds dispersed is small, as the probability that the seed disperses further is greater. Additionally, the limited extent of 10,000m of the simulated landscape lowers the smaller measures, as the spread is limited to the extent of the simulated landscape.

Both of these explanations for the significant differences between the velocities, based on the different measures, are valid. Further investigation into factors influencing these differences will contribute greatly to the understanding of the spread of a species. However, more simulations in larger simulated landscapes might be required to reject or verify whether stochasticity of seed dispersal is the cause of the significant differences observed or if they represent a real pattern.

An understanding of the relationship between the different measures will also enable the use of these measures in the field instead of just identifying the furthest spread individual plant ( $x_{0001}$ ). Especially in cases of species which have a high velocity  $V$ , the furthest-spread individual can be quite isolated from the other individuals and therefore difficult to locate. Consequently, misidentifying a closer individual as the furthest individual can lead to a (probably significant) underestimation of velocity  $V_{x_{0001}}$ . In contrast, the difference in distance between the 50<sup>th</sup> furthest and 51<sup>th</sup> furthest spread individual is likely to be less than between the first and second. Therefore the error in the determination of the velocity  $V_{x_{0050}}$  is likely to be considerably less than in  $V_{x_{0001}}$ , assuming that furthest-spread individual cannot be identified. Therefore the use of these additional measures adds a certain robustness to the estimate of the velocity  $V$  of the spread.

The dependence of the velocity on the expert estimate (in the simulation) is consistent with the mathematical predictions based on [Clark et al. \(2001\)](#). But no clear correlation could be found between  $V$  and  $\alpha$  or  $\gamma$  of the kernel. However, as will be discussed below, all seed dispersal kernels, which all were Weibull distributions, show a logarithmic relationship between seed production and  $V$ .

As expected,  $V$  is highly dependent on the seed production, with a logarithmic relationship between seed production and  $V$ . This relationship is, in most cases, highly significant and most of the  $R^2$  values were between 0.9 and 1. This logarithmic relationship is in contrast to [Richardson et al. \(1987a\)](#) who assumes an exponential relationship and predicts that “a 20% increase in seed numbers will increase maximum dispersal distance by 80%”.

Based on this logarithmic relationship, regarding the logarithmic axis of Figure 4.2 as a linear axis representing velocity, the dependence of the velocity  $V$  on the different biocontrol and fire interval treatments is clearly illustrated. The resulting graph now shows, even if the absolute scale of the y axis is not known, the impact of certain management actions (introduction of biocontrol agencies, manipulation of fire intervals) on the spread of *Hakea sericea*. This can assist in identifying the effects of management changes on the velocity of the spread or, if looking at one generation, at the expected spread of the population, and contributes to selecting the most appropriate management strategy to halt further spread and potential invasion of *H. sericea* at any given site. Based on the discussion above, we draw the following conclusions:

1. Changes in fire frequency can be substitutes for the introduction of biocontrol agents regarding the impact on the spread of *H. sericea*. A shorter fire interval leads to a lower seed production (see Figure 4.2) and an introduced biocontrol agent reduces the number of viable seeds. As a reduction of seeds is the aim, both strategies are valid and can substitute for each other. Consequently, a successful alien control or eradication strategy has to look at the possibility of using changes in fire frequency and biocontrol agents for controlling the invader. Changing the fire frequency must obviously consider the impact on the other species in the area to be burned, but in areas heavily infected with *Hakea sericea* an altered fire frequency is likely to be the lesser evil compared to the infestation by *Hakea sericea*. This strategy depends very much on the characteristics of the infected sites – many Fynbos species, particularly Proteaceae, may decrease in abundance or become locally extinct under fire cycles shorter than 8 years, as this prevents maturation of plants, resulting in little or no seed output.
2. If the fire interval is less then seven years, an introduction of a biocontrol agent has no real impact on  $V$ , for two reasons. Firstly, seed-feeding biocontrol agents need a certain amount of time to establish themselves after fire and to be effective in their destruction of seeds. Therefore, if the fire frequency is too short, any established biocontrol agents will be present only in small numbers and cannot destroy seeds as effectively as later after a fire. Additionally, *Hakea* only starts producing seeds after 3 years and the number of seeds produced is so low in the first years (see Chapter 3) that, because of the low germination rate, germination and establishment rate approaches zero (see Chapter 3). On sites with short fire intervals, no intervention is necessary.
3. As the fire interval increases, the introduction of biocontrol agents has a considerable impact on the velocity  $V$ , namely more then 50% when comparing no biocontrol with YFF (young follicle feeder) and MFF (mature follicle feeder) at fire intervals higher then 11 years. Again, if the fire intervals are longer, the biocontrol agents are established and about more than 99% effective (see Chapter 3). This effect is reflected in the effect on the velocity  $V$ . Biocontrol agents are thus favourable on sites that have naturally long fire intervals.
4. When the biocontrol agent MFF is present, i. e. for the treatments YFF & MFF and MFF, the seed production, and therefore the velocity  $V$ , has a local maximum at a fire frequency of 9 and 10 years respectively. This is more pronounced in the case of YFF & MFF with a reduction of the velocity  $V$  by approximately 20% when the fire frequency is increased to 11 years or by approximately 30% when decreased to 7 years. This maximum has not been confirmed in field studies, but can be explained by a faster increase of the seed production of *H. sericea* than the increase of the effectiveness of the MFF, leading to a net increase of number of seeds accumulated on the plant. In the following years, the effectiveness of the biocontrol agent increases

faster than the seed production, resulting in a net reduction of the number of seeds accumulated. A few years later, an equilibrium is reached which leads to a slow but constant increase of the seeds accumulated on the plant. If this behaviour can be confirmed in the field, these fire intervals resulting in maximal seed production should be avoided because shorter as well as longer fire intervals would result in less seeds dispersed.

Comparing the two methodologies, i.e. the simulation approach and the mathematical approach based on [Clark et al. \(2001\)](#), one must conclude that these provide the same answers in general. The main difference is in the information and data required to apply the models and the flexibility of the approach. As [Clark et al. \(2001\)](#) discuss in their paper, their approach needs a very limited set of data, namely the dispersal kernel and the net reproduction. By only using these two pieces of information, the mathematical approach can be used. In contrast, the simulation approach requires more information, and the amount and type of information needed depends on the complexity of the simulation model itself. In our case, information about seed production, germination, dependence on fire frequencies, mortality and dispersal kernel are required. On the other hand, a simulation approach makes it much easier to include other aspects like variability in the parameters, interactions among the individual plants (e.g. density-dependent seed production) and even two sexes, multiple-species systems or spatial heterogeneity in the simulation model. The effectiveness and efficiency of the approach to *Hakea* control, therefore, depends on the systems in question. In this study, the approaches are more or less equivalent.

In contrast to Chapter 3, in which no quantitative answers were given, we are now able to provide such answers on the effects of management strategies such as introduction of biocontrol agents and change in fire intervals. However, to correctly estimate the velocity  $V$  of *Hakea sericea* at certain fire frequencies and biocontrol treatments, detailed information on the dispersal kernel is required – more accurate than those currently available. Nevertheless, we can state with certainty that when  $\ln(\text{SeedProduction})$  is halved, the velocity  $V$  will also be halved.

Our results are directly transferable to other species with a similar dispersal kernel, and dispersal parameters within the range of those provided by the five experts. In this case, we can expect a linear relationship between  $\ln(\text{SeedProduction})$  and velocity  $V$ . As no detailed analysis on the behaviour outside the parameter range of the dispersal parameters was conducted, the expected linear relationship cannot be confirmed. However, the method can easily be adapted for other dispersal kernels regularly used (see [Clark et al. \(1999\)](#); [Nathan and Muller-Landau \(2000\)](#); [Skarpaas et al. \(2004\)](#) for examples), and further investigations are needed to identify commonalities and differences in spread pattern.





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## **Part III.**

# **Dispersal Modelling for Restoration**



## 5. Reconstructing West Coast Renosterveld: past and present ecological processes in a Mediterranean shrubland of South Africa

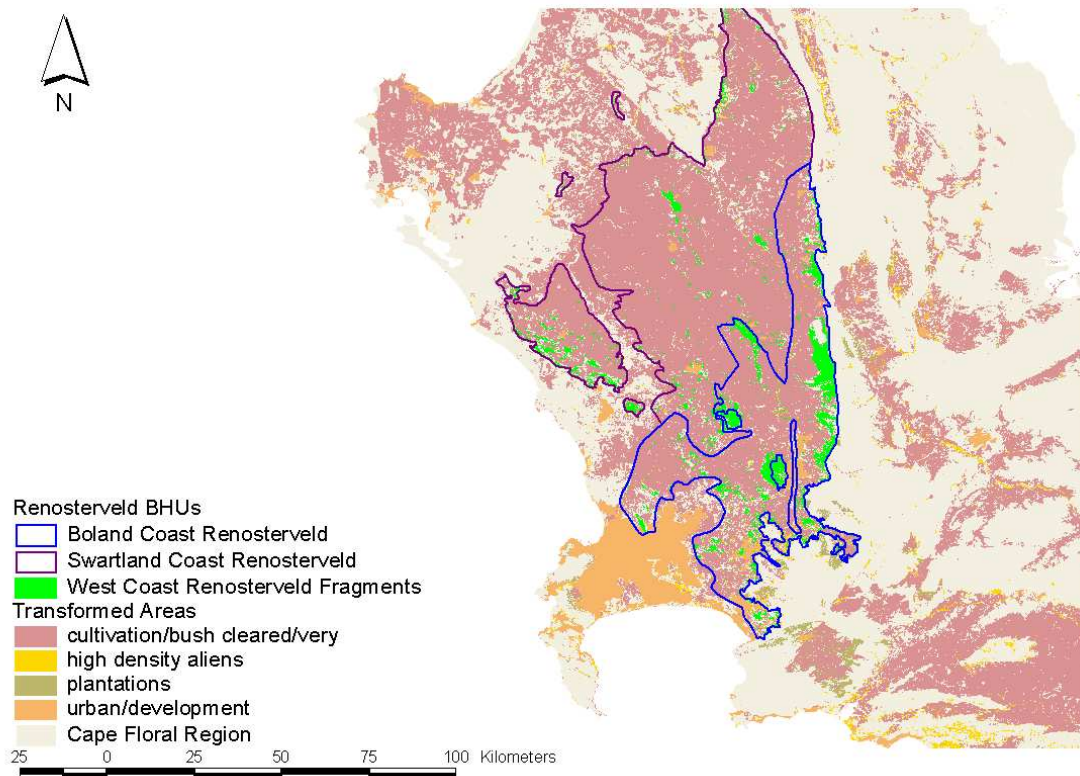
*This paper was authored by Rainer M. Krug (University of Stellenbosch), Cornelia B. Krug (University of Stellenbosch), Donald Midoko-Iponga (University of Stellenbosch), Benjamin A. Walton (University of Stellenbosch), Suzanne J. Milton (University of Stellenbosch), Ian. P. Newton (University of the Western Cape), Nicola Farley (Port Elizabeth Technikon) and Ndafuda N. Shiponeni (University of Stellenbosch), was presented at the 10th MEDECOS Conference, Rhodes, Greece, and is included in the conference proceedings. This chapter reflects the paper as published in the proceedings, except for editorial changes; the name *Elytropappus rhinocerotis* is replaced with *Dicerotheramnus rhinocerotis* throughout the document.*

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### 5.1. Introduction

Like many Mediterranean vegetation types, West Coast Renosterveld is one of the three forms of Mediterranean shrublands, as defined by [Di Castri \(1981\)](#), found in South Africa. It is exposed to a high degree of transformation and fragmentation ([Figure 5.1](#)) and less than 3% is left in a relatively-natural condition ([Low and Rebelo, 1998](#)). Furthermore, these remaining remnants are highly fragmented with only eight fragments of greater than 1000ha, and the largest fragment covering around 7400ha ([Newton, 2006](#)). Renosterveld is largely confined to fertile shale and granite soils ([Boucher and Moll, 1981](#); [Low and Rebelo, 1998](#)) with rainfall ranging from 250mm to 600mm. In areas receiving less rainfall, it is replaced by Karoo vegetation, in those with higher rainfall by Fynbos ([Boucher and Moll, 1981](#); [Low and Rebelo, 1998](#)). This combination of rainfall regime and soil results in a vegetation type which differs distinctively from Fynbos. In contrast to Fynbos, which can be characterised by restioid, ericoid and proteoid components, the predominant plant



**Figure 5.1.:** Fragmentation of West Coast Renosterveld. Dark Green areas indicate the potential distribution of West Coast Renosterveld; red areas indicate the remaining remnants. Broad Habitat Units by Cowling and Heijnis (2000), Renosterveld Fragments by Newton (2006).

types in Renosterveld are asteraceous shrubs, geophytic species belonging to the Iridaceae, Liliaceae and Orchidaceae, as well as bunch and lawn grasses (Moll et al., 1984; Low and Jones, 1995; Low and Rebelo, 1998).

Renosterveld can today be described as an asteraceous shrubland with grasses, mainly tussock grasses, and a high proportion and diversity of geophytic species (further descriptions of Renosterveld vegetation can be found in Boucher (1978, 1983); Cowling (1984); Moll et al. (1984); Jones (1986); Boucher (1987); Cowling et al. (1988); Joubert and Moll (1992); Heydenrych and Littleworth (1995)). The dominant species are the asteraceous shrubs. Main representations of this group are the Renosterbos (*Dicerotheramnus rhinocerotis*), which can grow up to two meters high but usually does not exceed 120cm, and *Stoebe plumosa*, which grows up to 50cm. Renosterbos is usually present in Renosterveld, but it is neither the case that Renosterveld can be defined through the occurrence of Renosterbos nor that the absence of Renosterbos negates Renosterveld as the vegetation type. Renosterbos can form very dense stands in which, during summer, mainly Renosterbos can be found. Nevertheless, these stands still maintain a high diversity of geophytes which are only ardent in spring when they flower. The name Renosterveld itself is derived from the Afrikaans word “renoster” which means rhinoceros. According to historical records, the black rhino was found resting or feeding in Renosterveld (which can be translated literally as “Rhino fields”) (Waterhouse, 1932). Others likened the colour (a greenish grey) and

structure of the shrubby vegetation, especially of *Dicerothamnus rhinocerotis*, to the hide of the rhino (Levyns, 1927), hence the name Renosterbos and Renosterveld (for a more detailed note on the derivations of name “Renosterveld”, see Boucher (1980)).

The fauna of the Fynbos Biome, unlike the flora, has received little attention from scientists. Bigalke (1979) gives a broad overview of the larger mammals inhabiting the Cape Floral Region, but unfortunately does not distinguish between Fynbos and Renosterveld vegetation. Among the medium-sized carnivores, mainly black-backed jackal (*Canis mesomelas*), Cape fox (*Vulpes chama*), bat-eared fox (*Otocyon megalotis*), polecat (*Ictonyx striatus*), caracal (*Felis caracal*) and even leopards (*Panthera pardus*) can be found in the mosaic of natural vegetation remnants and transformed areas. Today, antelopes are represented only by the smaller species, like Cape grysbok (*Raphicerus melanotis*), steenbok (*Raphicerus campestris*), grey rhebok (*Pelea capreolus*) and common duiker (*Sylvicapra grimmia*). The larger herbivores like eland (*Taurotragus oryx*), bontebok (*Damaliscus dorcas dorcas*), mountain zebra (*Equus zebra zebra*), red hartebeest (*Alcephalus buselaphus*) and gemsbok (*Oryx gazella*) are restricted to nature reserves and game farms with Renosterveld vegetation. Other surviving larger mammal species occurring in Renosterveld include the armadillo (*Orycteropus afer*) and porcupine (*Hystrix africaeaustralis*). The high levels of transformation and fragmentation to which this vegetation type has been subjected over the last 150 years, as well as the loss of the large mammal fauna, has supposedly lead to changes in ecological pattern and processes. Thus we suspect that Renosterveld might not always have been a shrubland, like it presents itself today. The objective of this review is to combine the results of different recent research projects on Renosterveld to come up with a hypothetical picture of processes governing Renosterveld. We will not be able to prove the scenarios statistically but will use indications from recent research and literature to argue in favour of our hypothesis.

## 5.2. 10 000 to 2 000 ybp (Prehistory)

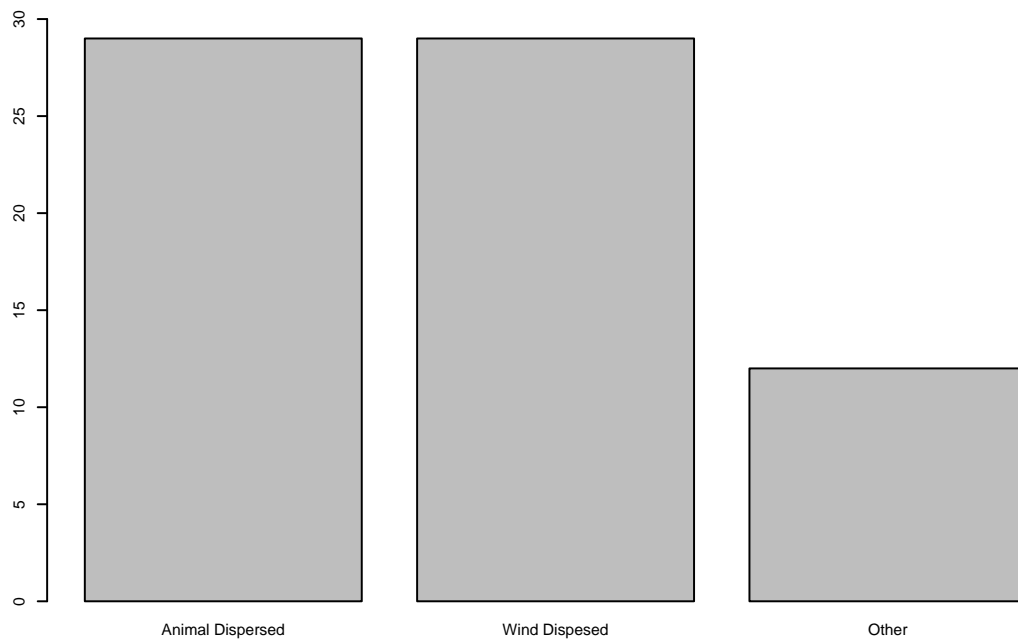
The vegetation in the West Coast Renosterveld region went through considerable climate-induced changes over the last 10 000 years. Around 10 000 ybp (years before present), when the climate was cooler and wetter than it is today, grasses were suspected to have dominated, due to a high grazer:browser ratio (Deacon and Lancaster, 1988). Around 5 000 ybp, the climate became hotter and drier, resulting in a vegetation dominated by shrubs (Deacon and Lancaster, 1988), with a cooler and wetter period occurring about 3 000 ybp, when grasses again became dominant. At 2 000 ybp, Renosterveld can be imagined as a landscape which was comprised of two components or subtypes: a shrubland component which covered the largest part of the area, and a grassland component. The shrubland was not dominated by a single shrub species, but was probably a mix of different shrub species with dominance determined by different local conditions (e.g. water availability, soil, nutrients and grazing pressure) and Renosterbos was not as dominant as it is today. Around 2 000 ybp, the climate and vegetation were similar to today, as the

**Table 5.1.:** Large herbivores occurring in West Coast Renosterveld at different times. G: grazer, B: browser; X: present at this time; E: extinct. Presence data from [du Plessis \(1969\)](#), [Klein \(1974\)](#) and [du Plessis \(1969\)](#) . Foraging strategies from [Skinner and Smithers \(1990\)](#).

		Foraging Style	2 000 ybp	1650	Today
<b>Perissodactyla</b>					
	Black Rhinoceros	B	X	X	
	Quagga	G	X	X	E
	Mountain Zebra	G	X	X	(X)
<b>Artiodactyla</b>					
	Hippopotamus	G	X	X	
	Eland	G B	X	X	
	Red Hartebeest	G B	X	X	
	Steenbok	B	X	X	X
	Grysbok	B	X	X	X
	Klipspringer	B	X	X	X
	Vaal Rhebuck	B	X	X	X
	Common Duiker	B	X	X	X
<b>Proboscoidea</b>					
	African Elephant	B	X	X	

fauna indicates, which included several larger herbivore species and carnivores. Notable are the occurrences of Eland (*Taurotragus oryx*), Red Hartebeest (*Alcephalus buselaphus*), Mountain Zebra (*Equus zebra zebra*), Elephant (*Loxodonta africana*) and Black Rhinoceros (*Diceros bicornis*). In addition to these herbivores, nearly all African carnivores could be found in Renosterveld, including Wild Dog (*Lycaon pictus*), Spotted Hyena (*Crocuta crocuta*), Brown Hyena (*Hyaena brunnea*), Leopard (*Panthera pardus*) and Lion (*Panthera leo*). A more complete and detailed list can be found in [Klein \(1977\)](#), [du Plessis \(1969\)](#) and [Skead \(1980\)](#). It is notable that, of the larger herbivores, only the Mountain Zebra can be considered as nearly-exclusive grazers ([Skinner and Smithers, 1990](#)), Table 5.1. Others can be classified as mixed feeders (e.g. Eland, Red Hartebeest), or browsers (e.g. black rhinoceros). This indicates strongly that the vegetation consisted of a varied asteraceous shrub component, as well as extensive grassy areas, consisting mainly of bunch grasses like *Ehrharta*, *Pentstemon*, *Merrimuella*, *Tribolium*, *Cymbopogon* and *Eragrostis* and the locally abundant species *Themeda triandra* and *Cymbopogon marginatus* ([Low and Rebelo, 1998](#)).

Humans inhabiting Renosterveld were the Khoekhoen. Until 2 000 ybp, they were mainly hunter-gatherers, using geophytes as an important component of their diet ([Parkington, 1977](#); [Deacon, 1992](#)). To increase the growth and abundance of geophyte species, they might have used burning on a relatively-small scale ([Deacon, 1992](#)). Around 2 000 ybp, fire and grazing can be assumed to be the two main processes shaping the ecosystem. Results from two experimental studies, one focusing on seed-dispersal distances and syndromes of Renosterveld plant species and the second looking at the impact of grazing and competition with grasses on the establishment of five selected Renosterveld species, indicate that grazing has to be considered as the driving factor in this ecosystem. Unlike



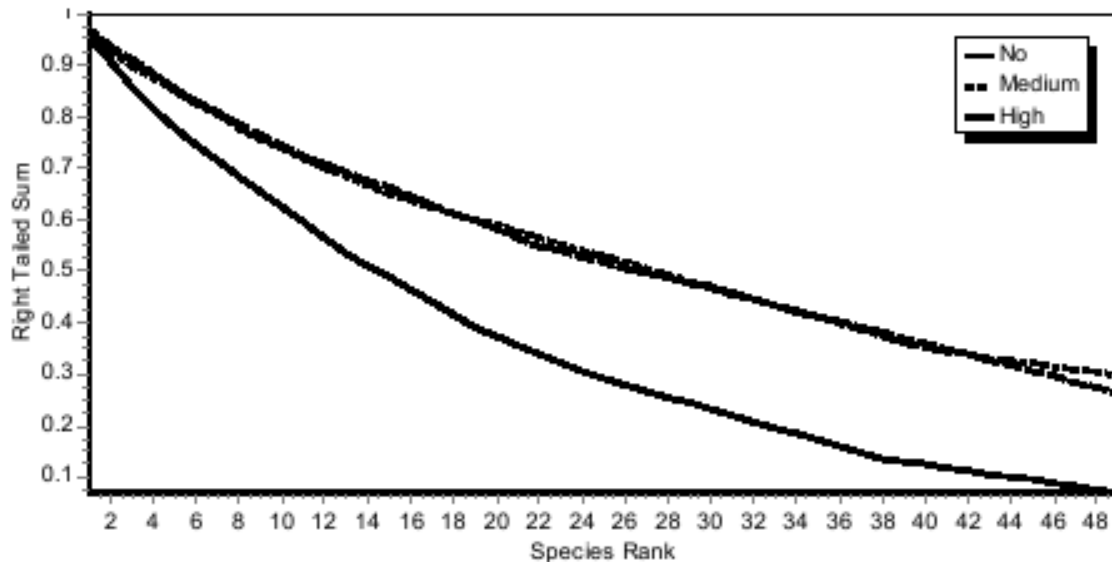
**Figure 5.2.:** Main dispersal syndromes for the species recorded in the seed dispersal study. Main dispersal syndromes were identified by visible adaptations in the morphology of the seeds. Data from Shiponeni (2003)

Fynbos, which is a fire-driven system, no adaptations of seeds to dispersal after fire were found. The two main seed dispersal vectors identified were wind (for asteraceous shrubs) and animals, mainly through the internal dispersal of seeds, (for grasses and geophytes), Figure 5.2.

In preparation for the establishment experiment, seeds of five selected Renosterveld species, four shrubs and one tree species, could be germinated in the nursery without the need for smoked water or heat treatment, as necessary for virtually all Fynbos species which are adapted to germination after fire. The establishment experiments in the field identified competition as the more important factor for the growth of the selected Renosterveld species (Midoko-Iponga et al., 2003). This can be seen as a strong indicator that the species are adapted to grazing by large herbivores. Another indicator that Renosterveld is an ecosystem driven by grazing is the species richness and diversity under different grazing pressures. Species diversity, as calculated with the Shannon-Wiener Index from data collected under three different grazing regimens (Walton, 2005), is significantly higher in the grazed than in the non-grazed plots (Table 5.2). No significant difference in species diversity could be found between the two grazed plots. This indicates a relative robustness towards grazing, especially when taking into consideration that the grazing pressure in the high grazing pressure site is twice as high as in the intermediate site. This observation is supported by the diversity ordering “right-tailed sum” graph (Figure 5.3). The two

**Table 5.2.:** Shannon-Wiener Diversity on plots with no, intermediate and high grazing. Measures obtained by using [Solow \(1993\)](#) with 10,000 random partitions. Data from Walton (in prep).

Grazing Pressure	H	Variance H	Lower 95%	Upper 95%	
No	3.8709	0.003662	3.55952	3.78377	A
Medium	4.426	0.0039158	3.97622	4.21146	B
High	4.3991	0.0030997	4.00772	4.21676	B



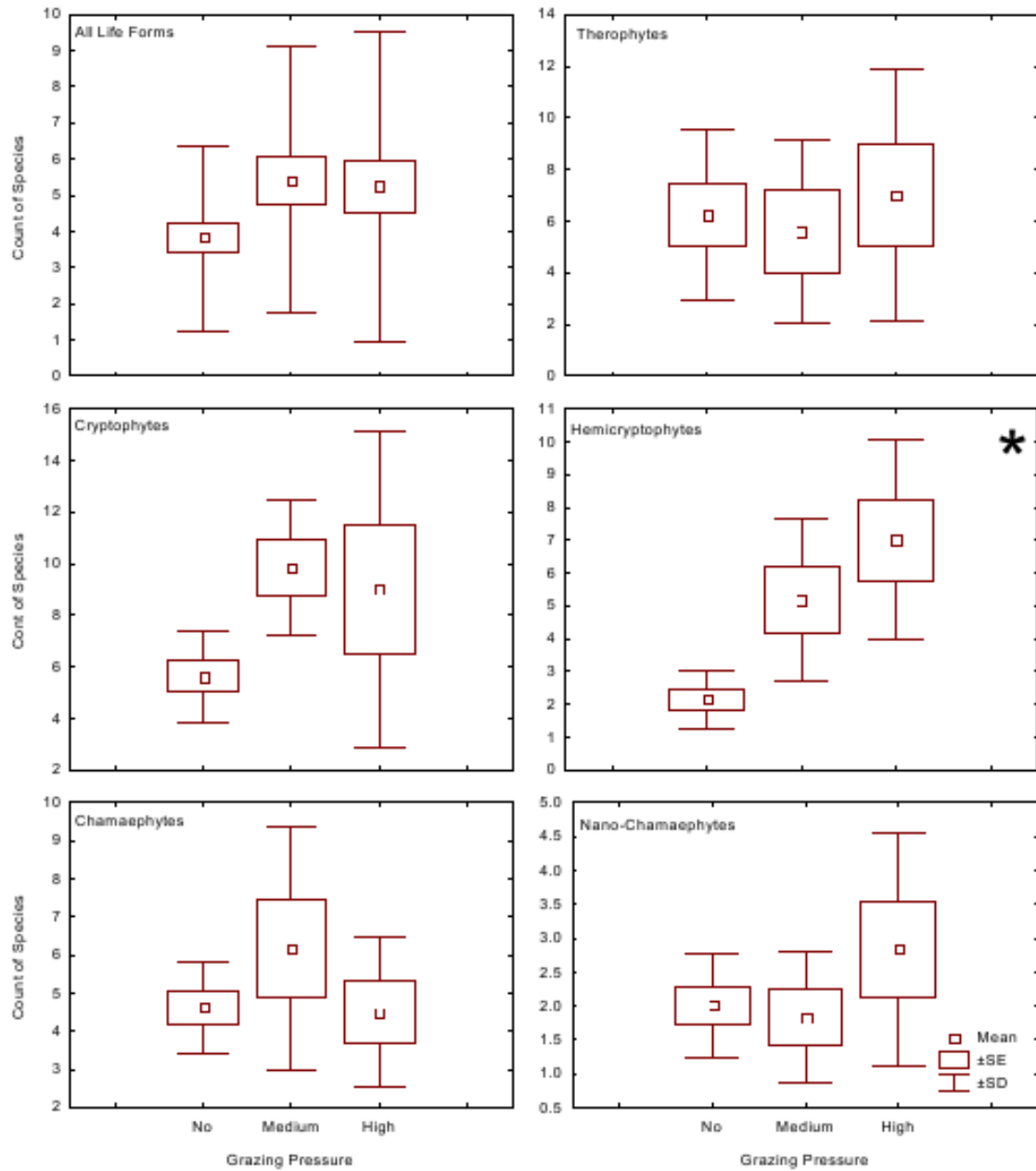
**Figure 5.3.:** Right-tailed Sum Diversity Ordering of all plant species under three grazing regimes. Right Tailed Sum equals the sum of the proportions of total abundance of all species with a higher rank. Data from Walton (in prep.).

curves for the grazed sites overlap considerably and are distinctly different to the one for the non-grazed sites. Curves for the grazed sites are also noticeably flatter than the one for non-grazed sites, indicating that many species have similar abundances.

Regarding life form types and number of species, only hemicryptophytes showed a significant difference between the three grazing regimes when a Sequential Bonferroni correction is applied, while cryptophytes showed a trend towards significance (Figure 5.4). This, and the results cited above, indicate that grazing had a lesser influence on species diversity than on abundance of species and life forms, and grazing lead to a more equal distribution and abundance of species. This supports the hypothesis that the landscape before the large herbivores were removed was not dominated by *Renosterbos* as much as it is dominated now.

Summing up, in the time before 2 000 ybp, West Coast Renosterveld can be seen as a grassland shrubland mosaic with high shrub species diversity. The shrubland covered the majority of the area. The processes which maintained this system were grazing by indigenous herbivores, trampling and, to a lesser extend, fires on a spatially-small scale. Fire played a role only in the opening of shrubby areas but the main process maintaining high species diversity was grazing.





**Figure 5.4.:** Number of species in plots subjected to three different grazing regimes. High grazing equals twice the number of animals than under medium grazing. Samples were taken at 10m2 plots. \* indicates significant differences with Sequential Bonferroni . Statistical values: All Life Forms: H2, N=111 = 3.131975  $p = 0.2089$ ; Therophytes: H2, N=19 = 0.3690402  $p = 0.8315$ ; Cryptophytes: H2, N=20 = 6.755395  $p = 0.0341$ ; Hemicryptophytes: H2, N=19 = 10.26947  $p = 0.0059$ ; Chamaephytes: H2, N=20 = 1.110550  $p = 0.5739$ ; Nano-Chamaephytes: H2, N=20 = 1.306121  $p = 0.5205$ . Data from Walton (in prep.).

### 5.3. 2 000 ybp – 1652

Approximately 2 000 ybp, another factor came into play: with the arrival of domestic stock (sheep, later followed by cattle), Khoekhoen adopted a herding lifestyle (Schweitzer and Scott, 1973; Schweitzer, 1979; Klein, 1986). At the same time, they began using fire on a larger spatial scale than previously, managing the natural vegetation to obtain suitable and sufficient grazing for their livestock (Thom, 1952). These fires played an important role in the system at this time, as they were on a large scale and with relatively short fire rotation times (Thom, 1952, 1954). This led to an increase in the grass component and thus to the creation of large areas of grassland. The impact on these enlarged grassy areas was substantial as the burning intervals were relatively short and the number of domestic live stock, mainly cattle and sheep, were rather high: records of the early settlers indicated herds of around 10 000 – 20 000 cattle and sheep (Thom, 1952). These grazing grounds were subjected to brief periods of intense grazing until the Khoekhoen moved on. Before moving on to a new area, the old “degraded” area was burned (Thom, 1952). They returned to the same area after 1–4 years (Thom, 1952; Smith, 1992) which indicates a heavy influence on these areas and their surroundings. In contrast to this, the hunting pressure on indigenous herbivores did not increase compared to earlier times, and the indigenous fauna did not change much (based on Klein (1974)). Their impact on the unburned areas therefore stayed the same. It can therefore be hypothesised that the shrub diversity did not change substantially during this time period, at least on the areas not used for grazing by the Khoekhoen. For this time period of nearly 2 000 years, the importance of processes in the ecosystems was split: in areas which the Khoekhoen used for grazing, the natural processes which previously drove the ecosystem were essentially eliminated: it is unlikely that herbivores used these areas as the palatable species were already grazed by cattle and sheep and the Khoekhoen returned as soon as the new vegetation came back. Fire became the major process, together with seasonal very heavy grazing of domestic livestock, determining the vegetation composition of the ecosystem. Summing up, the system became patchier than previously. In addition to the still existing but less extensive grassland – shrubland structure with high shrub diversity, large stretches were transformed to grasslands with relatively small number of remaining species appeared.

### 5.4. 1652 – 1900 European Settlers

With the arrival of the European settlers in the 17<sup>th</sup> century, the rate of transformation of the landscape increased, as the influence of the European settlers was different to that of the Khoekhoen herders in several regards. The settlers did not follow a nomadic life style, but established permanent settlements with gardens, paddocks and crop and live stock farming. The settlements themselves were relatively small, and at the beginning, the direct influence on the natural veld, apart from direct transformation, was relatively minor. Nevertheless, these settlements formed nuclei for the further transformations of

the landscape. Influences on the surrounding landscape were various, ranging from direct transformation for housing and infrastructure, through water use and waste disposal and expanding agriculture, mainly livestock and crop farming. The animals, mainly cattle and sheep traded from the Khoekhoen (Leibbrandt, 1901, 1902; Thom, 1952, 1954, 1958) but also, especially in the later stages, brought in from Europe, were not moved in a nomadic fashion. As indigenous animals, mainly game birds and large game, were very abundant in Renosterveld, hunting for domestic consumption (Thom, 1958) was introduced by the Europeans. This led to the local extinction of most of the larger indigenous herbivores, including the Bluebok (extinct about 1800 (Skinner and Smithers, 1990), but never recorded from West Coast Renosterveld in last 10 000 years (Klein, 1974)) and the Quagga (extinct about 1875 (Skinner and Smithers, 1990)). With the removal of these large herbivores, the main driving factors for the ecosystem were removed, namely grazing and trampling by these larger indigenous herbivores. Thus, the dispersal of the seeds of many species, especially geophytes and grasses, was reduced, while the seed dispersal of asteraceous shrubs, mainly by wind, was not impacted. With the disappearance of the herbivores, grazing of palatable shrubs and grasses and trampling ceased. These disturbances had previously opened gaps, which were important habitats for shade-intolerant species, like many geophytes. Without large herbivores, the shrublands remained closed and covered as continuous patches over large areas, therefore a shift in the dominance structure of shrub species occurred. As a lower disturbance regime favours longer-lived plants, it is expected that shrubs would have survived better; Renosterbos e.g. has a life expectancy of at least 50 years (Boucher, 1983). Another property of *Dicerothamnus rhinocerotis*, which led to a fast spread and dominance of large areas, is its invasiveness. *D. rhinocerotis* is an excellent invader of disturbed areas (Levyngs, 1929) due to its high seed production and huge dispersal distances. This, therefore, offers an explanation of why Renosterveld today is dominated by shrubby vegetation with the dominant shrub species being *Dicerothamnus rhinocerotis*. At the same time, the grassy areas decreased dramatically in size as *Dicerothamnus rhinocerotis* was able to invade grasslands, but lawn grasses seem unable to invade undisturbed shrublands (pers. obs.). As a kind of cascade effect from the removal of the large herbivores, the fire frequency, intensity and scale very likely changed dramatically in this time. A smaller number of large herbivores and an increase of shrubby vegetation lead to an increased fuel load in the landscape which was in addition also quite homogeneous for large areas. This led probably to hotter and larger-scale fires. This, in turn, promoted a further homogenisation of the landscape towards shrublands. Renosterveld provided excellent opportunities for crop farming due to its fertile soils and relative flat topography. In this context, *Dicerothamnus rhinocerotis* was considered as an indicator for good farmland (Talbot, 1947), as it grows on relatively fertile soil compared to Fynbos species like Protea species which grow on rather poor, usually-acidic soils (e.g. Kruger, 1979). Summarised, the removal of the indigenous large herbivores was the main early influence of the European settlers on the Renosterveld system. Through direct impact cascading effects on fire frequency, intensity and scale, it changed the system

from a rather heterogeneous grassy state with a variety of shrub species with *Dicerothamnus rhinocerotis* “one among others”, into a relatively-homogeneous shrubby system with *Dicerothamnus rhinocerotis* as the dominating species.

## 5.5. Modern Agriculture

The development of efficient transportation systems to serve the market caused by the discovery of gold and diamonds inland, led to the development of intense agricultural practices over much of the area that was home to West Coast Renosterveld (Talbot, 1947), (mainly wheat, vine, olives). This transformation led to a radical fragmentation of the remaining natural vegetation up to today where currently only about 5% of the original West Coast Renosterveld remains (Low and Rebelo, 1998), of which less than 1% is formally conserved (Low and Rebelo, 1998) and the largest patch is ca. 7400ha (Newton, 2006). Studies in other areas have shown that fragmentation can have a huge impact on an ecosystem and on the survival of species in isolated and small patches (see e.g. Saunders and Hobbs, 1991). An example of these impacts on Renosterveld was found e. g. in the pollinator – plant interactions. Donaldson et al. (2002) showed that abundances of certain pollinator species, like bees and monkey beetles, were significantly lower in small fragments than in large ones. In addition, four of the seven plant species examined showed a reduced fruit and seed set in smaller and isolated fragments. For one orchid species (*Pterygodium catholicum*), they showed through hand pollination that the reduced seed set was pollination-limited. Nevertheless, most of the effects of fragmentation on Renosterveld are speculative, as not much research has been done in this field (see e.g. Kemper et al. (1999) and Kemper et al. (2000)). In addition to the direct effects of fragmentation on the flora and fauna itself as discussed above, it also affects other processes, namely fire and grazing. Firstly, by the fragmentation of the habitat, more of the larger indigenous herbivores disappeared from West Coast Renosterveld, removing the previously-essential processes of grazing and trampling, as mentioned above. Secondly, due to the removal of the remaining large herbivores and the extremely small fragment size, the fire regime changed dramatically. On the one hand, the lower browsing pressure led to a much higher accumulation of fuel for fires, with consequentially hotter fires, as also mentioned above. Grazing pressure was probably higher, but more selective with domestic stock. This prompted farmers to brush cut Renosterveld patches, especially along roads, to minimise the danger of fires spreading from natural Renosterveld into farm land, essentially preventing all fires in these patches. Furthermore, several patches of Renosterveld are surrounded by urban development (e.g. Tygerberg Nature Reserve, Signal Hill) which also led to a strict exclusion of fires due to the risk of it spreading into the urban areas. Another threat to the remaining patches of Renosterveld is the increased use of agricultural chemicals (e.g. insecticides, pesticides, and fungicides), especially when sprayed by planes. Alien species play an important role as modern threats in Renosterveld. Among the plants, mainly Australian acacias, herbs (e.g. *Echium plantagineum* (Paterson’s curse)) and grasses (European pasture grasses)

play an important role as invaders. Up to now, it is unclear what effect they have had on Renosterveld. Their behaviour after fire, whether they invade freshly-burned areas or whether they are out-competed by indigenous plants, is an open question. Concerning alien invasive animals, feral pigs pose a big challenge as they severely disturb large patches ( $>100\text{m}^2$ ) while digging for geophyte bulbs (Peter Viljoen, pers. comm.). In contrast to the porcupine, which also digs for bulbs, a single disturbance caused by the feral pig is much bigger in scale and they are much less selective in their selection of bulbs (pers. obs.). Invasive ant species, particularly the argentine ant, do not play an as important role as invaders as in Fynbos, as it does not seem that ant dispersal is an important dispersal agent in Renosterveld (Bond and Slingsby, 1983; Shiponeni, 2003). Based on these transformations, Renosterveld today is an agricultural area with small isolated shrubland patches with no grazing from large indigenous herbivores. When fires occur, they affect a whole patch and enhance invasion by alien species.

## 5.6. Positive Trends

Apart from the above-discussed transformation of the fauna and the flora in Renosterveld through changes in the land use and modifications of the processes driving the ecosystem, there are also positive trends: the conservation of the remaining patches of natural vegetation and even restoration of a Renosterveld-like system. This is based on the possibilities of eco-tourism, mainly based on wildflower and game watching. In both instances, the veld needs to be in a relatively-natural state to provide the diversity of flowers and to form an important aspect in game farming (Farley in prep.).

## 5.7. Conclusions

Renosterveld consisted and still consists of two different forms of vegetation: a grassland and shrubland. The grassland formed the matrix and the shrubland the patches in the matrix. The balance between these two forms of Renosterveld was influenced by climate and human activities which led to the total extinctions of one species, the Quagga, and to the local extinction of all other larger herbivores. Today, we are only left with small, isolated fragments dominated by shrubs. These changes can be attributed to human actions, particularly the removal of the large herbivores and therefore elimination of grazing by these animals, in what is essentially a grazing-driven ecosystem. This, in conjunction with the fragmentation of the remaining Renosterveld, has led to a tremendous change in the nature of the fires occurring. To conserve West Coast Renosterveld, it is important not only to consider the conservation of the remaining patches, but also the restoration of abandoned lands in a “natural” state to enable them to be used as corridors, stepping stones or even additional habitat. In the context of restoration, the question of what is the goal for restoration needs to be addressed, i.e.: for what do we want to use the restored areas, and what do we want them to look like? Do we want them to resemble “natural”

Renosterveld, and if yes, how should it look? We suggest envisaging Renosterveld as a system which consists of the above mentioned forms of shrubland and grassland and a suite of other associated species. Restoration attempts should consider these two forms, as both forms play an important role in the dynamic of the system and enable farmers to use Renosterveld for game farming and even, if the veld is carefully monitored, for domestic livestock.

## 5.8. Acknowledgements

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## 6. Modelling Seed Dispersal for Restoration of Old fields in Renosterveld - from Area Source to Point Source

### 6.1. Introduction

Seed dispersal models play an essential role in predicting the rates of invasion of alien plants into natural vegetation (Higgins and Richardson, 1999), in understanding and predicting recolonisation rates of economically important tree species into clear-felled sites (Greene and Johnson, 1996), and in planning the conservation and restoration of species and vegetation (e.g. Bullock and Clarke (2000)).

Nathan and Muller-Landau (2000) classify seed dispersal models into two categories, namely phenomenological seed dispersal models and mechanistic seed dispersal models. Mechanistic models are directly based on the properties of the plant and its seed dispersal agent. They are usually quite complex and require considerable knowledge about the species, dispersal syndrome(s) and agent(s) and parameter(s) influencing the dispersal process. These models are therefore able to predict the seed rain. Phenomenological models are based on probability density functions (pdf), often referred to as seed dispersal kernel (Nathan and Muller-Landau, 2000) or dispersal term Greene and Calogeropoulos (2002), that are fitted to the observed seed-dispersion pattern (Nathan and Muller-Landau, 2000). The selection of the functional form of the dispersal kernel is based on the objective to describe the observed seed-dispersion pattern as closely as possible, independent of seed dispersal mechanisms, while minimising the number of parameters. Therefore these models describe the seed rain and usually do not have much predictive power outside the sampled distance range.

Although phenomenological models cannot be used to predict seed-dispersion pattern beyond the system studied (Nathan and Muller-Landau, 2000), they are suitable for comparing resulting seed dispersal kernels of different species and can be used to predict and analyse dispersal and potential spread of species.

When seed rain is measured in the field, seeds trapped rarely originate from a single plant, unless in a controlled experiment (e.g. Bullock and Clarke (2000)), but rather from several plants of which the positions are known (Nathan et al., 2001) or from a large number of plants which are covering an area relatively homogeneously (Greene and Johnson, 1996). The nature of the seed source (i.e. single point source, multiple point sources or area source) determines how to describe the seed dispersal kernel.



In the case of a single point source (e.g. [Bullock and Clarke \(2000\)](#)), all seeds originate from one single plant and the seed dispersal kernel is directly based on the observed seed-dispersion pattern. If the seed source consists of more than one point source with known locations, an inverse approach can be used to reconstruct the seed dispersal kernel of an individual ([Ribbens et al., 1994](#); [Clark et al., 1998, 1999](#); [Nathan and Muller-Landau, 2000](#)). For an area source, this reconstruction of an individual seed dispersal kernel is, in most cases, not possible due to a high number of point sources involved, missing information of their locations or if the extent of a single plant does not justify the use of a point source approach.

In landscapes where natural vegetation is highly transformed and fragmented by agricultural activities, conservation of viable vegetation fragments may depend on restoration of old fields to provide corridors among fragments or to increase fragment size ([McIntyre et al., 1996](#); [McIntyre and Hobbs, 1999](#)). The interventions used to restore natural vegetation to old fields will depend on the rate of natural recolonisation of the field. Where recolonisation is seed-limited, restoration of old fields might involve reseedling; but if abundant seeds are being dispersed onto the fields from the natural vegetation, then habitat amelioration (e.g. increasing water infiltration or reducing competition) might be more effective than reseedling.

An understanding of seed rain is pertinent to restoration of Renosterveld, a low shrubland vegetation of fertile soils in the winter-rainfall zone of the Western Cape of South Africa. This species-rich vegetation, which is a part of the Cape Floristic Region, is threatened as a result of past agricultural development that transformed 92% of the West Coast Renosterveld into agricultural lands ([von Hase et al., 2003](#)). The remaining natural vegetation fragments are small, with only 28% of the fragments being larger than 1ha ([von Hase et al., 2003](#)). Restoration of abandoned fields is being considered in order to link the existing fragments and to increase the area of Renosterveld under conservation. Hence, a basic knowledge about seed dispersal syndromes and dispersal distances for species in the natural vegetation is essential before planning restoration strategies.

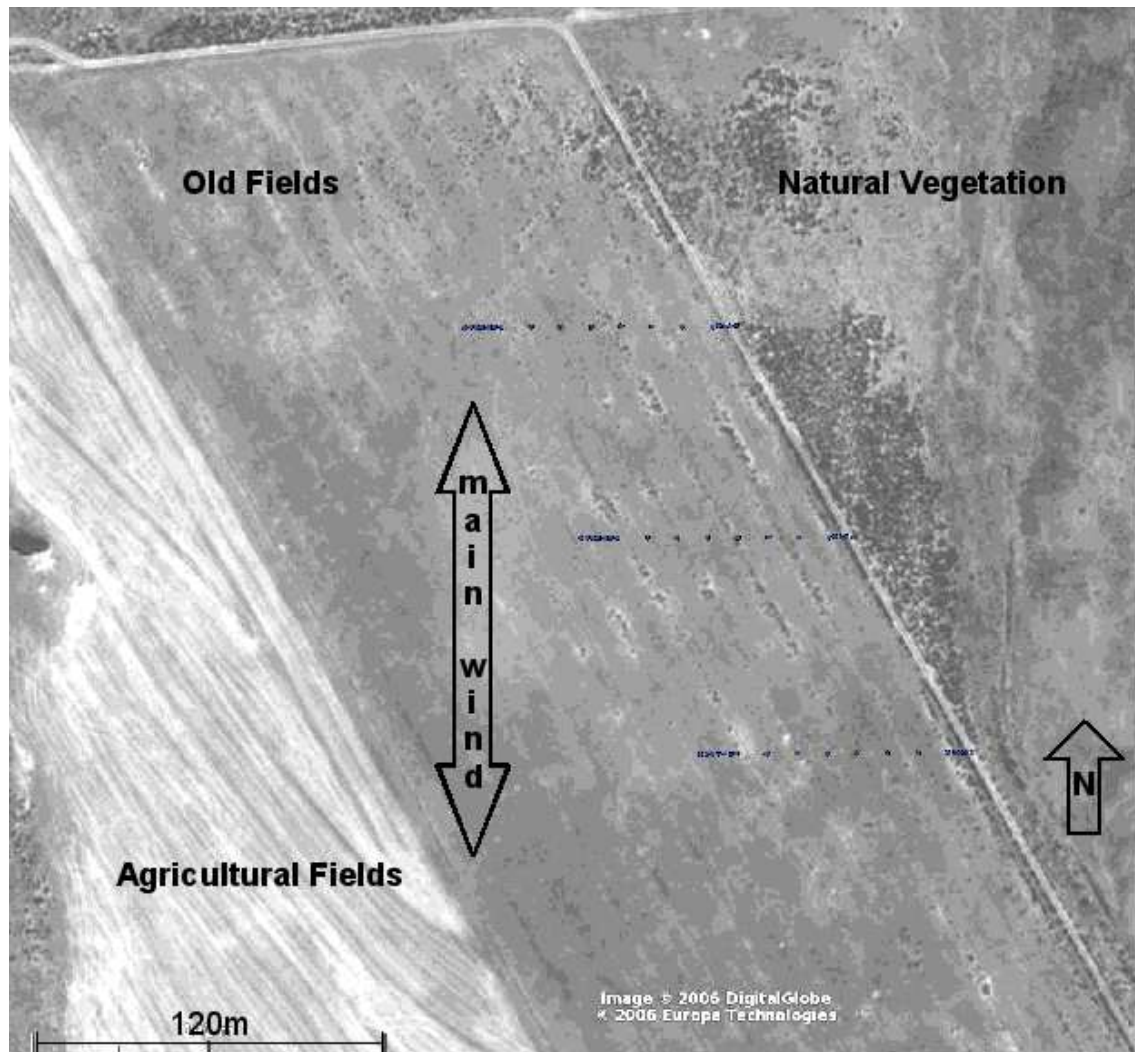
The objective of this paper is to describe the seed dispersal kernel from an area source of a wind dispersed asteraceous shrub, *Dicrothamnus rhinocerotis*, onto an abandoned agricultural field, by using phenomenological models and drawing conclusions for the seed dispersal kernel for a point source. This seed dispersal kernel from a point source will be useful to draw conclusions concerning restoration of Renosterveld.

## 6.2. Materials and Methods

### 6.2.1. Study Site & Species

The field aspects of the study were carried out in the Elandsberg Private Nature Reserve ( $19^{\circ}02' E$ ,  $33^{\circ}27' S$ ) in the Western Cape, where abandoned ploughed fields are adjacent to large areas of intact shrubland. The area has a typically Mediterranean climate with predominantly winter rainfall ([Baard, 1993](#)). Prevalent wind direction is south for most





**Figure 6.1.:** Study site at Elandsberg Private Nature Reserve. Dots indicate pit traps. “main wind” indicates the main wind direction in the study site, i. e. North–South. Satellite picture from Google Earth.

of the year, but becomes northerly in winter (unpublished data, Diemer, N). Historically, the reserve area was used for livestock grazing until 1973 when it was stocked with re-introduced indigenous antelope species. The cultivated fields investigated were abandoned in 1985, over-sown with European pasture grasses and used for livestock grazing until 1987, when they were incorporated into the reserve (Shiponeni, 2003). The sampling sub-area of 2.5ha (250m by 100m) was selected adjacent to natural vegetation and on the north-east corner of the field where the influence of active crop agriculture was negligible (Figure 6.1).

Natural West Coast Renosterveld vegetation, a low (1-1.5 m high) asteraceous shrubland, characterised by abundant grasses and geophytic species, is dominated by the shrub *Dicrothamnus rhinocerotis*. Other prominent shrubs include *Erioccephalus africana*, *Relbana fruticosa* and *Athanasia trifurcata* (Low and Rebelo, 1998), all of which are wind-dispersed. An indigenous perennial grass, *Tribolium hispidum*, dominates the grassy layer

of the natural vegetation up into the transition zone where pasture grasses take over. The vegetation on the old field is dominated by a perennial African lawn grass, *Cynodon dactylon*, in summer, and annual alien pasture grasses *Vulpia myuros*, *Briza maxima*, *Bromus diandrus*, *B. pectinatus*, *Lolium spp.* and *Poa annua* after winter rainfall. There is an ecotone of transition vegetation between the natural vegetation and old field. In this transition zone, some of the Renosterveld species are returning and waves of *D. rhinocerotis* can be observed encroaching into the field, mainly along ploughed furrows that run across the field and to the ecotone (see Chapter 7).

Empirical data obtained from seed trapping in an abandoned field are used here as the basis for modelling the seed dispersal kernels of an area source of *D. rhinocerotis*. Seeds of *D. rhinocerotis* are small ( $< 0.2\text{mm}$ ) and are equipped with a plumed pappus that enables them to become airborne (Herman et al., 2000).

### 6.2.2. Seed Trapping

Pit traps were constructed from metal cans, 9cm in diameter and 20cm high and an opening in the top with a surface area of  $63.6\text{cm}^2$ . The cans were sunk in the soil so that the lid was flush with the soil surface. This allowed both tumbling seeds and flying seeds to be trapped when the cans were open.

Three transects, each with 19 traps, were laid out in east – west direction, with the edge of the natural vegetation being north-east – south-west (see Figure 6.1). Distances of the traps from the edge of the natural vegetation ranged from 1.7m to 80.5m (see Figure 6.2 and Table 6.2). Distances specified throughout the paper will refer to the distance from the seed source, i.e. from the edge of the natural vegetation.

The distance between traps was 1.75m for the 5 traps nearest and for the 7 traps furthest from the source. The remaining 6 traps per transect (at distances of 8.7m to 70m from the seed source) were spaced at intervals of 8.75m. These differing trapping densities were chosen as a compromise between trapping effort and resolution. As the seed rain can be expected to show an early decline close to the source (e.g. Willson (1993) or Bullock and Clarke (2000)) a high resolution was required at distances close to the source to document this change. As the seed densities were expected to be low furthest away from the seed source, it was decided to have a higher trapping density at the end of the transect to describe even small seed densities and therefore the tail of the seed dispersal distribution. In the mid-range of the kernel, the trapping effort was reduced as changes in densities were expected to be small.

Seeds were trapped over four days every month over one year (September 2001 to September 2002). Each can was lined with a new plastic bag held open by a coiled strip of firm plastic and the lid was removed. At the end of the session, bags were removed and cans were closed. The seeds collected in the plastic bags were identified and counted using a dissecting microscope.

### 6.3. Analysis

Seeds of indigenous and alien species were trapped. However, only seeds from *D. rhinocerotis* were included in the analysis, since these seeds were most abundant in the traps and thus the species can be regarded as a representative of other wind-dispersed shrub species and as an important, if not a keystone, species, in West Coast Renosterveld.

Seed counts of *D. rhinocerotis* on the three transects, at each distance over the whole trapping period were summed up, resulting in a seed count for each distance. These resulting seed counts were fitted using eight seed dispersal models discussed below.

#### 6.3.1. Dispersal Models

We use the following general structure for our dispersal models to describe the one-dimensional seed rain originating from a rectangular area seed source:

$$S_N(D) = T_A p(D) \quad (6.1)$$

where  $S_N(D)$  is the total number of seeds deposited at distance  $D$ ,  $T_A$  is the total number of seeds dispersed out of the area source and  $p(D)$  describes the functional dependence on the distance  $D$ . If the seed source is a point source and  $p(D)$  a probability density function (pdf),  $p(D)$  can also be referred to as the seed dispersal kernel (Nathan and Muller-Landau, 2000). Other authors use this terminology more loosely, and use the term “seed dispersal kernel” even if  $p(D)$  is not a pdf (e.g. Bullock and Clarke (2000) for their mix model IP\_NE). As both pdf and non-pdf models are evaluated here, we use the more loose terminology of Bullock and Clarke (2000), with referring to the term  $p(D)$  as “kernel” regardless whether it is a real pdf or not.  $S_N(D)$  will be referred to as the dispersal model. This terminology, used for a point source, will be applied to an area source in our case.

The phenomenological models used to fit the data are separated into two categories, models which are pdfs and models which are not. The non-pdf models are the inverse power model (IP) and the mixed model (IP\_NE) (both Bullock and Clarke (2000)), a combination of inverse power and negative exponential. Pdfs are the negative exponential distribution (NE) (Clark et al., 1999; Bullock and Clarke, 2000), normal distribution (NM), the log normal distribution (LNM) (Greene and Johnson, 1989), the Weibull distribution (WB), a mixed model suggested by Higgins et al. (2003b) (WB\_NE) combining WEIBULL and NE and the 2DT distribution of Clark et al. (1999). The mathematical representation of the seed dispersal models and their parameters are listed in Table 6.1.

The dispersal models differ in the numbers of their parameters. IP and NE have two parameters, NM and LNM, WB and 2DT three, IP\_NE four and WB\_NE five parameters.

The parameter  $p_{WB\_NE}$  in the WB\_NE model, ranging from 0 to 1, determines which of the two components is more important: a  $p_{WB\_NE}$  of 1 indicates that the mixed WB\_NE model is equal to the first component (i.e. WB) while a  $p_{WB\_NE}$  of 0 indicates that the model is equal to its second component (i.e. NE).

**Table 6.1.:** Equations and fitted parameters used to fit the observed seed dispersal kernel  $p(D)$  for *D. rhinocerotis*. Parameter  $a_i$  of the equations was used to standardise the sum of all probabilities at trap distances to 1. Models below the horizontal line are not true probability distributions. References for the model are IP: [Bullock and Clarke \(2000\)](#), NE: [Clark et al. \(1999\)](#), 2DT: [Clark et al. \(1999\)](#), IP\_NE: [Bullock and Clarke \(2000\)](#) and WB\_NE: [Higgins et al. \(2003b\)](#).

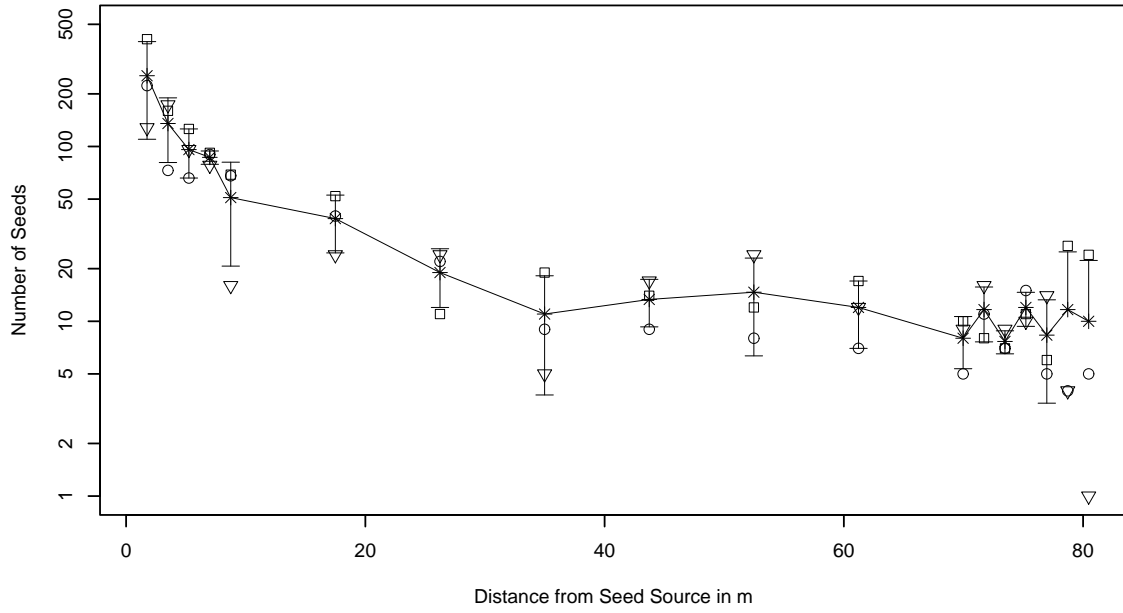
Model	Formula	Parameter	Type
Inverse Power (IP)	$a_{IP} a_{IP} D^{-b_{IP}}$	$a_{IP}$ $b_{IP}$	shape
Negative Exponential (NE)	$a_{NE} b_{NE} \exp(-b_{NE} D)$	$a_{NE}$ $b_{NE}$	shape
Normal (NM)	$a_{NM} \frac{1}{\sigma_{NM} \sqrt{2\pi}} \exp\left(-\frac{(D-\mu_{NM})^2}{\sigma_{NM}^2}\right)$	$a_{NM}$ $\mu_{NM}$ $\sigma_{NM}$	location shape
LogNormal (LNM)	$a_{LNM} \frac{1}{\sigma_{LNM} \sqrt{2\pi} D} \exp\left(-\frac{(\log(D)-\mu_{LNM})^2}{2\sigma_{LNM}^2}\right)$	$a_{LNM}$ $\mu_{LNM}$ $\sigma_{LNM}$	location shape
Weibull (WB)	$a_{WB} \frac{\gamma_{WB}}{\alpha_{WB}} \left(\frac{D}{\alpha_{WB}}\right)^{\gamma_{WB}-1} \exp\left(-\left(\frac{D}{\alpha_{WB}}\right)^{\gamma_{WB}}\right)$	$a_{WB}$ $\alpha_{WB}$ $\gamma_{WB}$	scale shape
2DT (2DT)	$a_{2DT} \frac{p_{2DT}}{\pi u_{2DT} \left(1 + \frac{D^2}{u_{2DT}^2}\right)^{p_{2DT}+1}}$	$a_{2DT}$ $p_{2DT}$ $u_{2DT}$	shape shape
Mixed Model (IP_NE)	$a_{IP\_NE} (IP + pNE_{IP\_NE} \cdot NE)$	$a_{IP\_NE}$ $IP_{IP\_NE} b$ $pNE_{IP\_NE}$ $NE_{IP\_NE} b$	shape IP weight shape NE
Mixed Distribution (WB_NE)	$a_{WB\_NE} (p_{WB\_NE} \cdot WB + (1 - p_{WB\_NE}) NE)$	$a_{WB\_NE}$ $p_{WB\_NE}$ $WB_{WB\_NE} \alpha$ $WB_{WB\_NE} \gamma$ $NE_{WB\_NE} b$	weight scale WB shape WB shape NE

### 6.3.2. Model Fitting and Evaluation

To fit and evaluate the models, a likelihood approach using the Poisson likelihood was chosen (e.g. [Clark et al., 1999](#); [Bullock and Clarke, 2000](#); [Jones et al., 2005](#)). For this, the likelihood  $L$  was numerically maximised by changing the parameter values. Instead of actually maximising  $L$ ,  $-\ln(L)$  was minimised following [Skarpaas et al. \(2004\)](#). As the models differ in the number of their parameters, a direct comparison of the likelihoods is not sufficient to identify a best-fitting model. We therefore used AIC ('An Information Criterion' or 'Akaike's Information Criterion') to differentiate between these models (for a detailed description of AIC see [Burnham and Anderson \(2002\)](#)):

$$AIC = -2 \log(L) + 2K \quad (6.2)$$

where  $L$  is the likelihood and  $K$  is the number of parameters in the model.



**Figure 6.2.:** Total numbers of seeds trapped on each of three transects at various distances from the seed source. Stars connected by the solid line depict the average seeds per distance, squares indicate transect one, circles transect two and squares transect three. Note the log scale on the y-axis.

As the ratio of sample size (i.e. the distances at which traps were set) over the number of parameters is small (between 2 and 3.6), [Burnham and Anderson \(2002\)](#) suggest using a second order AIC, called  $AIC_c$  instead of AIC, which incorporates a correction for small sample sizes

$$AIC_c = AIC + \frac{2K(K+1)}{n-K-1}$$

where AIC is the AIC as calculated in Equation 6.3.2,  $K$  is the number of parameters in the model and  $n$  is the number of observations. The Akaike weights, based on the  $AIC_c$  ([Burnham and Anderson, 2002](#)), were calculated to compare the fit of the models.

The functions named “mle” from the package stats4 and “AIC” in R ([R Development Core Team, 2005](#)) were used for the maximum likelihood estimation and to calculate the AIC values. The quasi-Newton Broyden-Fletcher-Goldfarb-Shanno method was used for maximisation of the likelihood. For WB and WB\_NE, the modifications of the Broyden-Fletcher-Goldfarb-Shanno method by ([Byrd et al., 1995](#)) were used as this allows for constraints of the parameter values to be fitted.

## 6.4. Results

### 6.4.1. Dispersal Distances

Overall, 2403 *D. rhinocerotis* seeds were caught. Seeds were caught at all distances in all transects (Figure 6.2). Number of seeds caught decreased considerably over the first traps. The decline at distances further than 30m away is relatively constant. 77.8% of the seeds

were trapped in the first ten meters (short-distance dispersal) while 8.7% were deposited further than 70m from the seed source (long-distance dispersal) (Figure 6.2, Table 6.2).

### Model Parameter and Model Evaluation

The  $AIC_c$  values (Table 6.2) show a clear grouping of IP, LNM, WB, IP\_NE and WB\_NE, with  $AIC_c$ s ranging from 150.2 to 157.0, and NE, 2DT and NM with  $AIC_c$ s ranging from 721.9 to 783.8. The differences in the  $AIC_c$ s can be attributed to the different number of parameters, as the number of parameters is increasing from IP to WB\_NE. The associated  $-\log(Likelihoods)$  are nearly identical. The mixed models, IP\_NE and WB\_NE, fitted the observed pattern better than their first components (IP and WB) (smaller -log likelihoods), but had larger  $AIC_c$ s than their first components due to larger number of parameters. The NE, the second component of both the mixed models, was the third-worst fitting model, only outperforming the 2DT and NM model. Therefore the IP is the best-fitting model of all the eight models analysed.

The Akaike weights, based on  $AIC_c$ , give an even clearer indication of the most likely best-fitting model. IP has a Akaike weight of 0.63, i.e. a 63% chance that it is the best fitting model, compared to the LNM, which has an Akaike weight of 0.18. IP\_NE, WB and WB\_NE are the only other models having Akaike weights larger than 0.01 (see Table 6.2).

The Akaike weights are interpreted as probabilities that the model is the best-fitting model of those analysed (Burnham and Anderson, 2002). Therefore, we can quite clearly say that the IP, LNM or WB must be considered as the favourites for best-fitting model with the IP being the most likely best-fitting model.

The cumulative seed dispersal kernels (Figure 6.4) show a similar picture as they also indicate two distinct groups: the first group constituting of IP, LNM, WB, IP\_NE and WB\_NE being convex (left-curved) for the whole plotted range up to 1000m. In contrast, NE, 2DT and NM display a sigmoidal shape in the range between 0m and 1000m (convex < 100m, concave > 100m).

### Seed dispersal from a point source

The IP was identified as the most-likely best-fitting model for the observed seed dispersal pattern from an area source. Assuming that the area seed source is unlimited, we can deduct that the seed dispersal model for a *D. rhinocerotis* point source is also an IP model (for a derivation see Appendix 1)

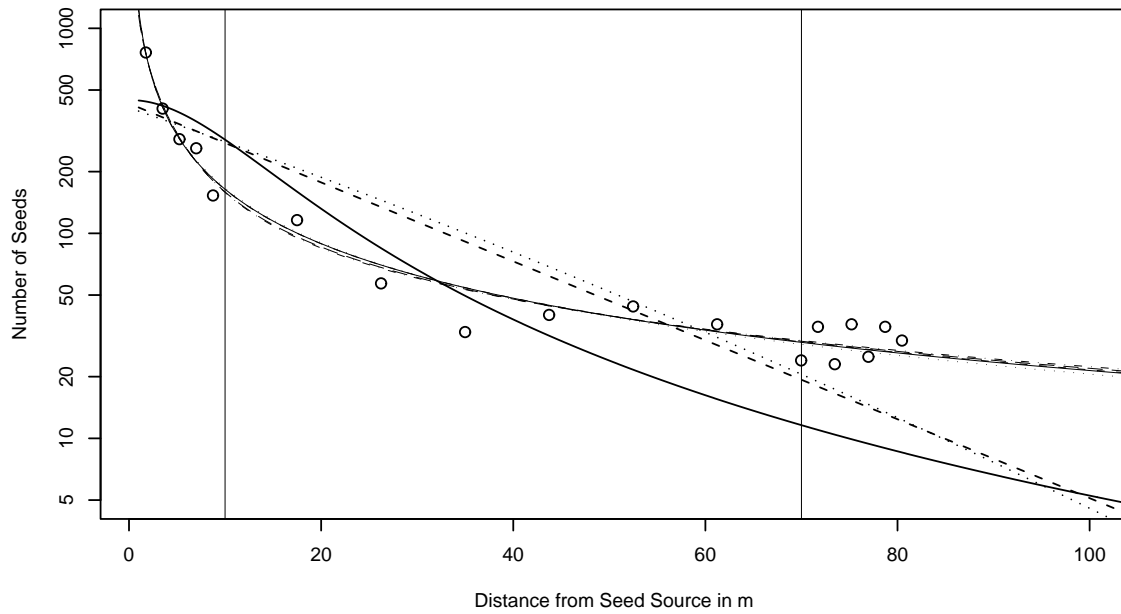
$$Q_X = 1449D^{-1.88} \quad (6.3)$$

where  $Q_x$  is the *seed* count at distance D, following the nomenclature from Greene and Calogeropoulos (2002). The exponent of -1.88 indicates a thick-tailed distribution, allowing dispersal over long distances.

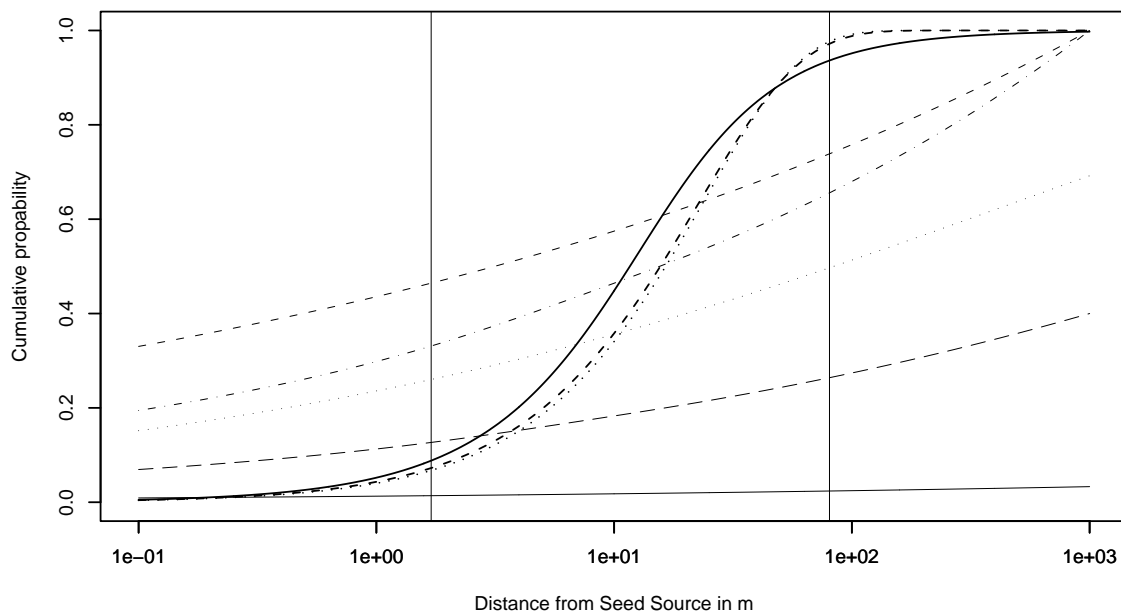


**Table 6.2.:** Likelihood, parameter estimates and estimated number of seeds for *D. rhinocerotis*. The fit of the different seed dispersal kernels is based on the observed seed count. AIC increases from left to right. The seed count per m<sup>2</sup> is provided for comparison with other seed dispersal studies. Dotted horizontal lines separate short-, mid- and long-range dispersal. Vertical lines indicating the borders of the rule of thumb given by [Burnham and Anderson \(2002\)](#), i.e.  $\Delta_i < 2$  the model having substantial support,  $4 < \Delta_i < 7$  having considerably less support and finally  $\Delta_i > 7$  having essentially no support and may be omitted from further analysis.

Distance (m)	Seed Count observed	per $m^2$	Predictions based on empirical seed dispersal models										2DT	NM
			IP	LNM	WB	IP_NE	WB_NE	NE						
1.7	762	117231	759.20	757.91	756.01	751.18	751.20	400.64	440.38			383.89		
3.5	406	62461	412.45	412.95	413.41	422.76	423.76	370.93	419.52			359.16		
5.2	288	44308	288.65	289.28	290.03	293.69	293.37	343.42	388.65			335.88		
7.0	260	40000	224.07	224.65	225.40	224.11	223.34	317.95	352.02			313.96		
8.7	153	23538	184.11	184.60	185.28	181.18	180.47	294.36	313.58			293.35		
17.5	116	17846	100.02	100.22	100.56	95.97	96.19	200.23	160.53			207.49		
26.2	57	8769	70.00	70.06	70.21	67.90	68.16	136.21	85.73			145.12		
35.0	33	5077	54.34	54.32	54.37	53.35	53.50	92.65	50.61			100.38		
43.7	40	6154	44.65	44.59	44.56	44.26	44.31	63.02	32.55			68.66		
52.5	44	6769	38.03	37.94	37.87	38.00	37.98	42.87	22.36			46.44		
61.2	36	5538	33.20	33.10	32.99	33.41	33.33	29.16	16.15			31.06		
70.0	24	3692	29.52	29.40	29.27	29.88	29.75	19.84	12.13			20.55		
71.7	35	5385	28.89	28.76	28.63	29.27	29.13	18.37	11.50			18.89		
73.5	23	3538	28.28	28.15	28.01	28.68	28.54	17.00	10.92			17.36		
75.2	36	5538	27.70	27.57	27.43	28.12	27.97	15.74	10.38			15.95		
77.0	25	3846	27.15	27.02	26.87	27.59	27.43	14.57	9.87			14.64		
78.7	35	5385	26.61	26.48	26.33	27.07	26.91	13.49	9.40			13.44		
80.5	30	4615	26.10	25.97	25.82	26.58	26.41	12.49	8.96			12.33		
Model Parameter			$a_{IP}$	$a_{LNM}$	$a_{WB}$	$a_{WB\_NE}$	$a_{IP\_NE}$	$a_{NE}$	$a_{2DT}$	$a_{NM}$				
			45	NaN	5278	367	234	217	2054927	10000000				
			$b_{IP}$	$\mu_{LNM}$	$\alpha_{WB}$	$p_{WB\_NE}$	$IP_{IP\_NEb}$	$b_{NE}$	$p_{2DT}$	$\mu_{NM}$				
			0.88	39.21	0.21	0.99	0.83	0.04	0.14	-254.00				
			0.02	3.39	0.03	0.01	0.06	0.001	0.01	5.49				
			$\sigma_{LNM}$	17.58	$\gamma_{WB}$	$WB_{WB\_NE\alpha}$	$pNE_{IP\_NE}$	$WB_{WB\_NE\alpha}$	$u_{2DT}$	$\sigma_{NM}$				
			2.05	2.05	521.17	0.21	0.66	0.05	209.38	82.20				
						$WB_{WB\_NE\gamma}$	0.81		22.90	1.82				
						$NE_{IP\_NEb}$	0.31	27791.47						
						0.11	12041.96							
						$NE_{WB\_NEb}$	0.34							
						0.13								
$-LogLikelihood$			72.7	72.8	73.4	72.3	72.5	358.6	358.2	388.3				
$AIC_c$			150.2	152.7	154.0	154.3	157.0	721.9	723.5	783.8				
$\Delta_i$			0.0	2.5	3.8	4.1	6.9	571.8	573.4	633.6				
Akaike Weights			0.63	0.18	0.09	0.08	0.02	$\ll 0.01$	$\ll 0.01$	$\ll 0.01$				



**Figure 6.3.:** Observed and predicted seed count of *D. rhinocerotis* for the most likely models. Open circles: observed seed count; dash-dot line: IP model; dashed line: MIX model; continuous line: WEIBULL distribution; dotted line: LOGNORMAL distribution; dash-dot-dot line: 2DT distribution. Vertical lines indicate thresholds for short, medium and long range dispersal. Note the log scale on the y-axis. IP: thin dashed, LNM: thin solid, WB: thin dotted, IP\_NE: thin dot-dash, NE: thick dashed, 2DT thick solid, NM: thick dotted.



**Figure 6.4.:** Cumulative seed dispersal kernels of all eight seed dispersal models. As IP and IP\_NE are not real pdfs, it is assumed that all seeds disperse up to a maximum distance of 1000m. The two vertical lines indicate the range of distances in which seed traps were set. Note the log scale on the x-axis. IP: thin dashed, LNM: thin solid, WB: thin dotted, IP\_NE: thin dot-dash, NE: thick dashed, 2DT thick solid, NM: thick dotted.



## 6.5. Discussion

### 6.5.1. Seed Dispersal Kernel: Area source

Looking at Figure 6.3, one can see that only the normal distribution (NM) is below the negative-exponential distribution (NE) and all other distributions have thicker tails than the NE at distances of more than 100m. This implies that all dispersal kernels, except NM, lead to jump dispersal instead of forming a closed front. This is in agreement with field observations which indicate isolated establishment from *D. rhinocerotis* away from the source (pers. obs.; see Chapter 7 for a more detailed discussion of the spread pattern of *D. rhinocerotis* onto old fields). The cumulative dispersal distribution (Figure 6.4) gives an even clearer picture on the dispersal distance which can be expected: essentially no seeds disperse further than 1000m from the seed source, except for the inverse power (IP) and Weibull (WB) and log-normal (LNM). In the case of the LNM, a unrealistically-fat tail can be observed which would lead to extremely high dispersal distances which are biologically impossible.

As a thinner tail indicates that fewer seeds are dispersed further, more seeds are dispersed over short and medium distances. This can be seen in Figure 6.3 where the NE and NM kernels, which have thinner tails in comparison to the better-fitting kernels, overestimate the medium distances substantially. This effect may not be observable in the field, if the spread is not seed limited but rather recruitment limited, as not the seed number but rather the availability of microsites determines the number of established plants.

The 2DT kernel produces a similar picture, describes the observed seed dispersal pattern quite well up to 40m, and underestimates the seed count substantially afterwards. Despite this underestimation, it still has a thick tail leading to jump dispersal.

The IP, WB, IP\_NE and WB\_NE follow the observed pattern and produce the thickest tail from all the analysed kernels therefore leading to the furthest dispersal distances and consequently less seeds dispersed at short and medium distances than the other used kernels.

Based on the rules of thumb provided by Burnham and Anderson (2002), differences between  $AIC_c$  can be interpreted as the relative strength of evidence between two models. More concretely, a difference in  $AIC_c$  of more than 10 between the best model (i.e. the smallest  $AIC_c$ ) and another model, indicates that the model can be excluded from further analysis as it has virtually no support compared with the best model (Burnham and Anderson, 2002). Using this guideline, we can exclude the NE, 2DT and NM model. These three models underestimate the thickness of the tail, and underestimate the seed rain at a distance of 100m by nearly an order of magnitude compared to the other models (Figure 6.3).

Although the IP law best describes the seed dispersal pattern, it has one main limitation: it is not a real pdf as the integral from 0 to infinity is infinite. However, if the exponent  $b_{IP}$  is larger than zero and smaller than one, the integral from 0 to any distance  $D$  can be calculated. The parameter value for  $b_{IP}$  and  $b_{IP\_NE}$  are 0.88 and 0.83 respectively

(Table 6.2) and we can calculate the cumulative IP distribution. The same applies to the mix model IP\_NE as it is a combination of IP and NE. Assuming a maximum dispersal distance (i.e. the chance of seed dispersing further than this distance is virtually zero), we can normalise the IP and IP\_NE kernel to represent a pdf. For an assumed maximum dispersal distance of 1000m, we obtain the cumulative seed dispersal kernels shown in Figure 6.4.

The singularity of IP, WB, IP\_NE, and WB\_NE influences the interpretation of the value of infinity at zero. We fitted the seed dispersal models to the seed count in the traps at specific distances. Therefore the seed dispersal models represent the number of seeds caught in a trap if a trap is located at distance  $D$ . As it is physically not possible to place a trap closer than half its diameter to the seed source, our number of expected seeds is not  $S_N(0)$ , which would be infinite, but  $S_N(\text{diameter of trap}/2)$ .

The seed dispersal kernel itself can also represent the probability of a single seed being dispersed a distance  $D$ . To obtain the number of seeds caught at any distance, we have to calculate

$$NoSeedsTrapped(D) = T_A \int_{D-d_T}^{D+d_T} p(x) dx \quad (6.4)$$

Following the reasoning above, we can convert the IP and IP\_NE to a pdf and adopt this interpretation despite the singularity.

Based on this, we can calculate the number of seeds which will be caught in a trap with diameter  $d_T$  at a distance  $D$ . This trap will trap seeds at distances ranging from  $D + d_T$  to  $D - d_T$ . To obtain the number of seeds caught at any distance, we have to calculate

$$NoSeedsTrapped(D) = T_A \int_{D-d_T}^{D+d_T} p(x) dx \quad (6.5)$$

If  $d_T$  is small, the change of  $p(x)$  over  $D + d_T$  to  $D - d_T$  can be assumed to be linear, the integral can be approximated by using  $p(D)$ , the average probability. This assumption is true in most cases but not if  $D$  is close to a singularity or a sudden change in the seed dispersal kernel. Therefore, the curve describing the seeds caught at a certain distance will deviate substantially around a singularity. At distances away from singularities, the seed dispersal kernel reflects the curve displaying the number of seeds caught at any given distance. If the seed dispersal kernel located closer to a singularity must be described, we need to use integrals to obtain the number of seeds expected in a certain area. As all the models identified as being the most-likely best-fitting models (IP, LNM, WB, IP\_NE and WB\_NE) have either singularities (IP, WB, IP\_NE and WB\_NE) or fast changes (LNM) at or close to zero, we cannot use the directly-fitted dispersal kernels to predict seed rain closer to the source. But even when using this technique, the number of seeds expected in the trap closest to the seed source, i.e. the centre of the trap at 4.5cm from the trap, would be 107 times as high as the number of seeds in the first trap at 1.7m in the case of the IP, and 69 times as high in the case of the WB. These high estimates for the number of seeds in the trap are clearly too high to be realistic. So even if real pdfs are used, it is

not possible to extrapolate to distances closer to zero than the closest trap. If traps are close to the seed source, it becomes necessary to use a different approach and to include the size of the trap in the analysis because, as discussed above, the assumption that the seed density changes linearly over the area covered by the trap is no longer necessarily true.

For a point source, Jones et al. (2005) argued that deviations from the fitted seed dispersal kernel are expected, especially in the tail of the distribution, and recommended the usage of kernels consisting of two components — one describing the pattern for shorter distances and the other, long-distance dispersal (Higgins et al., 2003b). The same argument can also be applied to an area source. In our study, both mixed models performed less well than their individual first components.

Thus, we can conclude that our distance range is either within the zone for short-range dispersal, or long-range dispersal, but not in the transition zone between these two as this intermediate would be better described by a mixed kernel. As the unrealistically thick tails of all the estimated kernels indicate, the distance range sampled seems to be in the short-range dispersal zone. This implies that seeds will be dispersed much further than distances sampled.

This is supported by the extremely fat tails predicted by all better-fitting models: these distributions imply that only a small proportion of all seeds dispersed are deposited within or closer than the sampled area. Considering the LNM model, only 3.3% of the seeds are dispersed up to a distance of 1000m. In contrast, WB\_NE predicts 40% and WB 69% (For the IP and IP\_NE, a maximum dispersal distance of 1000m was assumed). The predicted proportion of seeds dispersing further than 1000m is unrealistic for a shrub of less than 1m height, indicating that the models are not suitable for predicting dispersal distances much farther than sampled distance range. But as the IP, LNM and WB describe the observed seed dispersal rather well, and do not show an increasing deviation from the observed pattern at far distances but still overestimate the proportion of the seeds dispersing over long distances, the shape of the mixed kernel should be the same in the sampled range but thinner in the tail. One option to address this would be to use a broken stick kernel.

Even if it is not possible to predict seed densities outside the sampled range, using phenomenological models to describe seed dispersal pattern is of value.

### 6.5.2. Seed Dispersal Kernel: Point Source

The dispersal model identified for the point source, i.e. the IP model with  $b = -1.88$ , also shows an extremely thick tail compared to the exponents determined by Bullock and Clarke (2000). In contrast to the exponent of 0.88 for the area source, for which the integral from 0 to D could be calculated, the exponent of 1.88 makes it impossible to calculate this integral and therefore the cumulative probability from distance zero as the integral would be infinite. On the other side, the integral from any distance D to infinity converges to a finite number. To calculate the cumulative probabilities and normalise these to one, we have to start at a minimum distance  $D_{min}$  which represents the minimum distance for

which this model can be used. Since our minimum distance sampled was 1.7m, it makes sense to use 1.7m as  $D_{min}$ . If we do this, the seed dispersal model is given by, following the nomenclature from [Greene and Calogeropoulos \(2002\)](#):

$$Q_X = 1449D^{-1.88} = \int_{D_{min}}^{\infty} x^{-1.88} dx \cdot \frac{D^{-1.88}}{\int_{D_{min}}^{\infty} x^{-1.88}} = 2034 \cdot 0.71D^{-1.88} \quad (6.6)$$

Due to the restriction of the integral to distances larger than  $D_{min}$ , the number of seeds dispersed, here 2034, represents the number of seeds dispersed further than  $D_{min}$ .

[Cousens and Rawlinson \(2001\)](#) stated that the height at which the seed is released is usually in the same order of magnitude as the dispersal distance. This is definitely not the case for *D. rhinocerotis*, as the height of the shrubs in the study site is between 0.8m and 1.2m (pers obs.). However, the dispersal distances are two orders of magnitude larger than the height of the plant. [Tackenberg et al. \(2003\)](#) showed that turbulences play an essential part in the dispersal of seeds and determine essentially the resulting dispersal distance. As the seeds of *D. rhinocerotis* are adapted to wind dispersal (they are equipped with a pappus ([Herman et al., 2000](#))) and the ground surface is relatively open and the vegetation cover consists of mainly lawn grasses and bare ground, it is very likely that substantial turbulences exist which could cause this long-distance dispersal.

### 6.5.3. Relevance for Management

Seed dispersal is an important aspect of restoration. Depending on the number of seeds of indigenous plants arriving in the areas to be restored, it might be necessary to broadcast additional seeds or to establish “islands” of restored natural vegetation which can function as seed sources. One approach would be to simply measure the number of seeds arriving at a site by using seed traps. This can be a time-consuming exercise which can be avoided when information on the seed dispersal kernel of desired species is available.

Based on our study, the estimated dispersal distances for a *D. rhinocerotis* point source substantiate the claim by some authors ([Levy, 1927](#); [du Toit and du Toit, 1938](#)) of *D. rhinocerotis* being an invasive species. We can conclude that the return of *D. rhinocerotis* onto old fields is not seed-limited but rather limited through other processes like high seed mortality, low seed viability, low germination rate or low establishment rate. Consequently, restoration measures should address barriers to population recovery. Reseeding of *D. rhinocerotis* would not be necessary in the vicinity of established mature stands of this species. This information can assist in the successful planning of cost- and time-effective restoration strategies in Renosterveld.

## 6.6. Acknowledgements

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## 7. Spread from the edge—spatial spread pattern of a wind dispersed shrub, (*Dicerothamnus rhinocerotis*) onto an old field colonised by invasive grasses

### 7.1. Introduction

The study was conducted in West Coast Renosterveld, a Mediterranean-type shrubland in the Fynbos Biome of South Africa (for a detailed description see [Krug et al. \(2004b\)](#), and Chapter 5). The vegetation is dominated by asteraceous shrubs, lawn and bunch grasses and geophytes ([Moll et al., 1984](#); [Low and Jones, 1995](#); [Low and Rebelo, 1998](#)). Interactions between shrubs and grasses could be regarded as savanna-like, with dynamics driven by grazing and fire (see Chapter 5). In recent times, the vegetation type has been heavily transformed due to agriculture and urbanisation, leaving only scattered remnants ([von Hase et al., 2003](#)). Due to this high degree of transformation and extensive fragmentation of the remaining natural vegetation ([von Hase et al., 2003](#)), it becomes important to not only try to conserve the remaining Renosterveld fragments, but also to include restoration of e.g. abandoned agricultural lands into conservation strategies. Due to the nature of agriculture (crop and livestock farming), most of the abandoned old lands are covered by indigenous (mainly *Cynodon dactylon*) and alien grasses (e.g. *Bromus spp.*, *Lolium spp.*, *Vulpia spp.*, *Briza spp.*). An important aspect of restoration is therefore to facilitate re-establishment of indigenous species, particularly shrubs, on these old lands to obtain a vegetation structure similar to the presumed natural state ([Krug et al. \(2004a,b\)](#), and [Krug and Krug \(2007\)](#) in Appendix B), assuming that the restoration of structural similarity between the restored site and the presumed natural state will facilitate the return of a whole suite of other species dependent on the structural diversity.

Previous studies have shown that the recolonisation of old fields by shrub species is limited by the competition of the grasses ([Bakker and Berendse, 1999](#); [Midoko-Iponga et al., 2005](#)), or other weedy species ([Hobbs, 2001](#)), however, the removal of grasses by either hand-weeding or herbicide application to facilitate the return of the shrub species is exceedingly expensive ([Cione et al., 2002](#); [Midoko-Iponga, 2004](#)). Thus, approaches which facilitate the return of shrubs without necessitating the complete removal of the grasses become an important consideration. One approach would be to establish islands of shrubs in the old fields to facilitate the natural spread from these islands farther onto

the old fields, and to create microsites in which seedlings of shrub species can establish. An important aspect which needs to be considered, if this approach is chosen, is the optimal distance between these “islands of shrubs” in the “sea” of grasses. A compromise has to be found between shrubs planted close together (in clumps), i. e. faster recolonisation of the old fields but at higher costs, or planted further apart (isolated bushes), i. e. slower recolonisation of the old fields but at lower costs. This trade-off makes it important to obtain an understanding of the speed of recolonisation of the old fields by shrub species and of the external influential factors.

As experimental determination of the spread of a long-lived shrub species over several generations is not feasible, an ecological simulation model is the best approach. However, most simulation models, which analyse spread pattern, were only concerned with the dispersal of a single species, and establishment of the seedlings was not influenced by environmental factors at the establishment site (Higgins et al., 1996; Clark et al., 2001; Higgins et al., 2003a). Even if considering a homogeneous environment in which the seedlings will establish, this assumption does not hold true for a multiple-species system. In most cases, the seedlings are out-competed by the already-established plants (e.g. Milton, 1994; Holzel and Otte, 2003; Hooper et al., 2005; Midoko-Iponga et al., 2005; Picon-Cochard et al., 2006). However, seedlings might be able to out-compete the established individuals once they themselves are able to establish on a site (Cione et al., 2002; Holzel and Otte, 2003). Consequently, the recolonising species needs competition-reduced or -free microsites that are suitable for establishment (Milton, 1995; Chambers, 2000). These microsites may be caused by disturbances which remove established species, such as hoof action by larger animals, mole hills or diggings by small mammals (Reichman and Seabloom, 2002; Bragg et al., 2005). When the recolonising species establish on these microsites, they are able to out-compete the already established species and produce seeds. In addition, depending on the species, the established re-colonisers could facilitate further establishment of seedlings and therefore be the beginning of an accelerating recolonisation.

In the system we investigated, the main recolonising species is a wind-dispersed asteraeous shrub, *Dicerotheramnus rhinocerotis* (renosterbos), and the established species is *Cynodon dactylon* (bermuda grass), an animal-dispersed lawn grass. The old field had been abandoned 20 years previously, after cereal cultivation and livestock farming. Midoko-Iponga et al. (2005) showed that the establishment of shrubs on this field was mainly hindered by competition from the existing grasses. However, as soon as shrub species established on microsites that were created by hand-weeding, the shrubs were able to out-compete the grasses for, presumably, light but also for water and soil nutrients,.

To analyse the recolonisation potential and spread of *D. rhinocerotis* on a field covered with *C. dactylon*, I developed a temporal – spatial explicit, stochastic, individual-based, two-species simulation model and addressed the following questions:

- How does the availability of microsites on an old field covered by *C. dactylon* influence the recolonisation pattern of *D. rhinocerotis* (measured by % cover of *D. rhinocerotis* on the simulated patch) and the velocity of spread of *D. rhinocerotis*?



- How well do the recolonisation patterns, arising from the ecological simulation model, correspond with the recolonisation pattern observed on the the old field? This validation of the simulation model was achieved by comparing the simulated distance dependence of the density of *D. rhinocerotis* as well as average shrub density with data obtained from vegetation line transects running across the old field.
- How can the pattern and their responses to parameter changes, as identified in the model, be applied for restoration?

To assess the influence of selected parameters used in the model on the final model results, a sensitivity analysis using the following parameters was conducted.

- the size of the zone of influence of *D. rhinocerotis*
- the seed production of *D. rhinocerotis*
- the frequency of recruitment events for *D. rhinocerotis*

## 7.2. Methods

### 7.2.1. Description RenPatch

The model description follows the ODD protocol, a standard protocol for the description of individual-based models suggested by Grimm et al. (2006). ODD stands for the sections in the protocol, i. e. Overview , Design Concepts and Details. The philosophy of the protocol is to provide a framework which facilitates the comprehension of the model as the protocol covers all relevant aspects required for the understanding of individual-based models. In addition, due to the standardised order in which the different aspects of the model are presented, relevant information is more easily accessible and makes the comparison of different models more readily possible.

All parameters used in the model, unless otherwise stated, were estimated from field observations (Shiponeni, 2003; Midoko-Iponga, 2004; Walton, 2005; unpublished data) and from data available in the literature on similar species and situations (e.g. Guglielmini and Satorre, 2002 for competition for light in *Cynodon dactylon* and Levyns (1927); Cowling et al. (1986) for germination requirements of *Dicerotheramnus rhinocerotis*), as well as educated guesses, as no data was available on which to base some parameter estimates directly. This lack of scientific information on the ecosystem dynamics is mainly due to the fact that Renosterveld has been transformed for centuries, and was not recognised as an independent vegetation type until the 1950s. Furthermore, the (relatively) complex nature of some parameters used in the models, such as the relative zone of influence ( $ZOI_{rel}$ ), required estimations based on own observations, general literature and experience from other researchers working in West Coast Renosterveld.

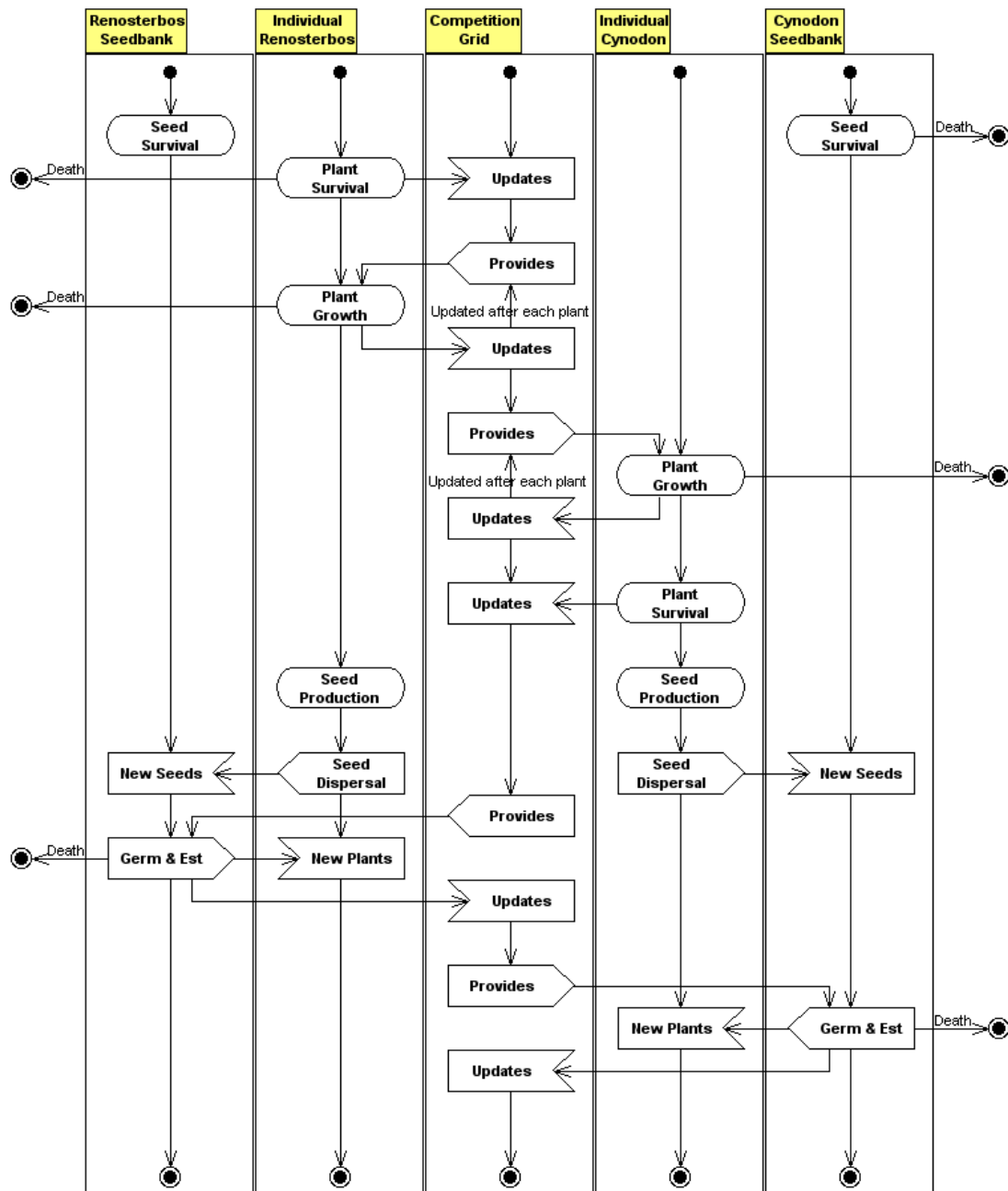
## Overview of RenPatch

**Purpose** The purpose of the model RenPatch is to investigate the colonisation of an old field by a wind-dispersed asteraceous shrub, *Dicerothamnus rhinocerotis* (renosterbos). As the old field is dominated by *Cynodon dactylon* (kweekgrass or bermuda grass), an animal-dispersed lawn grass, the resulting spatio-temporal dynamics of the two species will be examined, and the spread pattern of *D. rhinocerotis* in relation to grass cover and grass competitiveness will be investigated.

**State variables and scales** RenPatch is an individual-based, spatio-temporally explicit, stochastic simulation model developed in Delphi 7. It consists of three hierarchical levels, namely the individual plants, the two species and the simulated patch (= old field) with a size of  $25 \times 125\text{m}$ . The simulation model is a combination of an individual- (single plants) and grid-based approach (cell size  $10 \times 10\text{cm}$ ), where *D. rhinocerotis* is modelled using an individual-based approach, while for *C. dactylon*, a grid-based approach is used. The grid-based approach for *C. dactylon* was used as the species spreads vegetatively as well as via rhizomes, and individual plants are not easily delineated. For *D. rhinocerotis*, the canopy of one individual plant can cover several grid cells. Cover of *C. dactylon* in a cell is not determined; the species is either present, or not, in a cell. Growth of an individual plant is modelled as the occupation of a neighbouring cell. Therefore a cell colonised by *C. dactylon* is regarded as one individual. Parameters associated with a species (e.g. growth and germination rates) determine the extent to which plants of the same or different species can overlap, i.e. they determine intra- and interspecific competitive abilities. A grid is also used to model the interactions between individuals, i.e. competition, and the deposition of seeds into the seed bank. Individuals are characterised by their species, location on the grid (x and y coordinates), their size (radius  $r$ ), age and number of seeds on the plant. Species are characterised by attributes specifying the life history and competitiveness. The simulated patch is considered as being spatially homogeneous, i.e. conditions are the same across the patch and do not change in space or time. One time-step in the model reflects one year and temporal heterogeneity of environmental conditions is only considered to influence the germination of *D. rhinocerotis*, i.e. to determine whether, or not, germination occurs in a year.

**Process overview and scheduling** The simulation model consists of several processes which are executed sequentially. Processes act on one of four different entities. These entities are 1) *D. rhinocerotis* plants, 2) *D. rhinocerotis* seed bank, 3) *C. dactylon* plants and 4) *C. dactylon* seed bank. A fifth entity, the Competition Grid, links the species and allows for interaction between them. A flow chart of the processes and their sequence of execution is depicted in Figure 7.1, and the parameters and their initial values are shown in Table 7.1. If processes are on the same level, like seed survival in both species, the sequence of their execution is not relevant as they do not influence each other.

One point to mention is the delayed execution of PLANT SURVIVAL of *C. dactylon*. If



**Figure 7.1.:** Flowchart of the simulation model showing the different entities of the model (plants and seed banks of the two species and the Competition Grid), their different processes and how they interact. One time step progresses from top to bottom.

PLANT SURVIVAL of *C. dactylon* was executed before GROWTH of *C. dactylon*, all existing gaps in the *C. dactylon* cover would be closed up. As it is assumed that these gaps in *C. dactylon* cover represent microsites for *D. rhinocerotis* establishment, PLANT SURVIVAL of *C. dactylon* needs to be executed after GROWTH of *C. dactylon* to guarantee the gaps required for establishment of *D. rhinocerotis*. The survival rate of *C. dactylon* therefore represents the proportion of microsites available on the simulated patch.

The competition grid brokers the interaction between the two species and is based on the superimposed FONs (Field of Neighbourhoods) (Berger and Hildenbrandt, 2000) (for a detailed description on how the competition grid is obtained, see next paragraph). Plants of both species exert a certain amount of competition on their neighbourhood (Zone of Influence, ZOI). This competition experienced in a cell, caused by all plants on the grid, is stored in the Competition Grid. The competition experienced by an individual is indifferent to the individuals causing the competition, i.e. an individual plant cannot differentiate whether it is exposed to competition from an individual of the same species (intraspecific competition) or from a different species (interspecific competition). This assumption is reasonable, if we assume that light is the limiting resource for which the two species compete (Guglielmini and Satorre (2002) showed that light plays an important role in the radial growth of *C. dactylon*). In contrast to Berger and Hildenbrandt (2000) who used the same maximum competitiveness (*Comp*) for each species, the two species modelled here have different maximum competitiveness. This can be interpreted as the different heights of the two species in the context of competition for light. The processes GROWTH and GERMINATION & ESTABLISHMENT are influenced by the competition to which the plant or the seedling is exposed, and in return these processes update the Competition Grid. PLANT SURVIVAL only updates the Competition Grid. In the case of GROWTH, the Competition Grid is updated after a new seedling has established, while in the case of PLANT SURVIVAL and GERMINATION & ESTABLISHMENT, the Competition Grid is only updated after the process has iterated through all individuals.

## Design Concepts of RenPatch

*Emergence:* The life cycles of the individual plants are modelled using empirical rules and probabilities from which the community dynamics and spatial pattern of the simulated patch emerge.

*Sensing:* It is assumed that individual plants are aware of their age, the competition to which they are exposed relative to their own competitiveness, and their species. Examples are the age dependence of the seed production or the competition dependence of growth. In addition, it is assumed that seeds “know” their species and age as well as the competition in the location in which they will germinate.

*Interaction:* Interaction among individuals is modelled through competition following the FON approach (Field of Neighbourhood) described by Berger and Hildenbrandt (2000). Each plant exhibits a certain amount of competition in its neighbourhood, depending on its species. This is called the Zone of Influence (ZOI) (Czárán, 1998; Berger and Hildenbrandt,

2000). The size of the ZOI is determined by the size of the plant itself and a constant factor specific to the species,  $ZOI_{rel}$  the “relative ZOI radius”. The strength of the competition within this ZOI, the FON, is not constant, but is dependent on the distance  $r_p$  from the location of the plant following

$$FON(r_p) = \begin{cases} r_p \leq r & Comp \\ r_p \leq r \cdot ZOI_{rel} & Comp - (r_p - r) \frac{Comp}{r(ZOI_{rel}-1)} \\ r_p > r \cdot ZOI_{rel} & 0 \end{cases} \quad (7.1)$$

where  $r$  is the radius of the cover of the plant and  $Comp$  is the maximum competitiveness of the species.  $Comp$  differs between species based on their competitiveness, i.e. the species which can out-compete the other species is considered having a higher  $Comp$  value. The FONs of all plants, irrespective of species, are superimposed to obtain the competition at each given point  $(x, y)$  in space

$$F(x, y) = \sum_N FON_n(x, y) \quad (7.2)$$

and finally  $F(x, y)$  is stored in a grid which is updated by the processes PLANT SURVIVAL, PLANT GROWTH and GERMINATION & ESTABLISHMENT.

*Stochasticity:* RenPatch is a stochastic simulation model. All processes are stochastic, except for SEED PRODUCTION which is deterministic and only dependent on the plant age. PLANT SURVIVAL, SEED SURVIVAL, PLANT GROWTH and GERMINATION & ESTABLISHMENT are modelled as probabilities; the Seed Dispersal kernel follows an empirical probability distribution and the dispersal direction is randomly selected. Germination events are deterministic. The order in which the individuals are evaluated in the different modules follows the order in which they were created during the simulation (in most cases, this coincides with the age of the plants). In the case of PLANT GROWTH, the order is randomised to avoid any bias towards certain individuals evaluated at an earlier stage.

*Observation:* After completion of each time step, the locations and size of each individual is saved. In addition, cover summary statistics in the form of number of cells covered by *D. rhinocerotis*, *C. dactylon*, both, or bare ground is calculated and saved. Also, a log of when germination events occurred is generated and stored.

## Details of RenPatch

**Initialisation** As we simulate the return of *C. dactylon* onto an old field, each simulation is initialised with an patch covered with *C. dactylon*, an empty seed bank for both species and the assumption that a GERMINATION EVENT event occurred in the last year. The seed input of *D. rhinocerotis* leads to an accumulation of seeds over the number of years until the next GERMINATION EVENT takes place. The time until the first GERMINATION EVENT of *D. rhinocerotis* can be regarded as an initialisation phase during which *D. rhinocerotis* seeds accumulate.

**Input** The only external event in the model is the occurrence of a GERMINATION EVENT (see Chapter 7.2.1). To simplify the model, the occurrence of the germination event is deterministic with a given number of years between events (five and ten years). Apart from the occurrence of the germination event, all dynamics in the model are determined by the dynamics and interactions of the two species considered.

### Sub-models

**Germination Event** As *D. rhinocerotis* occurs in cohorts (pers. obs.), germination was not modelled as yearly events but as germination events. In reality, occurrence of these germination events should be linked to environmental factors e. g. exceptionally high rainfall (Cione et al., 2002). Some authors (Levyngs, 1927; Koekemoer, 2002) state that establishment is triggered by fire. However, germination does not seem to be dependent on fire (pers. obs.) and fire does not always trigger the germination and establishment of *D. rhinocerotis* (pers. obs.). As Koekemoer (2002) states, competition, or rather the lack of it, is important for successful germination and establishment of *D. rhinocerotis*.

To simplify the model, it was decided not to include climate scenarios, but to simulate deterministic germination events at five or ten year intervals, covering the range of intervals between these exceptional events. Whether *D. rhinocerotis* will germinate is determined at the beginning of each simulated year, subsequent germination events are based on a given number of years between events. Germination events influence only *D. rhinocerotis* and not *C. dactylon*. If a germination event occurs, the *D. rhinocerotis* seeds accumulated can germinate (see Chapter 7.2.1).

**Seed Survival** SEED SURVIVAL is represented as a probability for a seed. This probability is dependent on the age of the seed and an empirical age dependence is given. If the age of the seed exceeds the maximum age in the distribution provided, the probability of the last year is used. Due to a lack of empiric knowledge about seed survival in the seed bank, we assumed a survival of 0.5 for the first 7 years and no survival thereafter.

**Plant Survival** The process PLANT SURVIVAL is modelled in the same way as SEED SURVIVAL. In the case of *D. rhinocerotis*, survival refers to the survival of an individual shrub whereas in the case of *C. dactylon*, death refers to the clearing of a cell in the grid. Based on the surviving individuals, the competition grid is updated after this process.

**Plant Growth** Based on the difficulty of identifying individuals in *C. dactylon* and the different growth pattern (vertical growth in *D. rhinocerotis* and horizontal or creeping growth in *C. dactylon*), plant growth was modelled using different approaches for *D. rhinocerotis* and *C. dactylon*. In the case of *D. rhinocerotis*, growth was assumed to be vertical growth and the size of the individual plant changed. In the case of *C. dactylon*, growth was modelled as creation of new individuals in the neighbouring cells following

**Table 7.1.:** Parameter values for different processes and species. ZOI stands for Zone of Influence. More then one value specifies different scenarios.

Process	Value	
Parameter	<i>D. rhinocerotis</i>	<i>C. dactylon</i>
Species Parameter		
Relative ZOI radius ( $ZOI_{rel}$ )	2	1
Competitiveness ( $Comp$ )	2000	1000
GERMINATION EVENT		
Frequency	5	n/a
SEED SURVIVAL		
seed survival at age 0	0.5	1
seed survival up to age 6	0.5	0
afterwards	0	0
PLANT SURVIVAL		
survival probability	0.9	0.98, 0.99
GROWTH		
Maximum plant diameter in m	0.5	n/a
Maximum growth until relative competition	0.5	0.5
Zero Growth until relative competition	1.5	1.5
Death of plant above relative competition	2	1.7
Relative Growth	0.5	n/a
Maximum Number of cells deep	n/a	5
Probability of growing into neighbouring cell	n/a	0.5
SEED PRODUCTION		
at age 0 and 1	0	1
at age 2	10	1
at age 3	100	1
at age 4	1000	1
at age 5 and older	10000	1
SEED DISPERSAL		
Additional seeds	6250	100
Seed dispersal kernel	see Figure 7.2	uniform
GERMINATION & ESTABLISHMENT		
Germination at seed age of 0	0.02	1
Germination at seed age of 1	0.4	1
Germination at seed age of 2	0.5	1
Germination at seed age of 3	0.5	1
Germination at seed age of 4	0.4	1
Germination at seed age of 5	0.2	1
Germination at seed age of 6	0.03	1
Establishment probability	0.05	0.5
Maximum establishment up to competition of	1000	500
Zero establishment at competition higher then	2000	1000



an iterative algorithm, i.e. similar to a cellular automata approach where growth is modelled as cells occupied. The maximum radius increase of a plant in one year is specified by “Probability of growing into neighbouring cell” (see Table 7.1) and is set to five cells, which equals 50cm. Guglielmini and Satorre (2002) measured growth of *C. dactylon* up to 120cm within 53 days under lab conditions. Therefore the 50cm used here are likely an underestimate of the real growth of this species.

For vertical growth, the parameter “relative growth” represents the maximum relative growth of which a plant is capable if it is not exposed to any competition. Depending on the actual size of the plant and the parameter “maximum size”, this maximum relative growth rate is adjusted following the logistical equation

$$RelGrowth = MaxRelGrowth \cdot 1 - \left( \frac{PlantSize}{MaxPlantSize} \right) \quad (7.3)$$

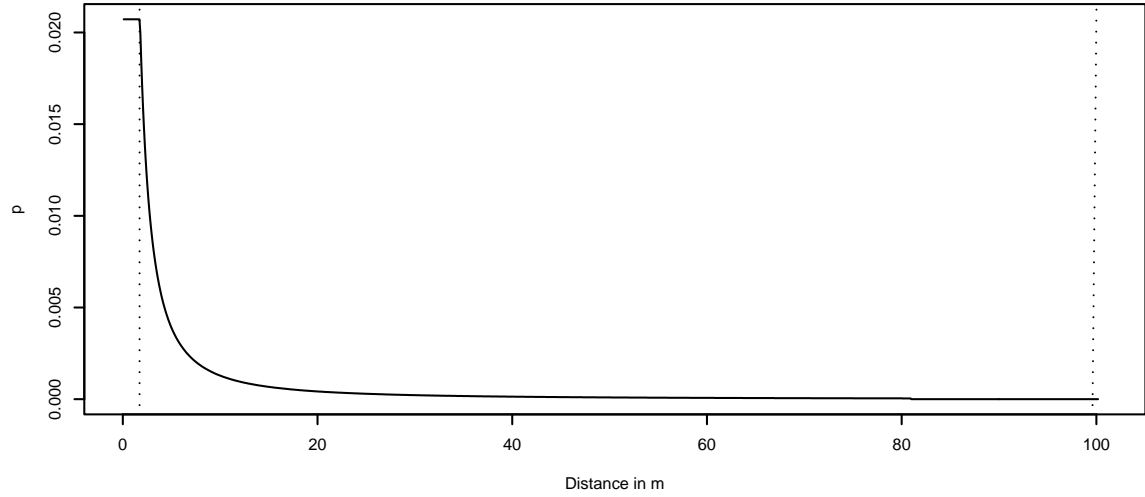
resulting in the maximum relative growth rate for small plants and zero growth rates for plants of “maximum size”.

In a final step, the resulting growth rate is adjusted based on the ratio of the competition the individual is exerting and the competition it experiences. One parameter specifies the maximum competition ratio up to which the growth rate is not impacted. A second parameter specifies the ratio at which the growth will be zero due to the competition. To allow for a shrinking of the plant due to competition, a third parameter was introduced which specifies the maximum ratio up to which the individual can still survive. If the ratio is larger, the individual will die. To obtain the resulting growth rate for intermediate ratios, the growth rates were linearly extrapolated.

**Seed Production** The number of seeds produced is dependent on the age of the plant and independent of the competition experienced by the plant. A vector is given as a parameter determining the number of seeds produced by a plant of a certain age. The number of seeds produced represent the number of seeds which will be dispersed up to 100m. This process is deterministic.

**Seed Dispersal** Depending on the dispersal syndrome of the species, two different modules were used to simulate seed dispersal. Seed dispersal of *D. rhinocerotis*, a wind-dispersed shrub, is modelled by determining the dispersal distance and direction for each seed on the plant. The direction is drawn from a uniform distribution from 0° to 360°, therefore showing no preference for any direction. The distance distribution is based on the seed-trapping experiments and the analysis presented in Chapter 6, i.e. following a uniform distribution from 0m to 1.7m, and following an IP law with an exponent of -0.88 between 1.7m and 100m. No seeds disperse further than 100m (see Figure 7.2). Therefore, the number of seeds produced represent the number of seeds which are dispersed up to a distance of 100m. In the case of the animal-dispersed *C. dactylon*, we assume that seeds are randomly distributed in the simulated area.





**Figure 7.2.:** Seed dispersal kernel for individual *D. rhinocerotis*. Vertical dotted lines indicate range trapped (see Chapter 6) from 1.7m to 81m. Distances smaller than 1.7m are assumed to have same probability as distance 1.7m, distances further than 81m are assumed to receive no seeds.

The dispersed seeds are then added to the spatial explicit seed bank described by a grid of a cell size of  $0.1 \times 0.1$ m.

**Germination & Establishment** The process GERMINATION & ESTABLISHMENT includes two separate sub-processes, germination and establishment. In the case of *C. dactylon*, germination takes place every year, in the case of *D. rhinocerotis* only if a germination event occurs (see Chapter 7.2.1). In both cases, germination is characterised by a vector providing the germination probability of a seed of certain age (for *D. rhinocerotis*, the probabilities are based on a study by Levyns (1927) and are further discussed in Cowling et al. (1986)).

After seed germination, establishment of the seedlings takes place. The probability of establishment is based on a maximum probability that a seedling will establish in a cell when no competition is present. The impact of competition on the maximum establishment is characterised by two parameters. One parameter specifies the maximum competition in a cell up to which the seedling is unaffected by the competition to which it is exposed. A second, higher competition specifies the amount of competition which results in the death of the seedling, i. e. a probability of establishment of zero. Between these two competition values, the probability of establishment is extrapolated linearly.

### 7.2.2. Sensitivity analysis

A parameter sensitivity analysis, evaluating the impact of parameter value changes on the distance-dependent density and the overall density, was conducted with selected parameters. Parameters used in the sensitivity analysis were selected based on their “reliability”, i. e. if the estimates were based on literature data or on educated guesses, their presumed importance on the results and previous simulations which are not included here. This se-

lection of parameters with which to conduct the sensitivity analysis and the limitation to two or three parameter values was necessary due the number of parameters incorporated into the model and the extensive computational requirements for a single simulation. The parameters identified for the sensitivity analysis and their values used in the analysis, in addition to the default values indicated in bold, are

- relative zone of influence radius of *D. rhinocerotis*  $ZOI_R = (1.5, \mathbf{2}, 2.5)$
- frequency of germination events of *D. rhinocerotis*  $gi = (\mathbf{5}, 10)$
- mean establishment probability of *D. rhinocerotis*  $me = (0.01, \mathbf{0.05}, 0.1)$

The sensitivity analysis was conducted by simulating the two base scenarios of different microsite availability ( $cs = 0.98$  and  $cs = 0.99$ , respectively) with the combination of the parameter values used in the analysis, and evaluating the impact of these parameter value changes on the base scenarios.

### 7.2.3. Data Collection

To allow for validation of the simulation model, data on shrub density and distribution were collected on the same site as used for the seed dispersal experiments in Chapter 6. For a detailed description of the study site, see Chapter 6.2.1.

To obtain density estimates of *D. rhinocerotis*, line transects were laid out on the old field to determine the distribution and the plants' sizes. Transects of 100m were oriented perpendicular to the natural vegetation, leading away from the edge and starting 20m away from the area seed source, to avoid the impact of the irregularly-used track separating the natural seed source and the old field and its resulting disturbances. All *D. rhinocerotis* rooted within 0.5m left or right to the transect line were recorded with location on transect, and width, length and height of the bush. In addition, it was recorded whether or not the individual was located in a furrow (parallel to the field edge and perpendicular to the transects).

### 7.2.4. Analysis Field Data

Average *D. rhinocerotis* density was calculated from the data collected along the transects, separated for plants within or outside furrows (drainage lines). A  $\chi^2$ -test was used to compare the observed count of plants in the furrows with the observed count of plants outside the furrows.

To compare the average shrub density with the average shrub density of the simulations, all plants were pooled and the average density for all transects was calculated. Similarly, the distance dependence of the density was calculated: all transects were combined and a density estimation by using the function *density()* in R (2005) was used, which results in a probability density function (pdf). To obtain a consistent density estimation for both field and simulation data, the values for the following parameters were set to the following

values:  $bandwidth = 8$ ,  $from = -50$ ,  $to = 200$  and  $n = 512$ . Due to restrictions in the density-estimation method and the fact that transects started at 20m away from the edge, estimates do not reflect expected densities at distances closer than 36m. Despite this, the deviation is consistent and differences between two pdfs derived by the same parameter values but different input data, reflect differences in the input data set.

In addition, the distance of the individual furthest away from the edge was determined for each transect and mean, median and standard deviation was calculated over all transects.

### 7.2.5. Analysis Simulation Data

As outlined in Table 7.1, 36 scenarios were simulated and each scenario simulation was repeated 5 times.

To analyse cover change over the simulated time span of 100 years and the influence of selected parameters on species cover, we plotted the change of the proportion of cells covered by *C. dactylon*, *D. rhinocerotis*, mixed (i.e. a cell occupied by both) and bare ground. To determine if the cover reached an equilibrium after the simulated 100 years, we used a t-test in R (R Development Core Team, 2005), with the two variances assumed to be not equal, and compared the cover values of *D. rhinocerotis* of the years 80–90 with 90–100. If the t-test showed no significant differences, the scenario was classified as having reached an EQUILIBRIUM. To determine if any changes occurred over the simulated time span, we used the same approach and compared *D. rhinocerotis* of the years 20–30 with 90–100. If the t-test did report any significant differences, we classified the scenario as CHANGING. These time intervals were chosen to be at least as long as the germination interval and to not include the first years as some initial fluctuations, based on the initial conditions, could be expected.

To further investigate the spread of *D. rhinocerotis*, we used three measures discussed in Chapter 4 to describe the spread. A “measure”, in this context, is defined as a characteristic distance in units of meters of the dispersed plants from the seed source. Therefore, “velocity of the measure” is the distance by which the “measure” increases per time-step, which was one year in our context. These measures are calculated as follows: the individual plants in the simulated landscape were sorted according to their distance from the seed source in descending order, i.e.  $N_i^{dist}$  refers to the  $i^{th}$  furthest individual which is located at distance  $dist$  and consequently individual  $i = 1$  is the individual furthest away from the initial seed area source. The measures which we used were the distance of the  $i^{th}$  individual with  $i$  equal one (x0001), ten (x0010) and 100 (x0100) respectively. The measure x0001 is equivalent to the one used by Clark et al. (2001) and Cannas et al. (2003), which is the distance to the furthest-spread individual, measured from the western edge of the simulated landscape. These measures were determined for all plants ( $x0001_{all}$ ,  $x0010_{all}$  and  $x0100_{all}$ ) and all plants older than 5 years ( $x0001_5$ ,  $x0010_5$  and  $x0100_5$ ). Based on these six measures, the velocity of spread was determined using linear regression for each scenario and the results were plotted.

For the field validation of the simulation, the average density was calculated for an area 20m from the edge to 120m into the field which corresponds to the length of the line transects. These average densities were calculated for all simulated scenarios (base scenarios plus the scenarios used in the sensitivity analysis) and for each year. The density measures obtained for all simulated scenarios were plotted on a logarithmic scale versus the year and compared to the observed value.

For the distance-dependent density, a density probability density function (pdf) was estimated using the function *density()* in R (2005). This density pdf represents the probability density function of an individual being located at distance  $x$  from the edge in the simulated area. All parameters in the density estimation were at default values except for *bandwidth*, *from*, *to* and *n* which were set to the same values as used for the analysis of the field data (*bandwidth* = 8, *from* = -50, *to* = 200 and *n* = 512). We calculated the sum of squares (ssq) for each scenario and each year, and the likelihood  $L = -\ln(ssq)$  as a likelihood estimator was plotted as the dependent variable for each scenario, with the year as independent variable. A high  $L$  indicates a high “similarity” between the observed and the simulated pdf while a low  $L$  indicates a low “similarity”.

The sensitivity analysis was conducted by visually comparing the results from the different scenarios simulated. A representation of the impact in relation to a change in input parameter value was not useful due to the small number of different values of parameter values which could be assessed.

## 7.3. Results

### 7.3.1. Field Data

We counted 52 plants inside and 150 outside the drainage lines, with an overall average density of 0.1 plants per sqm. Of the overall transect length, 350.4m were inside and 1749.6m were outside furrows. A  $\chi^2$  test showed the distribution of plants inside / outside the drainage lines was significantly different from the expected distribution ( $\chi^2_1 = 11.9191$ ,  $p = 0.0006$ , see Figure 7.3).

The pdf of the distance-dependent density estimate of the plant, i. e. the expected density at any given distance from the edge, is shown in Figure 7.4. The distance of the furthest dispersed plant per transect ranged between 38.7m and 119m with a median of 98.4m and a mean of 88.8m.

### 7.3.2. Simulation Data

#### Density

For most of the 36 scenarios, *D. rhinocerotis* cover increased while cover of *C. dactylon* decreased. The exception were the scenarios where the parameter MEAN ESTABLISHMENT (me) equalled 0.01. In these scenarios, no observable change occurred, although statistical tests showed significant differences over time in all scenarios, but only three reached an

EQUILIBRIUM (see Figure 7.5 and 7.6 for details). All other scenarios showed a significant increase of *D. rhinocerotis* cover and a decrease of *C. dactylon* over time. Mixed cover, i. e. cells covered both by *C. dactylon* and *D. rhinocerotis*, followed *D. rhinocerotis* cover changes. Cover of Bare Ground was very low in all scenarios, with no observable changes, except for some scenarios, where small fluctuations occurred simultaneous with the germination events of *D. rhinocerotis*.

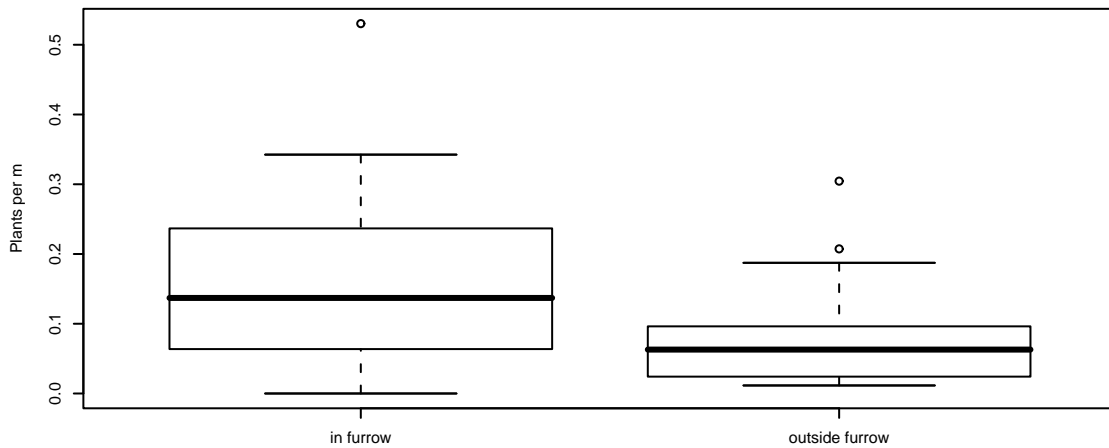
Even though the time-span simulated was 100 years, two of 36 scenarios did not change and only six scenarios reached EQUILIBRIUM.

### Base scenarios and sensitivity analysis

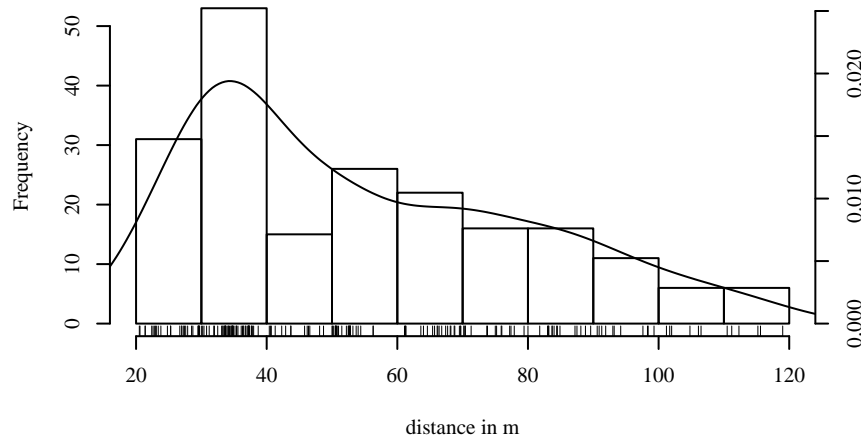
As stated above, the two base scenarios showed a decreasing *C. dactylon* cover and increasing *D. rhinocerotis* cover (Figure 7.5 and Figure 7.6) over time. As expected, with a lower availability of microsites (i. e. survival of *C. dactylon* (cs) increase from 0.98 to 0.99), the change is substantially less pronounced and *C. dactylon* was still the dominant species after 100 years of simulated time.

At the end of the simulated 100-year period, the following parameters had an impact on the EQUILIBRIUM level and time until EQUILIBRIUM of *D. rhinocerotis* (a summary can be found in Table 7.2):

**rz (relative ZOI radius):** An increase of rz leads to an increase of the cover of *D. rhinocerotis* when EQUILIBRIUM is reached (e. g. scenarios 25, 26 and 27). A similar observation can be made for most of the scenarios. With increasing relative ZOI (rz) of *D. rhinocerotis*, i.e. increasing area affected by the individual plant through competition, the cover of *D. rhinocerotis* increases, while mixed cover, i. e. cells covered by



**Figure 7.3.:** Density of *D. rhinocerotis* within and outside furrows on old field. Each transect is treated as a sample.  $\chi^2$ -test shows significant differences between observed and expected distribution of plants within and outside furrows ( $\chi^2_1 = 11.9191$ ,  $p = 0.0006$ ).



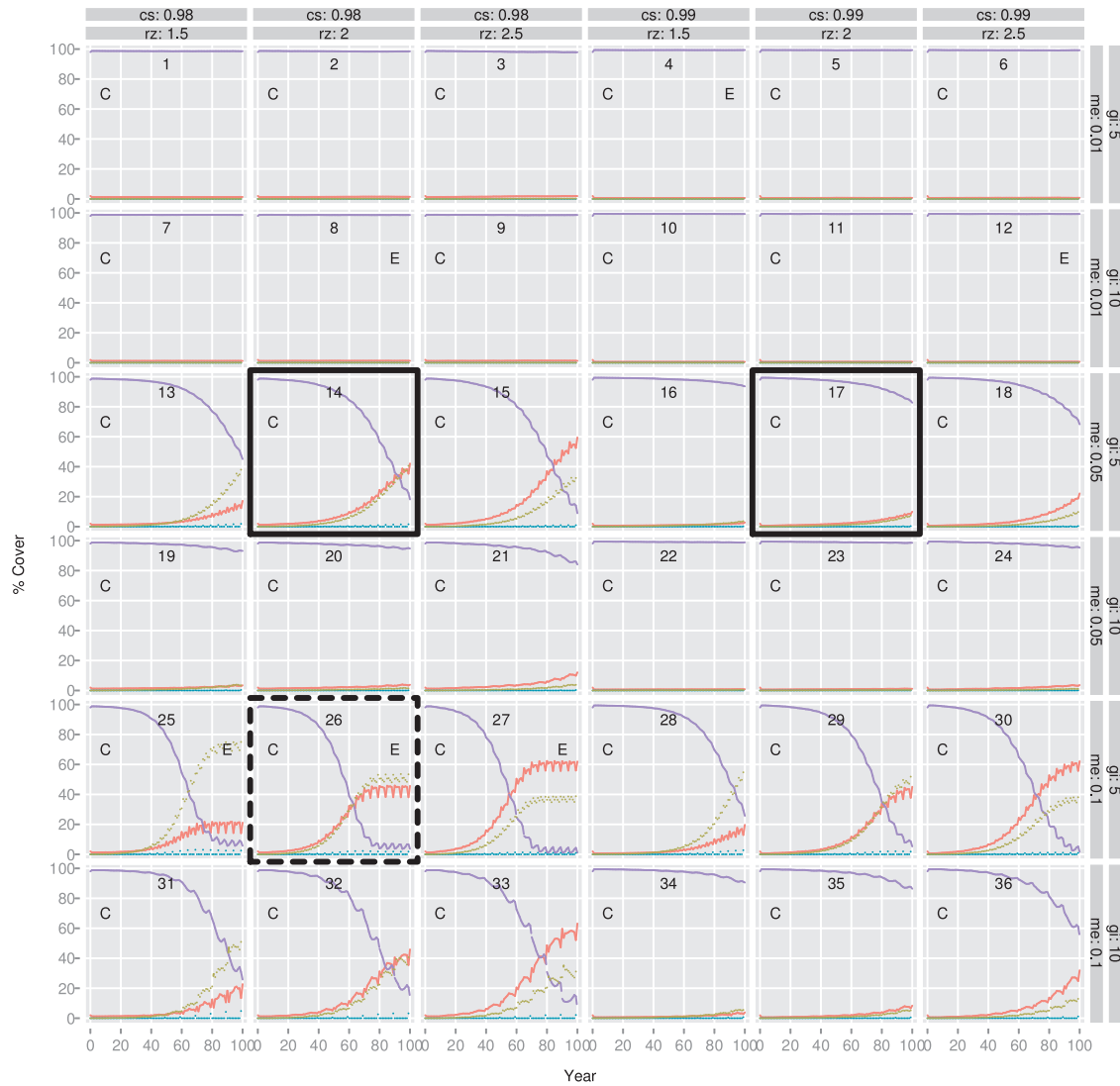
**Figure 7.4.:** Distance dependent density pdf. The histogram indicates the frequency distribution of the distance of the individuals in the old field, the line the estimated pdf and the vertical ticks below the chart represent the individuals.

*D. rhinocerotis* and *C. dactylon*, decreases. For rz of 1.5, mixed cover was higher than *D. rhinocerotis* cover, for rz of 2.0, these were approximately the same or mixed cover slightly higher, while in scenarios with a rz of 2.5, mixed cover was lower than *D. rhinocerotis* cover;

**cs (*C. dactylon* survival):** An increase in the survival probability from 0.98 to 0.99 leads to a slowing down of the return of *D. rhinocerotis*, i.e. an EQUILIBRIUM is reached later. However, the level of the EQUILIBRIUM seems to remain the same (e.g. scenarios 28, 29, 30 compared to 25, 26, 27). In the case of the two base scenarios, an increase of cs from 0.98 to 0.99 causes a delay in the recolonisation by *D. rhinocerotis*. The cover values of *D. rhinocerotis* at the end of the cs=0.99 base scenario were already reached in the cs=0.98 base scenario around year 63, i.e. in two-thirds of the time;

**gi (Germination interval):** An increase in gi from 5 to 10 years also seems to slow down the return of *D. rhinocerotis* (e.g. scenarios 16, 17, 18 compared to 28, 29, 30). No information is available on the level of the EQUILIBRIUM, as within the simulated time frame, only scenarios 25, 26 and 27 reached EQUILIBRIUM. Concerning the base scenarios, the doubling of gi from 5 to 10 years caused a dramatic increase in the time required to reach EQUILIBRIUM. Although the density of individual *D. rhinocerotis* is still increasing with a longer germination interval (Figure 7.6), the amount of change over 100 years is considerably reduced: it is only one order of magnitude compared with four orders of magnitudes for gi=5 years.

**me (Mean Establishment rate of *D. rhinocerotis*):** At a mean establishment rate of 0.01,



**Figure 7.5.:** Change of cover over time. A “C” in the upper left corner indicates a CHANGING scenario, an “E” in the upper right corner indicates the the scenario has reached an EQUILIBRIUM within the simulated time of 100 years (see Chapter 7.2.5 for details). Line colour indicates: violet: *C. dactylon* cover, brown: mixed cover, red: *D. rhinocerotis* cover, turquoise: bare soil. Numbers in the upper centre indicate the number of the scenario. The two base scenarios of the model are framed with a solid line, the ideal scenario, as defined in the discussion, is framed by a hashed line.

**Table 7.2.:** Summary of impact of parameter increase on EQUILIBRIUM level and time till EQUILIBRIUM will be reached.  $\uparrow$ : increasing with increasing parameter,  $\downarrow$ : decreasing with increasing parameter,  $\Leftrightarrow$ : no change with increasing parameter and ? impact unclear

Parameter	Impact on					
	<i>D. rhinocerotis</i>		<i>C. dactylon</i>		mixed	
	level	time	level	time	level	time
rz	$\uparrow$	$\Leftrightarrow$	$\downarrow$	$\Leftrightarrow$	$\downarrow$	$\Leftrightarrow$
cs	?	$\uparrow$	?	$\uparrow$	?	$\uparrow$
gi	?	$\uparrow$	?	$\uparrow$	?	$\uparrow$
me	?	$\downarrow$	?	$\downarrow$	?	$\downarrow$

only a very small change in the density of *D. rhinocerotis* is observed (scenarios 1 to 12). When me is increased to 0.05 and 0.1, a dramatic increase in the rate of increase of *D. rhinocerotis* density can be observed (e. g. scenarios 1, 2, 3 compared to 13, 14, 15 and 25, 26, 27). No information is available on impact of me on the EQUILIBRIUM, as only scenarios 25, 26 and 27 reached EQUILIBRIUM. Nevertheless, when comparing scenarios 13, 14, 15 with 25, 26 and 27 respectively, it can be expected that the impact is rather low. For the base scenarios, a decrease of me from 0.05 to 0.01 caused a switch from a spreading to a constant / stable population. No increase in *D. rhinocerotis* density (Figure 7.6) was observable over 100 years. The identification of CHANGING in Figure 7.5 was caused by random fluctuations due to individuals establishing and dying, as confirmed by the densities depicted in Figure 7.6.

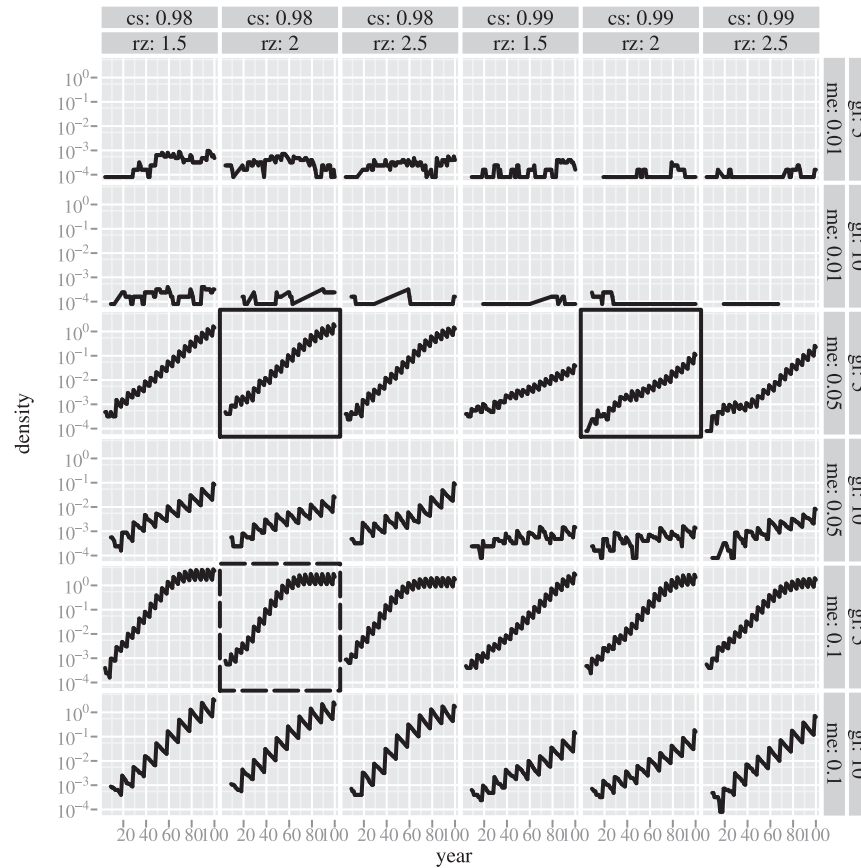
### Field validation

Simulated *D. rhinocerotis* densities are shown in Figure 7.6. Scenarios with me=0.01 did not show any substantial increase and remained below the observed density of 0.1 for the whole 100 year time period . The first base scenario (cs=0.98) reached the observed density after 60 years, the second base scenario (cs = 0.99) only after 95 years. In both base scenarios, the time it took to reach the observed density increased with increasing Zone of Influence rz, Germination Interval gi and decreasing mean establishment me and vice versa. In all cases, the change of rz had the least impact of three parameters investigated.

Based on the sum of squares (ssq) of the two distance-dependent density pdfs (observed versus simulated) (Figure 7.7), the picture changes: the cs=0.98 scenario has two peaks, the higher at 85 years and the lower one at 15 years. These peaks are quite robust with a change in rz, changing only by  $\pm 5$  years. The first peak becomes even more pronounced when increasing me from 0.05 to 0.1 but then the influence of rz on the strength of the peak is more pronounced.

The cs=0.99 scenarios also have two peaks, but these are of approximately the same amplitude at 25 and 60 years. In contrast to the base scenario of cs=0.98, an increase as well as decrease of rz leads to a disappearance of the first peak and a more pronounced





**Figure 7.6.:** Sensitivity of average *D. rhinocerotis* density increase over time to variation in the parameters me (mean establishment rate of *D. rhinocerotis*), rz (radius of zone of influence), gi (germination interval), cs (*C. dactylon* survival). The scenarios framed with solid black are the two base scenarios, the one framed with hashed black is the ideal scenario as defined in the discussion. Average density of field data are 0.1.

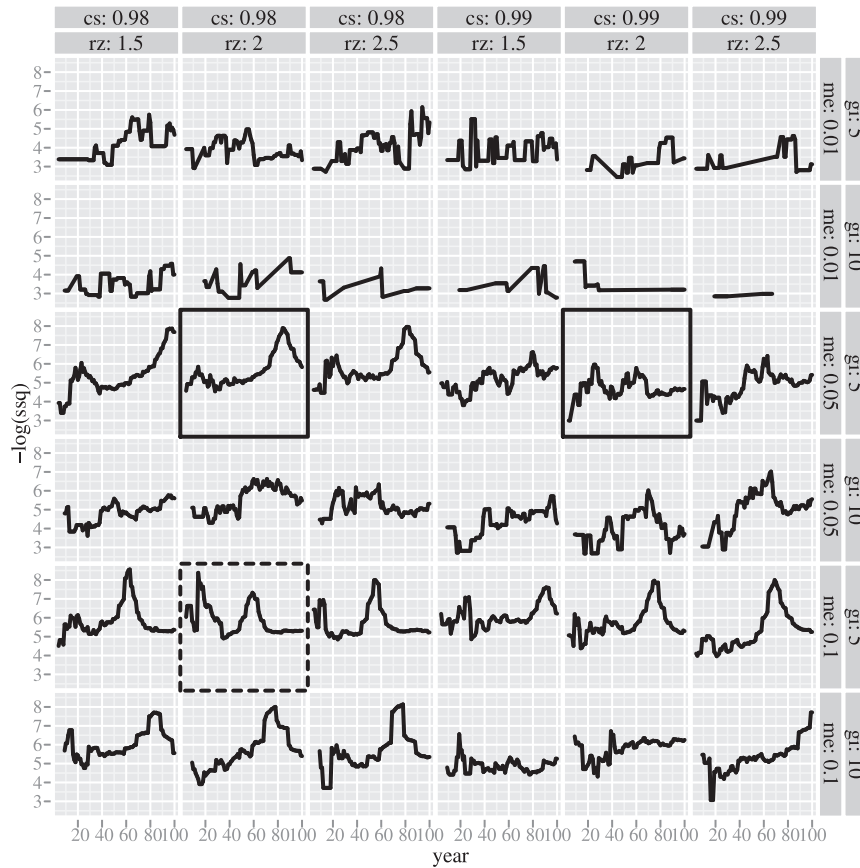
appearance of the second. An increase of gi has essentially the same effect as an increase in rz.

The peaks observed in two base scenarios (15 years with  $cs = 0.98$  and 25 year with  $cs = 0.99$ ) correspond well with the age of abandonment of the old field, which is 20 years. Based on these two scenarios, the microsite availability on the old field can thus be expected to be between 0.01 and 0.02 percent cover. Unfortunately, no field data are available to validate this estimation.

### Velocity

To analyse the velocity of the spread of *D. rhinocerotis* in the simulations, we combined the results of all five simulations. Consequently, for each year, a maximum of five distances for each measure is available. Figure 7.8 shows an example of one simulation per scenario. Results obtained from the other simulations provided similar pictures.

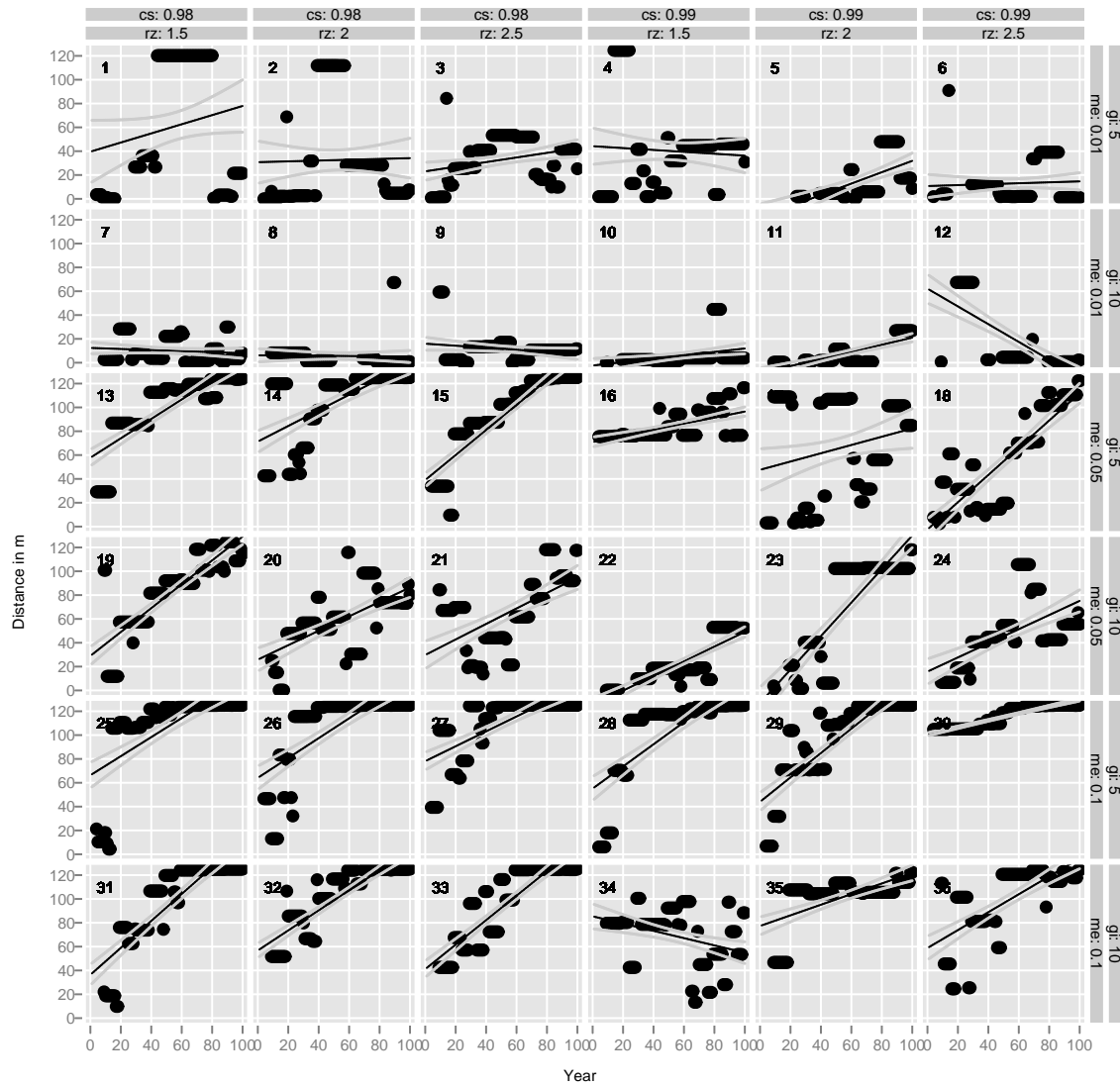
Linear regressions of the combined data, to determine the velocity of the spread for the three different measures (x0001, x0010, x0100), vary greatly between measures. The



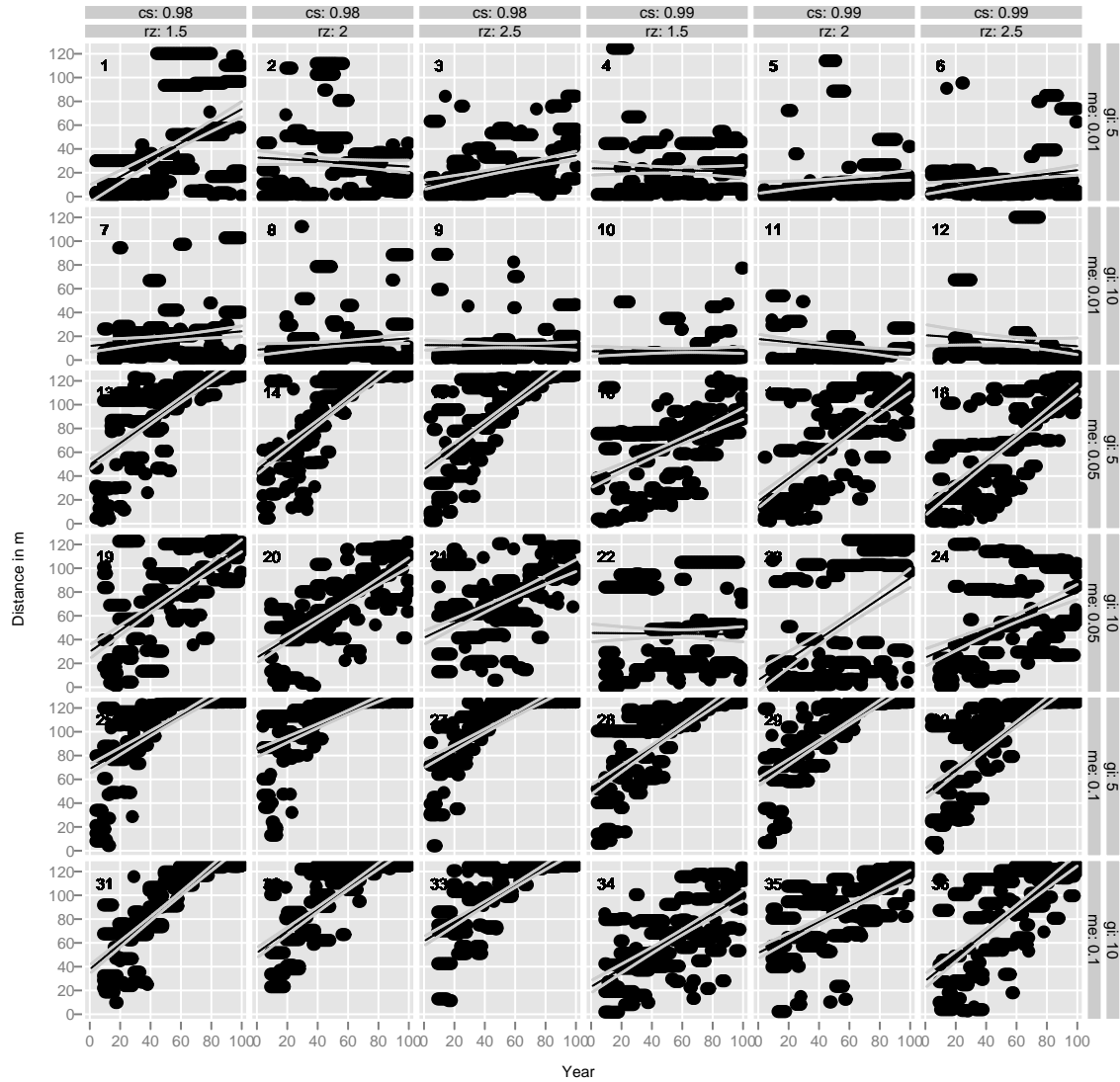
**Figure 7.7.:** Sensitivity of  $-\log(ssq)$  of observed and simulated distance dependent pdfs over time to variation in the parameters me (mean establishment rate of *D. rhinocerotis*), rz (radius of zone of influence), gi (germination interval), cs (*C. dactylon* survival). The scenarios framed with solid black are the two base scenarios, the one framed with dotted black the ideal scenario as defined in the discussion.

velocity of the individual dispersed furthest away (x0001) cannot be clearly determined by this method (Figure 7.9). Scenarios one to twelve show an inconsistent picture, with seven of these even having negative velocity (Negative velocity would mean that the *D. rhinocerotis* is not spreading but retracting). The other scenarios, 13 to 36, all show a positive velocity: *D. rhinocerotis* is spreading. A commonality between all scenarios is the large spread of the points, and for scenarios 13–21 and 25–33, that the distance between the plant closest to the edge and the edge is increasing over time. The distances of the individual dispersed furthest, in the ideal scenario identified above, correspond very well with those obtained from field observations; the mean of the ideal scenario is around 95m after 20 years, that of the field observations is 88.8m (median 98.4m).

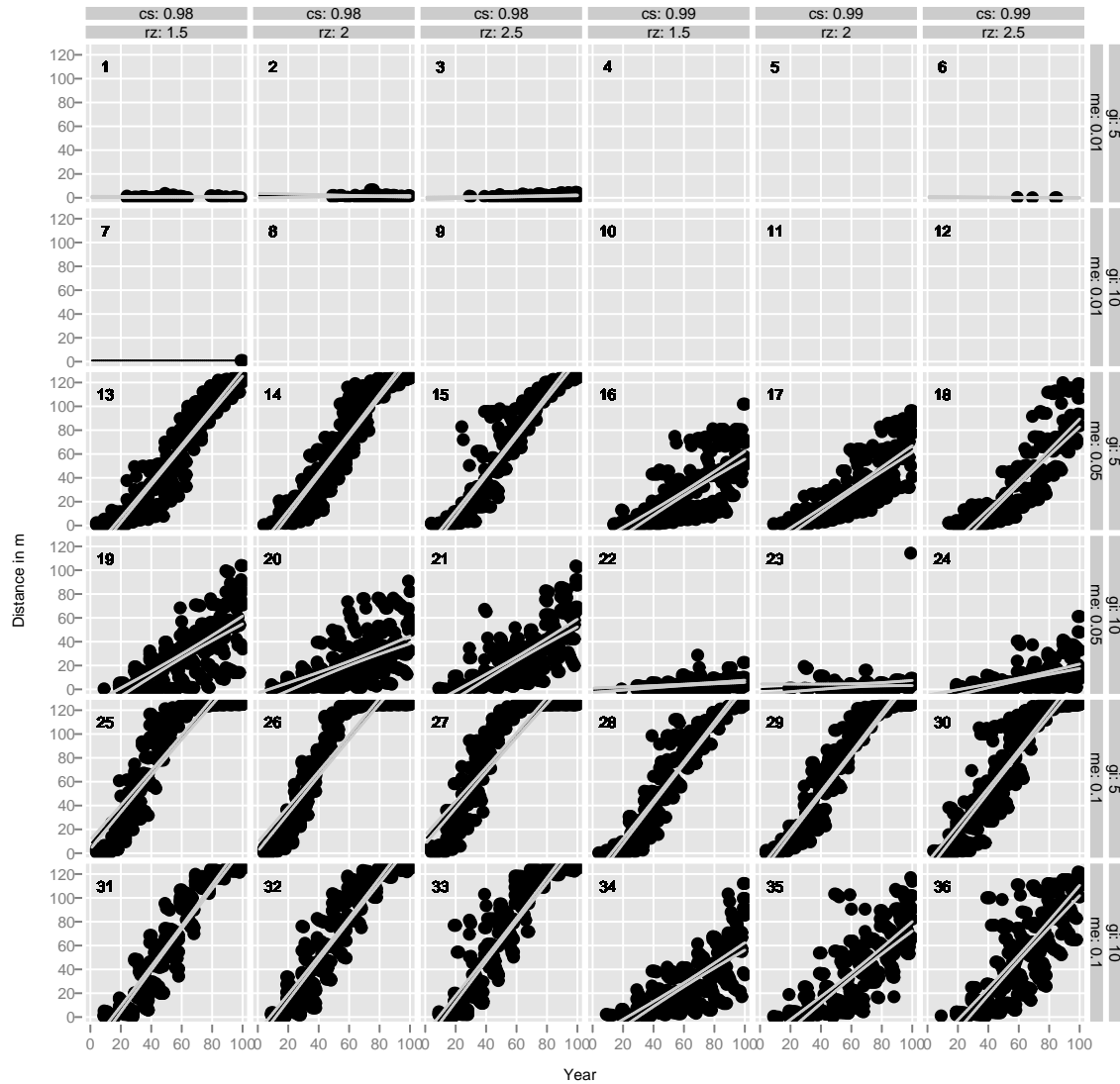
Based on the same analysis, when using measure x0010 (Figure 7.10), all velocities, i.e. slopes, are positive and the spread of the points is less pronounced, as can be seen in Figure 7.9. In addition, in scenarios 25–33, a sigmoidal shape of the cloud of points emerges, increasing slowly at the beginning then showing an approximately-linear increase and a flattening towards the end of the simulated time span. The velocities and the shape



**Figure 7.8.:** Distance of the furthest plant from the initial seed source (measure  $\times 0001$ ) of a single simulation over time versus variation in the parameters me (mean establishment rate of *D. rhinocerotis*), rz (radius of zone of influence), gi (germination interval), cs (*Cynodon* survival). Linear regression lines indicate the expected velocity. Data are from one single simulation. Numbers in the upper left corners indicate the number of the scenario.



**Figure 7.9.:** Distance of the furthest plant from the initial seed source (measure x0001) of all simulations combined over time versus variation in the parameters me (mean establishment rate of *D. rhinocerotis*), rz (radius of zone of influence), gi (germination interval), cs (*Cynodon* survival). Linear regression lines indicate the expected velocity. Data are combined from all simulations. Numbers in the upper left corners indicate the number of the scenario.

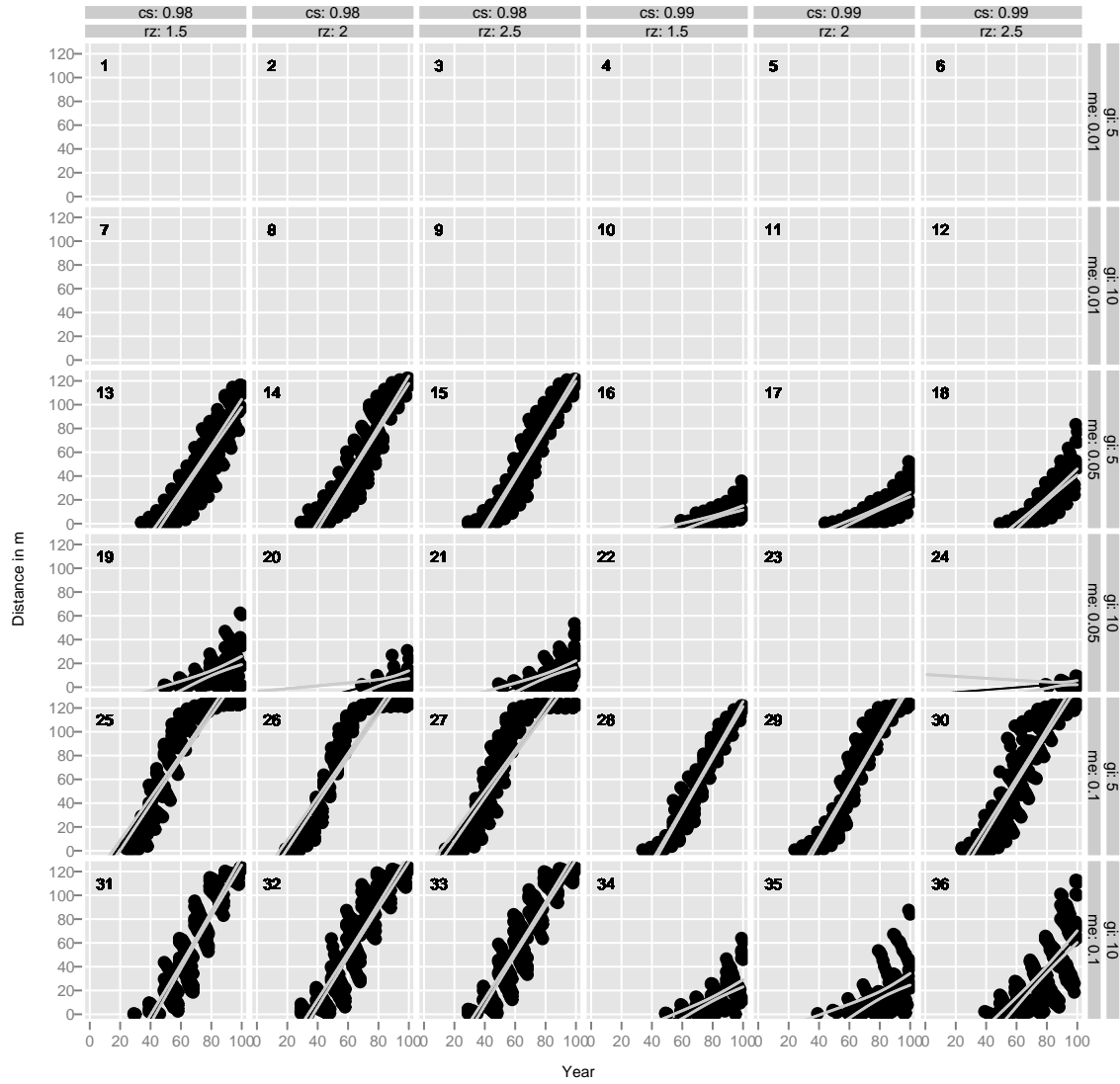


**Figure 7.10.:** Distance of the 10<sup>th</sup> furthest plant from the initial seed source (measure x0010) of all simulations combined over time versus variation in the parameters me (mean establishment rate of *D. rhinocerotis*), rz (radius of zone of influence), gi (germination interval), cs (*Cynodon* survival). Linear regression lines indicate the expected velocity. Data are combined from all simulations. Numbers in the upper left corners indicate the number of the scenario.

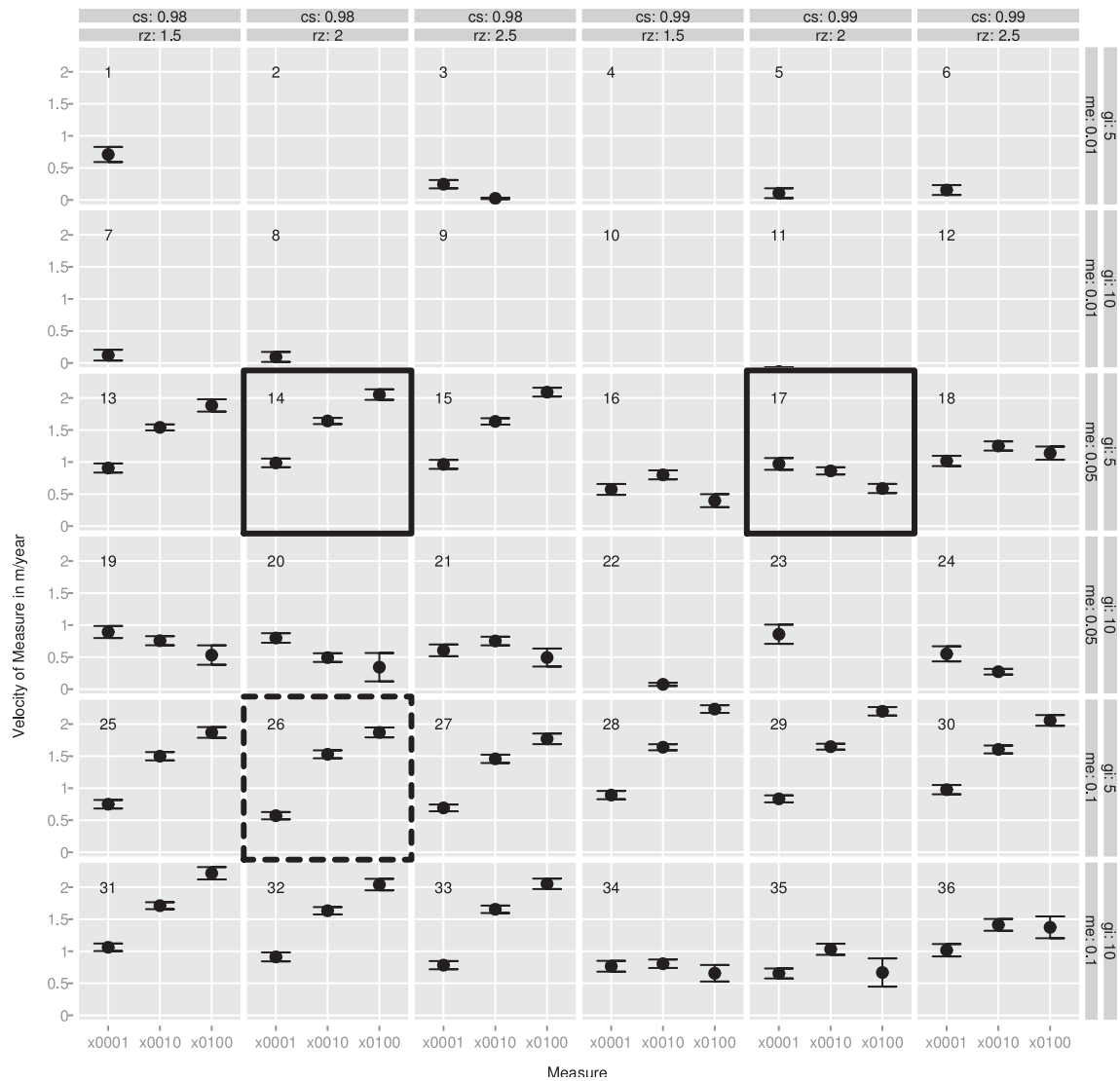
of the cloud of points are not greatly affected by the change in the parameter rz. In contrast, me has a considerable impact as no spread occurs with me of 0.01 and the velocity, i.e. the slope, increases with increasing values of me.

The measure x0100 gives the clearest pattern for velocity. A sigmoidal shape of the cloud of points emerges in essentially all scenarios in which *D. rhinocerotis* is spreading. These pictures remain when plants younger than 5 years are excluded from the analysis (see Appendix E).

Comparing the velocities obtained through linear regression for all scenarios and the three measures used, no clear pattern emerges. For some scenarios the velocity increases



**Figure 7.11.:** Distance of the 100<sup>th</sup> furthest plant from the initial seed source (measure x0100) of all simulations combined over time versus variation in the parameters me (mean establishment rate of *D. rhinocerotis*), rz (radius of zone of influence), gi (germination interval), cs (*Cynodon* survival). Linear regression lines indicate the expected velocity. Data are combined from all simulations. Numbers in the upper left corners indicate the number of the scenario.



**Figure 7.12.:** Estimated velocity of spread over 100 years based on all simulations over different the measures versus variation in the parameters me (mean establishment rate of *D. rhinocerotis*), rz (radius of zone of influence), gi (germination interval), cs (*Cynodon* survival). Only significant velocities are shown. Error bars indicate 95% confidence intervals. The scenarios framed with solid black are the two base scenarios, the one framed with dotted black, the ideal scenario.

with increasing measure ( $x_{0001} < x_{0010} < x_{0100}$ ) (scenarios 13–15 and 25–33), others decrease (scenarios 17, 19, 20) while some show no pattern at all (scenarios 16, 18, 21 and 34–36). Scenarios 1–12 and 22–24 do not have velocities based on all three measures.

## 7.4. Discussion

### 7.4.1. Recolonisation Pattern and sensitivity to parameter value changes

#### Density dynamics

The time taken to reach EQUILIBRIUM, as well as the average percentage cover of *D. rhinocerotis* at EQUILIBRIUM, strongly depend on the values of the parameters analysed, namely rz (relative ZOI radius of *D. rhinocerotis*), cs (survival probability of *C. dactylon*), gi (germination interval of *D. rhinocerotis* in years) and me (mean establishment of *D. rhinocerotis*). I will discuss the impact of each respective parameter, as well as the sensitivity on the level of and time to EQUILIBRIUM, in the paragraphs below.

**rz (relative ZOI radius of *D. rhinocerotis*)** The only parameter which does not seem to have an impact on the time taken until EQUILIBRIUM is rz, but an increase in rz increases the EQUILIBRIUM level of the average percentage cover of *D. rhinocerotis*. This seems to be a paradox, as the ZOI radius determines the zone in which competition affects other individuals. Therefore a larger rz increases the FON (Field of Neighbourhood) and consequently the area which is affected by the competitiveness of a single plant. It is important to note, however, that the average percentage cover “mixed”, i.e. coverage by both *C. dactylon* and *D. rhinocerotis*, decreases while the cover of *D. rhinocerotis* increases. When combined, these two cover types stay constant when rz changes from 1.5 over 2.0 to 2.5, as can be seen in the scenarios 25–27 and 28–30. Hence, the relative ZOI radius of *D. rhinocerotis* rz can be interpreted as one of the factors governing the coexistence of the two species: a low rz provides niches which can be colonised by *C. dactylon*, whereas a high rz would lead to a higher separation between the species in space.

This effect does not seem to be influenced by other parameters: a change of gi from 5 to 10 years (scenario 25–27 versus 31–33 and 28–30 versus 34–36) indicates the same pattern as described above. The same applies for a change in cs (25–27 versus 28–30) and me (13–15 versus 25–27).

**cs (survival probability of *C. dactylon*)** Survival of *Cynodon dactylon*, cs, has a different effect as it does not seem to influence the level of the EQUILIBRIUM, but rather the time it takes to reach said EQUILIBRIUM. This indication is given by comparing scenario 25–27 with 28–30. As cs represents the availability of microsites, i.e. small sites which provide a zone free from competition by *C. dactylon*, on which *D. rhinocerotis* can establish, this has important implications for restoration. The number of microsites available to species for establishment depends on frequency, intensity and type of disturbance (Holzel and Otte, 2003; Midoko-Iponga, 2004; Moyes et al., 2005). Nevertheless, it is important that in the parameter combinations we have used in our scenarios, even the slightest change in the survival probability of *C. dactylon* from 0.99 to 0.98 increases the time until EQUILIBRIUM is reached by at least 50% (in scenario 26–28, EQUILIBRIUM is reached at around year 70, and in scenario 29–31, not before year 100).



As in the case of the above discussed impact of  $rz$ , the pattern of an increase of the time until EQUILIBRIUM is reached with decreasing  $cs$ , is not influenced by the other parameter as can be seen in 13–15 versus 16–18, 25–27 versus 28–30 and 31–33 versus 24–36.

Due to this sensitivity, our simulation model demonstrates that *D. rhinocerotis* is not seed-limited but rather recruitment-limited by the availability of microsites for germination. This is supported by observations that *D. rhinocerotis* plants are found more often in old drainage lines (furrows) on the old field, than on the ridges. We hypothesise that *C. dactylon* is not as dense in the furrows as they are waterlogged in winter, therefore providing more microsites, as well as more moisture, for germination and establishment of *D. rhinocerotis*. Further investigation is needed to support this hypothesis, and indeed such investigation is underway (Memiaghe, in prep.). Similar observations have been made in European flood-meadows (Holzel and Otte, 2003), where regular flooding of experimental plots suppressed competitors, and at the same time, provided favourable conditions for germination of target species.

As outlined in Chapter 7.2.1, the growth rate of *C. dactylon* is an underestimate of the potential growth rate. Nevertheless, in all simulations at all times, all areas not covered by *D. rhinocerotis* were covered by *C. dactylon* (taking the competition interaction into consideration). Therefore even though a faster growth is possible, the limiting factor for growth of *C. dactylon* was not the parameter specifying the maximum growth, but rather the inter- and intra-specific competition.

**gi (germination interval)** An increase of the germination interval of *D. rhinocerotis*  $gi$  increases the time until an EQUILIBRIUM is reached and seems not to influence the level of the EQUILIBRIUM. As *D. rhinocerotis* seems to be recruitment-limited rather than seed-limited, a doubling of the germination interval should thus lead to a doubling of the time required to reach an EQUILIBRIUM. However, in scenario 27 with a  $gi$  of 5 years, *D. rhinocerotis* reaches 60% cover around year 75, but in scenario 33, where the  $gi$  is double that of scenario 27, in year 100. A similar observation can be made when comparing several other scenarios (between 25 and 31, 26 and 32 and 33 and 36), and for average percentage cover mixed — those scenarios with  $gi$  of ten do not require twice the time to reach EQUILIBRIUM compared to those with a  $gi$  of five. This can be explained, potentially, by the size of the plants: the same amount of cover can be produced by many smaller plants or few larger plants. As the growth of plants is higher for a period of 10 years than for five years, this could explain the expansion of cover independently from germination. In a scenario with a germination interval of ten years, more, older individuals are present in the population, as plants have had more time to establish without being exposed to repeated competition from new arrivals. In addition, as plants of age ten are larger than plants of age five, they therefore have a greater competitive advantage against newly-establishing individuals.

Due to the long time needed to reach EQUILIBRIUM and the consequently low number of scenarios reaching EQUILIBRIUM within 100 years (only three out of the 36 scenarios

reached EQUILIBRIUM and three to four more could be classified as nearly having reached EQUILIBRIUM), it is difficult to say what is the impact of the other parameters on the pattern of change of  $g_i$ . Nevertheless, when comparing scenarios 25–30 with 31–36, the same pattern can be seen: the change in the cover values happens in the scenarios 31–36 more slowly than in the scenarios 25–30, indicating an increase in the time until EQUILIBRIUM is reached. In the cases where a flattening of the curve can already be observed (scenarios 32 and 33), the level of the equilibrium seems to be the same as in 26 and 27.

Comparing scenario 32 (increase of  $g_i$  from 5 to 10 years based on scenario 26) and 29 (increase of  $cs$  from 0.98 to 0.99 based on scenario 26), shows a very similar pattern: at between 80 and 90 years, all percentage cover values, except of bare ground, are the same in these two scenarios and the values after 100 years are similar. Similarities can also be found in scenarios 31 and 28, 33 and 30 and even scenario 20 and 17, in which the mean establishment of *D. rhinocerotis* ( $me$ ) is 0.05. One can therefore conclude that the impact of an increase of  $g_i$  from 5 to 10 has effectively the same impact as an increase of  $cs$  from 0.98 to 0.99 (which is equivalent to a decrease of the availability of microsites from 2% of the area to 1%).

The impact of the germination interval on the time until EQUILIBRIUM is reached is used to develop restoration strategies in which favourable conditions for germination are mimicked and the time period between favourable events can be reduced. As germination of *D. rhinocerotis* in furrows is higher than on ridges, irrigation could be used to mimic high rainfall years. Due to the same effect of a decrease of  $g_i$  as an increase of the availability of microsites, management actions increasing the availability of microsites can also be used instead, like opening gaps in closed grass cover. Nevertheless, as very little is known about triggers for the germination of *D. rhinocerotis*, this approach requires more research into factors influencing germination of this species as well as other Renosterveld shrubs.

**me (mean establishment of *D. rhinocerotis*)** Similar to  $cs$ , the mean establishment rate of *D. rhinocerotis*,  $me$ , does not impact on the level of average percentage cover of the species, but rather on the time required until EQUILIBRIUM is reached (scenario 13–15 compared to 25–27).

As  $me$  also influences establishment, impact on the time until EQUILIBRIUM is reached is similar to that of  $cs$ : comparing scenario 29 (an increase of  $cs$  from 0.98 to 0.99 compared to the ideal scenario (26)) with scenario 14 (decrease of  $me$  from 0.1 to 0.05), one can identify similar pattern although the scenario 29 is changing slightly faster than 14. The same can be seen when considering scenario 28 versus 13 and 30 versus 15. When looking at scenarios with  $g_i=10$ , the difference in speed of change becomes more apparent: scenario 36 has similar cover % values in year 70 as scenario 21 in year 21, but the ratios between the different cover values are similar. This pattern does not seem to be influenced by a change in parameter values of  $g_i$  and  $rz$ .

Another pattern can be identified: a doubling of  $me$  from 0.05 to 0.1 can be counter-balanced by an increase of  $g_i$  from 5 to 10 years. Comparing scenarios 13–18 ( $g_i=5$  years,

me=0.05) with 31–36 (gi=10 years, me=0.1), the pattern of cover change are the same apart from the fluctuations in density after germination events, which are occurring twice as often in the gi=5 years scenario then in the gi=10 years scenario. This counterbalancing of me and gi is not influenced by a change in rz or cs.

Overall, we can conclude that the recolonisation pattern is most sensitive to the availability of microsites, represented by the parameter cs, and that even a small change from 1% to 2% availability of microsites has a dramatic impact. The second parameter to which the recolonisation pattern is sensitive, is me: a small change from 0.01 to 0.05 has a huge impact. Nevertheless, the parameter me has to be considered together with gi as these two can balance each other out: a change of me from 0.05 to 0.1 is balanced out by an increase of gi from 5 to 10. The parameter rz does not have a strong impact on the recolonisation pattern, but rather on the coexistence between the two species.

### Velocity of spread

The distance of the measure x0001 is positively related to simulated year, i.e. *D. rhinocerotis* is spreading onto the old field in most of the scenarios (Figure 7.9). However, this picture is misleading, especially in simulations 1, 3, 5–8, 10, 11 and 23, as the linear regression indicates a positive velocity. In fact, no actual spread occurs for the velocity based on the measures x0010 and x0100 (Figure 7.10 and Figure 7.11). These scenarios show no spread at all, or, in the cases where no points are plotted, less than 10 or 100 individuals, respectively, are located on the simulated patch. Measure x0001 is therefore extremely sensitive to the position of a single individual. This is an important feature in the case of spread of an alien species (see Chapter 4), as one individual spread far out may become the nucleus of a new infestation. In contrast, in the context of restoration, it is of concern whether (and why) a target species does not spread further in a patch. As the position of x0001 and the velocity of x0001 is very variable, relying on calculations of e. g. distances of stepping stones between potential establishment habitats, on the velocity of spread indicated by x0001 includes a certain risk. To ensure that the propagules indeed reach suitable patches, predictions based on a velocity estimate based on a measure like x0010 or even x0100 are much safer, as this will increase the chance of establishing a viable population in the new habitat patch. This is especially important in highly-fragmented ecosystems with a high degree of isolation between patches, such as Renosterveld.

The sigmoidal shape of the point clouds indicates that there are two processes influencing the spread: the first one is an initial phase in which the dynamics of the simulation are determined by the initial conditions and parameters set. As the seed dispersal, from the area source to the west of the simulated patch, is based on the actual seed dispersal kernel of the species (see Chapter 6), the only parameter influencing the initial phase is the number of seeds dispersed into the simulated patch. Should fewer seeds than from an actual area source be dispersed into the simulated landscape, the velocity would increase initially until it reaches its “normal” or “actual” velocity of spread. This phenomenon can be observed in most of the scenarios analysed using the measure x0100 (Figure 7.11),

and in several when using x0010 (Figure 7.10). The other anomaly which can be observed in the plots is the flattening of the point cloud towards the end of the simulated time frame. This is caused by the plants reaching the eastern side of the simulated patch and therefore not being able to disperse any further. This is therefore an artifact which could be avoided if a larger patch were to be simulated, which was not possible due to computational constraints. Combining these two artifacts, the velocities obtained from the linear regressions are lower estimates of the real velocity of spread. In the context of restoration, where the aim is to bring a species back into a patch, this is acceptable, as an underestimate in velocity of spread will lead to planning for shorter distances between patches and increases the chances of colonisation. However, in the case of alien spread, an underestimate is not desirable, since the aim is to prevent the spread of a species.

An interesting picture emerges when comparing the velocities based on the different measures (Figure 7.12). Those scenarios which show a flattening of the point cloud at the end of the simulated time frame also show an increase in velocity with increasing measure. Scenarios 13–15, and 25–33 for x0010 (Figure 7.10) all show flattening while having increasing velocities with increasing measure. Those point clouds, which do not flatten at the end of the simulated time frame (scenarios 16–24 and 34–36) all have velocities that are not significantly different, i.e. non-overlapping confidence intervals as in scenario 24, or show no consistent pattern. As the simulated landscape is closed to the east, no further spread at the end of a simulation time frame is possible, and the velocity for this measure is reduced. As smaller measures reach the eastern edge of the simulated landscape before the larger measures, velocities of smaller measures are slowed down earlier and more rapidly than those of larger measures. Over time, when the target species recolonises the whole simulated landscape to capacity, all velocities will be reset to zero. Nevertheless, the estimates based on linear regressions will still show that the smaller measures spread with a larger velocity, as the former reached the eastern edge of the simulated patch before the latter did.

#### 7.4.2. Field Validation

When comparing simulation results with actual observation, different pictures emerge: regarding the overall density of *D. rhinocerotis*, neither of the two base scenarios reach the observed density of *D. rhinocerotis* at around 20 years, the age of the old field. In contrast, the likelihood analysis indicates that there is a good correspondence between the shape of the simulated distance dependence of the invasion wave at around 20 years and the one observed in the field at an age of 20 years. This holds true for both base scenarios. In the case of the first base scenario with  $cs=0.98$ , there is a second, more-likely peak at around 85 years. It is difficult to say why the second peak is more likely than the first but after 85 years, the increase of the density in the simulated patch is already flattening which indicates that the simulated area is covered evenly by *D. rhinocerotis*. In contrast, this is not the case on the field site. Therefore, we can conclude that this peak at 85 years does not represent the observed pattern, even when disregarding the age of the old field.

In contrast, for the second base scenario ( $cs=0.99$ ), there is no indication that the density increase is flattening and therefore the reasoning to reject the peak at 85 years (as per the first base scenario) cannot be applied here. As at the time of the first likelihood peak both scenarios, as well as other scenarios showing this peak, are still expanding without experiencing the effect of the limited area; one can conclude that the first peak represents a feature of the scenarios caused by the processes included in the model and the parameter values. This first peak can be found in several other scenarios and the one which provides the best correspondence with the field data for the distance dependence of the density and the overall density is base scenario one with  $me=0.1$  instead of 0.05. In that scenario, the overall density observed in the field is reached after 40 years and the peak in the likelihood graph is very pronounced at around 15 years. In this “ideal” scenario, we would expect the cover of *D. rhinocerotis* and *C. dactylon* to be the same in year 60 and a relatively-stable cover ratio to be reached in year 80. This EQUILIBRIUM would consist of 40% of the cells covered by *D. rhinocerotis*, 50% covered by both species and around 10% covered by *C. dactylon*. These predictions should definitely not be taken as absolute predictions as further studies are required to verify these long-term predictions. Nevertheless, the prediction that after 60 years areas are covered again by *D. rhinocerotis* can be confirmed by [Walton \(2005\)](#) who found that sites which were ploughed 60 years ago are covered by *D. rhinocerotis*, and are very similar in vegetation structure to adjacent natural vegetation.

Comparing the distance of the furthest individual in the ideal scenario (Figure 7.9) with the observed distances, ranging from 38.7m to 119m with a median of 98.4m and a mean of 88.8m, one can see the same pattern: the simulated furthest distances range from around 40m to 120m, which is the same range as the observed ones, with the linear regression indicating a distance of around 90m after 20 years, which also corresponds with the observed mean and median.

### 7.4.3. Management implication

Based on the results, one can draw the following conclusions for management to increase the recolonisation potential of *D. rhinocerotis*. Our simulations indicate that *D. rhinocerotis* is very sensitive to changes in the availability of microsites for germination. This is supported by [Levyngs \(1927\)](#) and [Koekemoer \(2002\)](#) who argue that competition is a limiting factor for germination and establishment. Consequently, one management action could be to increase the number of available microsites through tilling or harrowing.

Another potential management action could increase the mean germination rates. As not much is known about the biology of *D. rhinocerotis*, especially its germination requirements, this management intervention requires further research. The same applies to the manipulation of the germination intervals. A decrease of the germination intervals would result in increased colonisation rates of *D. rhinocerotis*, but before this can be attempted, an understanding of the triggers of *D. rhinocerotis* germination events is required. [Levyngs \(1927\)](#) argues that fire is a trigger of germination in *D. rhinocerotis*, but this contradicts observation on our study site, where germination took place without fires and no ger-

mination was observed on a burned site which (by contrast, another burned site showed successful *D. rhinocerotis* recruitment). Alternatively, germination events could occur only during wet years, which is supported by the observation that *D. rhinocerotis* density is higher in the furrows, where water collects in winter. In Californian coastal sage scrub, Cione et al. (2002) recorded germination of indigenous shrubs seeds, oversown onto old fields, only during a wet year.

Considering the lack of knowledge about germination requirements and the triggers of germination events of *D. rhinocerotis*, the only viable current management option seems to be to increase the availability of microsites through the management actions suggested above while, at the same time, making sure that the microsites are not colonised by alien invasive species.

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## **Part IV.**

# **General Discussion and Conclusions**





## 8. Conclusions and Discussion

As discussed in Chapter 1, restoration ecology and invasive species control are both concerned with the spread potential of species. Therefore, there is potential for information sharing among these disciplines. Before comparing the two studies in Part II, “Dispersal Modelling for Invasion Control” and Part III, “Dispersal Modelling for Restoration” to identify the commonalities and the differences and finally to identify aspects which are profitable for both, I will present a short summary of the main findings of the two studies.

### Main Results “Dispersal Modelling for Invasion Control”, Part II

To be able to address the key questions of the impact of biocontrol agents on the spread of *Hakea sericea*, it was essential to obtain information on the shape of its seed dispersal kernel. In the absence of hard data, we used an innovative approach using expert estimates of the cumulative dispersal kernel and then fitting these to mathematical models. As it was impossible for us to reject certain expert opinions on the dispersal kernel, we used each of them plus the average for all further simulations. The problem of limited hard data availability is a very common problem, and our approach can be used as a model for other studies.

In Part II, I showed that seed-destroying biocontrol agents have an impact on the velocity of spread of *Hakea sericea*. In addition, I was able to quantify the effect of seed production on the velocity of spread. This has not been quantified previously, and as seed-destroying biocontrol agents and fire frequency influence the seed production per generation, this provides the means to determine the effects and impacts that different management scenarios have on the velocity of spread, and thus to predict more easily the potential spread into natural areas. The seed rain from an area source was estimated based on a determined dispersal kernel and seed production from a point source. However, as most spreads of alien invasive species originate from area sources, being able to estimate seed rain from an area source is important information to estimate the risk of spread from a given population. Although Clark et al. (2001) provide a method to calculate the velocity of spread of non-exponentially-bound seed dispersal, they do not provide a way of obtaining confidence intervals for these. I present a method which enables us to calculate these confidence intervals, and therefore provide a possibility to compare different velocities statistically. The results in summary are:

- I.1. Biocontrol agents have a significant negative impact on the velocity of spread;

I.2. Seed production influences the velocity of spread logarithmically:

$$V \sim \ln(\text{SeedProduction})$$

I.3. As fire frequency and biocontrol agents both influence seed availability of viable seeds, changes in fire frequencies can mimic the effect of biocontrol agents on the velocity of spread;

I.4. Management actions to control the spread of *H. sericea* should include:

- a) Introduction of appropriate biocontrol agents to destroy the seeds accumulating on the plant. A combination of YFF and MFF has the biggest impact;
- b) Increase of fire frequency to reduce seed production between fires. This needs to be approached with caution to minimise the detrimental effect of fire on the natural vegetation. However, a dramatic increase of the fire frequencies at sites heavily infested with *H. sericea* might be the most effective method to control the alien species;
- c) When the MFF is introduced, the number of seeds accumulated on plants is highest at a fire interval of nine years. Therefore fire intervals between eight and ten years should be avoided in order to decrease the seed accumulation. Further investigations are needed to determine if this model-predicted peak in seeds accumulated on the plant can be confirmed in the field.

## Main Results “Dispersal Modelling for Restoration”, Part III

As not much was known about the processes and pattern in Renosterveld due to its high degree of transformation and resulting habitat fragmentation, the first task was to use historical ecology to reconstruct potential pattern and processes shaping the ecosystem. This provided new insights into the anticipated biodiversity pattern, and processes governing this, in this vegetation type had transformation and fragmentation not occurred. The ecological processes identified were then used to plan the restoration experiments on an old field largely surrounded by Renosterveld. By determining the seed dispersal kernel of *Dicerothamnus rhinocerotis* from an area source, as well as deriving the point source kernel analytically from the area source kernel, I confirmed the field observation that the return of *Dicerothamnus rhinocerotis* is not seed-limited. In addition, the seed dispersal kernel from a point source was an essential piece of information required for simulating the small scale dynamics of *Dicerothamnus rhinocerotis* and *Cynodon dactylon*, a creeping grass covering the old fields. Modelling the small scale dynamics and interactions of these two species provided further insights into grass-shrub dynamics, and contributed to the understanding of factors limiting the establishment of shrub species on old lands dominated by grasses. The results are in summary:

- R.1. A sensitivity analysis showed that a change of the parameters *cs* (*C. dactylon* survival), *gi* (germination interval *D. rhinocerotis*), *me* (mean establishment of *D. rhinocerotis*) and *rz* (relative ZOI radius) have a considerable impact on the velocity *V* of spread, the time until the cover values in the simulated patch are in EQUILIBRIUM, and the levels of average percentage cover in the simulated area. All these factors influence and change the recolonisation potential of *D. rhinocerotis*;
- R.2. Time to EQUILIBRIUM and average percentage cover are extremely sensitive to a change in *cs*, i.e. availability of microsites for germination for *D. rhinocerotis*, and changes in *me*, i.e. changes in the mean establishment of *D. rhinocerotis*;
- R.3. Management actions to increase the recolonisation potential of *D. rhinocerotis* (and likely most other indigenous shrub species) include:
- a) Increasing the availability of microsites for germination by removing *C. dactylon* through weeding or herbicide application or introduction of small scale disturbances such as tilling or harrowing which create microsites for the germination of *D. rhinocerotis*;
  - b) Increasing the mean germination rates of *D. rhinocerotis* by improving conditions more favourable to germination. These management actions could include irrigation, as the species seems to establish after particularly wet winters, but further investigations into the biology of *D. rhinocerotis* is necessary to determine which factors inhibit germination and establishment when microsites are indeed available;
  - c) Influencing germination intervals (*gi*) by application of appropriate measures. Before this can be attempted, the triggers for establishment events, such as high rainfall or fire, need to be investigated through further research into the biology of *D. rhinocerotis*.

In addition, results from both studies confirm [Buckley et al. \(2005\)](#), highlighting the importance of long-distance dispersal, germination biology, juvenile survival and seedling establishment for the spread of a species.

## Differences and commonalities—How can the two disciplines inform each other?

Although both restoration ecology and invasion biology are interested in the dispersal potential and spread potential of a species, the objectives are very different. While the colonisation of a patch is desirable in restoration, the objective of invasive species control is to prevent colonisation. (For a summary of measures and their desirability in these two disciplines see [Table 8.1](#)) Nevertheless, both disciplines need to understand the factors influencing dispersal and colonisation potential, and thus the processes governing the spread

**Table 8.1.:** Desirability of values of measures in restoration biology and alien invasion biology.

Measure		Value	Desirability in	
			restoration	invasion
Velocity				
	x0001	↑↑	++	---
		↓↓	-	+++
	x0100 <sup>a</sup>	↑↑	+++	---
		↓↓	-	+++
EQUILIBRIUM				
	% cover <sup>b</sup>	↑↑	+	---
		↓↓	-	+
	time <sup>c</sup>	↑↑	-	+
		↓↓	+	-
Parameter				
	Sensitivity <sup>d</sup>	↑↑	+	0
		↓↓	+	0

<sup>a</sup>Representative for any measure larger the x0001<sup>b</sup>Percentage cover of target species<sup>c</sup>Time until EQUILIBRIUM is reached<sup>d</sup>Sensitivity of measures to change

of a species. In addition to gaining a basic understanding of the functional processes, both disciplines seek a qualitative understanding of how parameters change with the implementation of management actions in order to determine the most effective strategy (cost, time or any other measure for effectivity) to deal with the problem—be it the restoration of a patch of indigenous vegetation or the limitation of the spread of an invasive species into pristine habitats. Obtaining and providing information on the quantitative impact of management interventions would be ideal, but even though qualitative predictions are possible, quantitative predictions are often impossible to make.

Although dispersal processes and spread pattern are similar for both disciplines, differences occur mainly in the parameter range analysed using simulation models and in the interpretation of the results. When using a simulation model to address a particular problem for one of the disciplines, appropriate parameter values are chosen and results are valid for this problem only. Therefore predictions are also discipline- and problem-specific. Nevertheless, findings can be “translated” and interpreted in such a way that they are relevant for the other discipline. The guiding principle in this translation process is that if we know what limits the spread, we can also infer how to facilitate the spread and vice versa. One complication in the transfer of the management recommendations is that, in many cases, it is not possible to change the same parameter in both directions. One example would be irrigation: it is possible to irrigate and therefore facilitate the germination of a species, but it is not possible to reduce the rainfall in order to inhibit germination. Therefore, the management recommendations cannot be simply negated, but other management solutions need to be investigated based on dependencies identified in the system.

Certain conclusions of Part III, “Dispersal Modelling for Restoration”, are directly ap-

plicable to invasion control. Should the aim be to keep the shrub out of a patch, the results and conclusions concerning the processes and the impact of the parameters on the spread, i.e. restoration recommendations [R.1](#) and [R.2](#), are the same. To translate the management recommendations it is essential to examine if the parameter, that is influenced by the management actions, can be influenced into the other direction as well. In the case of the management recommendation [R.3a](#), whether the availability of microsites can be reduced must be considered, as this inhibits establishment. As the availability of microsites is heavily influenced by the disturbance regime, it becomes essential to control (and avoid) certain disturbances which create microsites for germination of the target species (see e.g. [Elton, 1958](#); [Richardson, 2001](#)). Management recommendation [R.3b](#) calls for the change of conditions to increase the mean establishment rate of the target species. In the context of alien control, the aim would be to reduce the mean establishment rates of the target species. Therefore, environmental conditions which reduce the mean establishment rate must be identified. In the context of restoration, an understanding of the biology of the target species is essential to change conditions for the target species without influencing the natural vegetation unnecessarily. Similar arguments can be made for management recommendation [R.3c](#): an understanding of the biology of the target species is essential to identify the germination event triggers. After these are identified, the decision has to be taken if and how they can be influenced without adversely affecting the native vegetation. [Holmes and Richardson \(1999\)](#), for example, suggest using fire to initiate recruitment as a potential restoration strategy for Fynbos.

Considering the study on invasion (Chapter [II](#)), the identification of the parameters to which the system is sensitive ([I.1](#)) is the same for restoration, but the management options ([I.4](#)) must be translated and adjusted accordingly. The introduction of biocontrol agents was identified as one important management action ([I.4a](#)) to limit the velocity of spread. An option to facilitate the spread of a target species into adjacent sites, would be to increase the seed production and seed output of the natural vegetation. This can be achieved by increasing the number of individuals in the natural vegetation, reducing the number of seed predators and / or managing the environmental conditions for an increased seed production. The feasibility of such an approach depends entirely on the action to be taken to achieve this and potential negative impacts on the other species in the natural patch. Another translation of the management action of using seed-destroying biocontrol agents in alien control, is to use broadcasting of additional seeds in the patch to be restored as this increases the number of seeds available (e.g. [Poschlod and Biewer, 2005](#); [Holzel and Otte, 2003](#)). In addition to increasing the availability of seeds in the to-be-restored sites, this can be regarded as modifying the dispersal kernel of the target species. Alternatively, (mature) individuals of the target species can be transplanted to form nuclei for further spread of the species ([Robinson and Handel, 2000](#)), assuming that the dispersal agent of the target species is present in the system.

The second management recommendation ([I.4b](#)) to increase the fire frequency, to limit the seed production in the area infested by the target species, is similar to the previous

one as the aim is also to control the seed production in the source population to increase or decrease the seed dispersal into un-colonised patches. Although this might be a viable management action with regard to the target species, it is, as with all management actions, essential to consider the whole system: a short fire frequency might control the target species, e.g. *Hakea sericea*, but at the same time promote the growth of alien grasses (Musil et al., 2005; Midoko-Iponga, 2004; Milton, 2004; Cione et al., 2002; Vila et al., 2001), which impacts negatively on the return of natural vegetation (Midoko-Iponga et al., 2005; Midoko-Iponga, 2004).

The idea of applying management to the natural vegetation to increase the chances of restoration was already discussed in Wijdeven and Kuzee (2000), but this focused more on increasing (or rather maintaining) the indigenous species pool.

The third management recommendation (I.4c) to avoid 9 to 11 year fire intervals in *H. sericea* stands infested by the mature follicle feeder (MFF), is highly species-dependent. Nevertheless, it highlights that it is important to consider non-linear relationships as they can result in unexpected anomalies, like the reduction of seeds accumulated on plants between the ages nine to eleven when MFF are introduced.

It should to be noted that invasive species control is mainly operating in landscapes already infested, while restoration operates mainly on patches to be restored, i. e. patches in which the target species is not present or present at a low densities. As discussed above, management can and should also include, in the case of restoration, the source of the target species or, in the case of invasions, the target of the invasive species in the planning of the most effective strategy to reach the goal of restoration or control / eradication of an invasive species. In essence, pro-active management actions can increase the effectiveness (costs and time) of reactive management actions. Nevertheless, the two are closely linked, as both ultimately have the same aim: to return the system to a (more) natural state. This is done by controlling and, where possible, eradicating alien species from the system, while at the same time promoting colonisation of the sites by indigenous plant species. To achieve this goal, both disciplines have to work together as alien clearing alone does not result in a more natural system (Holmes and Cowling, 1997; Richardson and van Wilgen, 2004; Yelenik et al., 2004), because the cleared sites provide excellent microsites for the colonisation by other alien species, e.g. alien grasses or weedy annuals (Yelenik et al., 2004). To facilitate the colonisation of a site by indigenous (desired) species while at the same time avoiding colonisation by alien (undesired) species, restoration efforts and alien control actions have to happen simultaneously. Consequently, management actions which both assist the clearing / control of alien species and re-colonisation by indigenous species are the most effective. By considering the above-outlined examples on how to transfer results and management actions from restoration to invasion biology and vice versa, it will be easier to identify management actions which will have positive effects on restoration as well as invasion control.

The presence of alien invasive grasses poses serious obstacles for the restoration of native shrub vegetation in a number of Mediterranean vegetation types (Hobbs, 2001; Cione et al.,

2002). Thus, research is required urgently to develop management strategies for sites invaded by these grasses. Research presented in this thesis investigates the interactions of shrubs (*Dicerotheramnus rhinocerotis*) and a grass species (*Cynodon dactylon*). Although *C. dactylon* is not an invasive species per se in South Africa, the problem is the same: *C. dactylon* inhibits the return of *D. rhinocerotis* onto the old fields. Hence, these results and management recommendations are transferable to the understanding and restoration of sites colonised by alien invasive grasses.

The restoration study addresses two important questions: how do grass–shrub dynamics manifest themselves? How can shrublands be restored on sites that are colonised by (invasive) grasses or weeds? This question is relevant in most of the highly-transformed Mediterranean ecosystems, especially in the new world (Fox, 1982; Cione et al., 2002; Milton, 2004; Clarke et al., 2005; Gillespie and Allen, 2006) and is becoming more and more relevant in South Africa (Milton, 2004), where the restoration of sites colonised by invasive grasses is a unsolved problem (Milton, 2004). Restoration is often done on a small scale (e.g. Cione et al., 2002; Midoko-Iponga, 2004; Midoko-Iponga et al., 2005), which is not applicable to a larger scale or even landscape scale (Ogden and Rejmanek, 2005). A similar problem applies to upscaling the model as, due to computational constraints, it is usually not possible to simply increase the simulated area. In addition, assumptions like homogeneity of the landscape are violated when upscaling. Especially for restoration, habitat heterogeneity plays an important role and must be taken into consideration, as local conditions and heterogeneity influence (a) the state of the system; (b) the goal of the restoration effort; (c) the restoration strategies; and (e) ultimately, the success of the restoration effort. An appropriate approach for upscaling would be to obtain rules from the small scale individual based model which can then be used in the landscape, grid-based model, to simulate the dynamics there.

As the specific management actions are site- and species-specific, our study cannot supply recommendations for every situation and target species, but can provide information on critical parameters and processes from which management recommendations for the specific situation studied can then be drawn. The first important aspect is the availability of microsites for the return of the shrubs on the grassland, as illustrated by Hobbs (2001) for weedy alien invaders. Although seeds of alien herbaceous species are able to arrive on the sites, their establishment is limited by the availability of microsites (Hobbs and Atkins, 1991). These studies, which were concerned with alien herbaceous species, confirm our findings for an indigenous shrub from the modelling approach: the return of the shrub is microsite-limited and not seed-limited. In our study, we could show that even a slight change of availability of microsites (1% of the area to 2% of the area) has a dramatic impact on the recolonisation of shrubs. In the context of management, all actions which produce even a small number of microsites for the establishment of the target species will assist in the recolonisation of the site to be restored. It is important to note that this management strategy does not require detailed knowledge about the biology of the target species.



All other management options require an understanding of the biology of the target species, especially about germination requirements and triggers. Two management strategies can be employed: shortening of the germination interval, i.e. management of the conditions triggering germination (through e.g. irrigation), or the increase of the mean establishment rate of the target species. Identification of potential management strategies can aid in directing further research on specific aspects of the biology of the target species, which in turn then assist in developing appropriate management strategies. Better knowledge of the biology of a species can then feed back into the simulation model, enabling fine tuning and even better identification of the factors facilitating or inhibiting successful recolonisation and restoration of e.g. old fields. This feed-back process of identifying crucial aspects through modelling, validating these in field work and providing better estimates of crucial parameters, where necessary, improves the model, which in turn then informs further fieldwork. An integration of modelling and fieldwork approaches provides a framework for optimising fieldwork and modelling, enabling the selection of most appropriate and effective management strategies.

Alien clearing and the necessary restoration following the clearing of the alien vegetation, become more and more important (see e.g. Richardson, 2001). Even though the costs of alien clearing are very high (Marais et al., 2004), progress has been made in the control and clearing of some species; however, at the current rate of clearing, many other species will not be under control in the next decades (Marais et al., 2004). Marais et al. (2004) also emphasised the role of biological control as a sustainable, effective and inexpensive solution. In this study, we look at the effectiveness of seed-destroying biocontrol agents and try to determine their effectiveness in the fight against *Hakea sericea*. As discussed above, this question was addressed by e.g. Hoffmann (1990); Hoffmann and Moran (1998); Myers and Risley (2000), but no coherent picture emerged. Through our study on *Hakea sericea*, we were able to supply additional information on the subject and show that seed-destroying biocontrol agents have a definitive impact on the spread of an invader. Additionally, we were able to quantify the effect of two different biocontrol agents (YFF and MFF) on the velocity of the spread and thus contribute to an understanding of spread rates under different biocontrol regimes, Richardson and van Wilgen (2004) identified as a research priority. This quantification of the effect of biocontrol makes it possible to evaluate the cost-benefit ratio of an introduction of any of these two biocontrol agents. Consequently, a more cost-effective alien control is possible.

In addition to the use of biocontrol agents, we were able to deduct alternative management strategies for the control of *Hakea sericea*. As with all management recommendations, they have to be evaluated in the context of the site-specific situation where they should be applied—i.e. increased fire frequencies might be an option in a situation where *H. sericea* has formed dense stands with nearly no remaining natural vegetation, but in a site in which natural vegetation is found, high fire frequencies are not suitable as they would negatively impact on those as well. This shows again that the use of models for assessing management strategies can play an important role in evaluating their effectiveness and

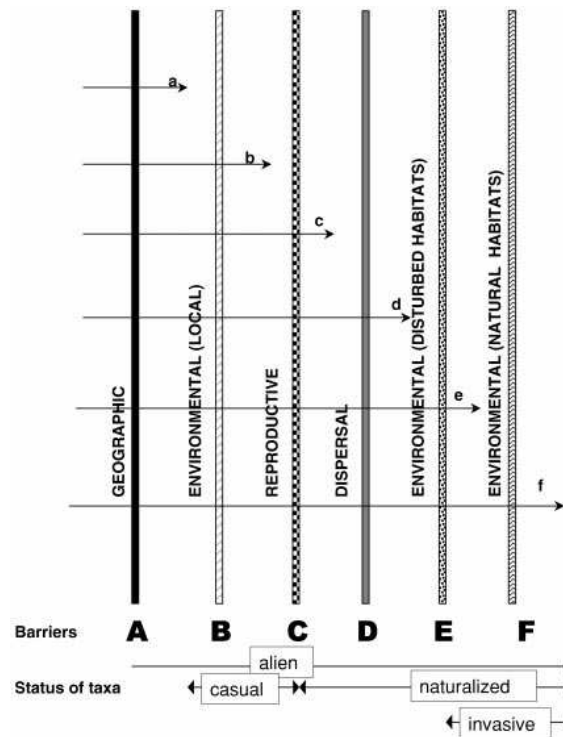


their cost–benefit ratio. This cost–benefit ratio can be used in policy discussions to provide additional backing for the use of biocontrol agents in the fight against aliens. The position of using biocontrol agents has already been adopted by South Africa, but other countries are still not utilising biological control agents (Richardson et al., 2004). As *H. sericea* is not only invasive in South Africa (Sousa et al., 2004) and due to the possibility of evaluating different scenarios according to their costs, this study could be a starting point for the promotion of the use of biocontrol agents in other countries as well as justification and evaluation of biocontrol agents in South Africa. To make this possible, the model needs to be up-scaled to landscape scale and, due to computational restrictions, move from individual-based model to a grid-based model. This will include using the results and predictions from the individual-based model concerning velocity and distance of spread in one generation and implementing these in the landscape model to simulate the spread. Other factors which should be included in the landscape model are topography, land use, land-use change and possibly climate change scenarios and spread pattern of biocontrol agents. This landscape model will enable us to simulate the effectiveness of different alien management strategies over time and to make a cost–benefit analysis.

Apart from these overlaps between invasion biology and restoration ecology, other areas also overlap. Looking at the barriers a species must overcome to become invasive (Figure 8.1, already introduced in Chapter 2 and reproduced here for clarity), other areas can be identified in which invasion biology and restoration ecology share opposite goals, but the required understandings are very similar.

Barrier C is the reproductive barrier which prevents the production of offspring. Alien species have to pass this barrier to become naturalised. This is one of the barriers at which the biocontrol agents discussed in Part II act: by destroying seeds, the biocontrol agents endanger the regular and successful reproduction of *Hakea sericea* after fires. Restoration ecology tries to maximise the possibility of regular and successful reproduction of the target species. But for both restoration ecology and invasion biology, a detailed understanding of the reproductive biology of the target species and how the reproduction is, or can be, influenced by external factors is necessary. Young et al. (2005) highlights the importance of looking at the ecology of ontogeny and ontogenic niche shifts in restoration ecology. The same case can be made for invasion biology: if plants occupy different niches during their life cycle and the niches during recruitment are narrower than their broader adult niches, it is important to not only look at the niche requirements of adult invaders, but also their niche requirements during recruitment. This might add to the understanding why certain casual alien species become naturalised and others not. In addition, this offers additional possibilities for management of aliens as it identifies possible management options based on the requirements during recruitment.

Dispersal (barrier D) plays, as shown in this study, an important role in invasion biology and restoration ecology, as this determines the spread potential of a species. Even if a species produces a large number of seeds, it will only spread if those seeds are dispersed. This is an important aspect to consider in restoration: in a natural, functioning ecosystem



**Figure 8.1.:** A schematic representation of major barriers limiting the spread of introduced plants. Barriers can be separated in spatial barriers (A and D) which need to be overcome through dispersal and environmental / physiological barriers (B, C, E and F). Barrier A is usually overcome through intentional or unintentional human activities. For further details see [Richardson et al. \(2000\)](#). Figure reproduced with permission from [Richardson et al. \(2000\)](#)

all necessary dispersal vectors are present. Nevertheless, when restoring a system, one needs to keep in mind that a plant species which is producing seeds does not necessarily spread any farther should the necessary dispersal vectors be absent. An additional complexity is added as many species have two different dispersal syndromes, and therefore vectors, for short- and long-distance dispersal and the presence of one does not necessarily guarantee the presence of the other. As most restoration studies focus on plant diversity, the aspect of animals and their role as dispersal vectors is often neglected.

As the spread of a species is not only determined by seed dispersal but also through seed production, barrier C has a large influence on the effectiveness of the dispersal of a species. For *H. sericea*, this can be seen in the effect of the biocontrol agents, which, by reducing the number of viable seeds, reduce the viable seed rain at long distances (see Chapter 3).

Even if species overcome these barriers, they are not necessarily invasive yet, as this requires that they can overcome barrier E, i.e. that they can cope with a modified environment, or even barrier F, that they can invade natural, undisturbed habitat. For this, the potential invader has to be able to cope with the conditions present in the system it is invading, i.e. anthropogenically disturbed (barrier E) or natural (barrier F). This latter barrier includes abiotic and biotic interactions and is the final barrier to naturalised

plants to become invasive. Restoration ecology is trying to restore a system by, among other actions, introducing indigenous or endemic target species. These target species also have to cross the same barrier, but the existing system is either a system severely affected by anthropogenic disturbances and / or alien invasive species. Hence, an understanding of what enables a plant species to become invasive will assist restoration ecology to choose appropriate target species which can be re-introduced or re-established more easily than others. D'Antonio and Meyerson (2002) go so far as to suggest that, in certain cases, it might be advantageous to choose alien species as initial restoration tools in order e.g. to decrease erosion or to ameliorate site conditions where land uses have resulted in loss of soil fertility. Therefore, the alien species will be the target species for the initial phase of restoration and will be replaced later with indigenous species when the conditions have improved. To apply this idea successfully, an understanding of the invadability of the intermediate system (dominated by the alien target species) by indigenous species target species is essential to be able to move from the alien-dominated intermediate system to a more natural system (in which the initial invasive alien target species is eliminated or only a casual alien species).

The understanding of the impact of the local environment (abiotic conditions and climate) on the target species (barrier B) becomes especially important in the context of climate change. Climate change can lead to an increase of the potential habitat of alien species and therefore their spread into previously uninvaded areas, or to naturalised species becoming invaders. It is therefore important to include this understanding of the potential climate change in the planning of alien control activities. In addition to the response of the individual naturalised / invasive species to climate change, it is important to understand the impact of the climate change on the system, as an increased, unchanged or decreased invadability is possible. Only the combination of these two impacts makes a prediction of the impact of climate change on invasions possible.

Climate change could affect the fire frequency to which *Hakea sericea* is exposed; the seed production per generation; the effectivity of the biocontrol agents; and the establishment probabilities. In the model presented, a change in establishment probabilities can be reflected as a change in the number of viable seeds dispersed. As one of the results of the model is a relationship between viable seeds produced and the velocity of spread, the impact of climate change can be directly read from this graph as soon as the impact of climate change on the number of viable seeds dispersed can be quantified.

Restoration ecology is confronted with a similar problem of specifying restoration aims : if the climate is changing, it is not sufficient to restore a system which can survive at the given climatic conditions, but it should also be able to sustain itself despite the climate change, or be resilient in the face of climatic changes. Therefore it becomes important to understand the impact of climate change not only on the target species, but also on the system itself.

Based on the discussion above, I argue that the model described by Richardson et al. (2000) can also be used in restoration ecology to identify obstacles in the reintroduction

of indigenous species into a disturbed / alien-invaded / transformed environment. It can form a basic framework for these two disciplines to design studies which enable invasion biology as well as restoration ecology to draw valuable *understanding* from the other's studies.

This framework will make it considerably easier to develop more holistic strategies for research and management in these two disciplines. Management which does not see alien control and restoration as two distinct management objectives, or stages of the process, can cover both objectives at the same time. Further, doing so, would likely be much more time- and cost-effective than a two-stage process in which alien plants are cleared first, leaving a highly-disturbed landscape, which is then, in a second stage, restored to a more natural state. [Sheley and Krueger-Mangold \(2003\)](#) demonstrate for weed control, that only the tight integration of invasion control and restoration can lead to success. Equally, incorporating this framework into research planning will produce research which provides valuable knowledge usable for both disciplines with less time and financial means needed than if the equivalent questions were be addressed in both fields separately.

This framework should be developed further and extended to include succession, assembly rules and disturbances to provide a decision-making framework combining restoration and invasions. This would ease the communication, co-operation and cross-fertilisation between these disciplines as both are working towards the same goal: to manage and maintain biodiversity.

# References General Discussion and Conclusions

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**Part V.**

## **Appendix**



## A. Restoration of West Coast Renosterveld: facilitating the return of a highly threatened vegetation type

*This paper was authored by Cornelia B. Krug (University of Stellenbosch), Rainer M. Krug, D. Midoko-Iponga (University of Stellenbosch), N.N. Shiponeni (Directorate of Scientific Services, MET), B. A. Walton (University of Stellenbosch) and S. J. Milton (University of Stellenbosch), was presented at the 10th MEDECOS Conference, Rhodes, Greece, and is included in the conference proceedings. The main author, Dr. Cornelia B. Krug, has agreed that this paper is included into my PhD as an appendix. This appendix reflects the paper as published in the proceedings, and no further changes were made. Additional information is provided in foot notes.*

*This appendix should be cited as follows:*

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### A.1. Background

As West Coast Renosterveld is associated with fertile shale soils (Boucher and Moll, 1981) and a rainfall regime suitable for crop production, most of this vegetation type has been transformed into agricultural areas over the last 150 years, leaving less than 5% of this vegetation type in a relatively natural state (Low and Rebelo, 1998). These remaining natural remnants are highly fragmented and isolated. Resulting from this is an interruption or even loss of natural ecological processes (see e.g. Bakker and Berendse, 1999; Cameron, 1999; Kemper et al., 1999; Donaldson et al., 2002; Tschardt et al., 2002). In addition to this, an IUCN recommendation states that 10% of each vegetation type should be formally conserved (Low and Rebelo, 1998), but of West Coast Renosterveld, less than 4% are is under formal protection, and many of the vegetation remnants are on private lands. To reach the IUCN conservation goal, and re-instate ecological processes by creating habitat corridors, and re-connecting fragments, degraded natural areas and abandoned agricultural areas need to be restored and incorporated in the current conservation network.

Restoration of these transformed areas further augments the area under conservation, as eco-tourism and game farming become viable alternatives to "standard" farming practices, and landowners are increasingly becoming aware of the value of natural veld (Winter and Hanks, 2002), and possibilities for the sustainable use of the vegetation. Observations have shown that the return of indigenous species to abandoned agricultural areas is slow, and certain suites of life forms and species never recover fully. Bakker and Berendse (1999) show that the return of European heathland communities is restricted by the absence of seeds in the seed bank, and seed dispersal is limited in a fragmented landscape. To facilitate the restoration of Californian sage scrub, a Mediterranean shrub land, Cione et al. (2002) use herbicide application and hand-weeding to control alien annual grasses. Aims of the Renosterveld Restoration Project are to investigate the mechanisms of secondary succession in West Coast Renosterveld, inspecting the seed dispersal mechanisms and related restoration capability constraints, investigating the effect of alien pasture grasses on the establishment of indigenous species and to devise feasible methods to facilitate the return of indigenous vegetation to previously transformed areas.

## A.2. Restoration Experiments

### A.2.1. Study Area and Experimental Site

Studies for the Renosterveld Restoration Project were conducted on Elandsberg Private Nature Reserve on the Farm Bartholomeus Klip (19°03' E, 33°27' S), at the foot of the Elandskloof Mountains, Western Cape. The vegetation in the low-lying areas of the reserve is classified as West Coast Renosterveld (Low and Rebelo, 1998), which is replaced by Mountain Fynbos on the mountain slopes. The reserve was proclaimed in 1973, initially to protect the geometric tortoise, *Psammobates geometricus*, a West Coast Renosterveld endemic, and indigenous game species were reintroduced. Currently, the reserve covers 3 600ha, of which about 1 000ha are true Renosterveld. Incorporated into the reserve are a number of abandoned agricultural fields of different ages, of which the youngest serve as grazing ground for the game species. All these agricultural fields were subjected to ploughing, and were planted with oats in the 1960s and 1970s. Analysis of aerial photographs allows for classification of these fields into different successional stages according to age class: last ploughed before 1997 (5 years of recovery), 1987 (15 years) and 1967 (35 years). The abandoned field where all the experiments are conducted (seed dispersal, establishment, restoration trials), was incorporated into the reserve in 1987. Prior to 1985, oats (*Avena*) was the main crop on the field. Subsequently, the field was over-sown with European pasture grasses (*Briza* sp., *Lolium* sp. and *Vulpia* sp.), and used for sheep grazing (Mike Gregor, pers. com). Even though this field is directly adjacent to an extensive patch of natural vegetation, the alien grasses still dominate the vegetation on the old field today, and very little indigenous vegetation has established. Some shrub species (mainly *Elytropappus rhinocerotis*, but also other indigenous species) have established at the edge of the field, close to the border to the natural vegetation.

### A.2.2. Methods

Natural restoration by means of secondary succession was monitored on abandoned agricultural fields of three age classes (5 years, 15 years and 35 years of abandonment), and compared to vegetation in untransformed (unploughed) areas of the reserve (Walton in prep.<sup>1</sup>). 10m<sup>2</sup> plots were established, number of species in these recorded, and cover of each species assessed using the new Braun-Blanquet scale. For the statistical analysis, the Braun-Blanquet values were translated into the corresponding percentage cover value. Each species was allocated to one of the following Raunkiaer life forms: phanerophyte (trees), chamaephyte (shrubs), nano-chamaephyte (subshrubs), hemicryptophyte (bunch grasses, restios), cryptophyte (geophytes) and therophyte (annual grasses and forbs). Chamaephytes and nano-chamaephytes were grouped for the statistical analysis. Seed dispersal onto the old field was estimated by sinking pitfall traps level into the ground along three parallel transects (Shiponeni, 2003). Seeds were collected at monthly intervals for one year, with traps opened four to six days each month. Seeds were counted and identified under a dissecting microscope. In addition, nursery trays filled with vermiculite were set up at four points of each transect, and replaced after seven months. The second set of these traps was removed after four months, at the end of the experiment (Shiponeni, 2003). The seed trays were transferred in the nursery, and emerging seedling identified and counted. To estimate endozoochoric dispersal by the game species present in the reserve, dung was collected on a monthly basis along six 100m transects across the experimental site parallel to the edge to the natural vegetation. The dung was air-dried after collection, and the dry weight determined. Dung samples were crushed, spread on nursery trays and seeds in the dung were left to germinate. Emerging seedlings were identified and counted. The soil seed bank was analysed by taking six soil samples with a 5cm soil corer on each of three transects (Shiponeni, 2003). The soil was spread onto seedling trays and seeds were left to germinate in the nursery over a six-month period. Emerging seedlings were identified to species level where possible. The influence of grass competition on the establishment of indigenous shrub seedlings was monitored through exclusion experiments (Iponga in prep.<sup>2</sup>). Grass was totally removed by hand weeding on ten 1m<sup>2</sup> plots, and these were paired with unweeded plots. Half of each weeding treatment was subjected to natural grazing by large herbivores, the other half was protected by exclusion cages. Seeds of four indigenous shrub and one tree species were germinated in the nursery, and seedlings were transplanted once they reached a height of about five centimetres. Seedlings of one indigenous annual, *Crassula glomerata*, established naturally on the experimental plots, and were included in the experiment. On a monthly basis, height and survival of the seedlings was recorded. To determine possible restoration techniques for West Coast Renosterveld, twelve plots of 100m<sup>2</sup> size were subjected to one of four treatments (Iponga

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<sup>1</sup>Walton, B.A. (2005). Vegetation patterns and dynamics of Renosterveld at Agter-Groeneberg Conservancy, Western Cape, South Africa. Unpublished MSc thesis, University of Stellenbosch, South Africa.

<sup>2</sup>Midoko-Iponga, D. (2004). Renosterveld restoration : the role of competition, herbivory and other disturbances. Unpublished MSc thesis, University of Stellenbosch

in prep.<sup>3</sup>): burning (March 2003), mowing/brush cutting (May 2003), herbicide (Gallant) application (May 2003) and control. Within each of these plots, 12 1m<sup>2</sup> plots were staked out to record number of species and estimate species cover using the new Braun-Blanquet scale. Data was collected on a monthly basis from May 2004 onwards. Braun-Blanquet values were translated into the corresponding percentage cover values for the data analysis, and species were classified according to Raunkiaer life form.

### A.2.3. Statistical Analysis

Species richness, i.e. number of species, in fields for the different stages of secondary succession as well as for the different restoration treatments, were compared using one-way ANOVA and Scheffé post-hoc test in STATISTICA 6.0 (StaSoft, 2001). To determine species diversity, the Shannon Wiener Index was calculated using the programme Species Diversity and Richness (Henderson and Seaby, 2001). With the same programme, the upper and lower confidence intervals of the Diversity Index were estimated using bootstrapping. The comparison of the diversity between age classes (secondary succession) and treatments (restoration trials) was done using the Shannon-Wiener index with 10000 random partitions (Solow 1993 in Henderson and Seaby, 2001), also built into the programme. To assess the differences in life form cover at various successional stages, as well as for different restoration treatments, F-statistics were calculated using the Resampling Stats Add-in for Microsoft EXCEL (Microsoft Corporation, 2001). The same statistical test was used to detect differences in the height of shrub seedlings between weeded and non-weeded experimental plots. The observed vs. expected 2-test in STATISTICA 6.0 (StaSoft, 2001) was employed to assess differences in survival of shrub seedling on weeded vs. non-weeded plots. Survival rates on weeded plots were taken as observed values, survival rates on non-weeded plots served as control (observed values).

## A.3. Results

### A.3.1. Natural Restoration – Secondary Succession

Overall species richness was lowest in the early successional stage (Table A.1). On average, 15 species were found in these plots. With increase in time, and advance of secondary succession, species richness increased steadily, although the latest stages of succession investigated did not reach the same level of species richness as the untransformed plots (One-way ANOVA:  $F_{3,32}=5.141$ ,  $p<0.01$ ).

The number of chamaephytes (shrub species) is significantly higher in the late successional stage and untransformed areas than in the intermediate successional stage (One-way ANOVA,  $F_{2,43}=6.666$ ,  $p<0.01$ ), (Figure A.1). Cryptophytes (the geophytic species) show a similar pattern, number of species increases with the advance in secondary succession,

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<sup>3</sup>Midoko-Iponga, D. (2004). Renosterveld restoration : the role of competition, herbivory and other disturbances. Unpublished MSc thesis, University of Stellenbosch

**Table A.1.:** Overall species richness (mean  $\pm$  SD of the successional stages monitored. Differing letters indicate significant differences between successional stages (Scheffé post-hoc test). Data from Walton in prep.<sup>a</sup>

Recovery	Number of species/10m <sup>2</sup>	N	
natural	28.00 $\pm$ 11.06	6	a
35years	23.75 $\pm$ 3.28	8	ab
15years	19.75 $\pm$ 5.83	12	ab
5years	14.17 $\pm$ 4.92	6	b

<sup>a</sup>Walton, B.A. (2005). Vegetation patterns and dynamics of Renosterveld at Agter-Groeneberg Conservancy, Western Cape, South Africa. Unpublished MSc thesis, University of Stellenbosch, South Africa.

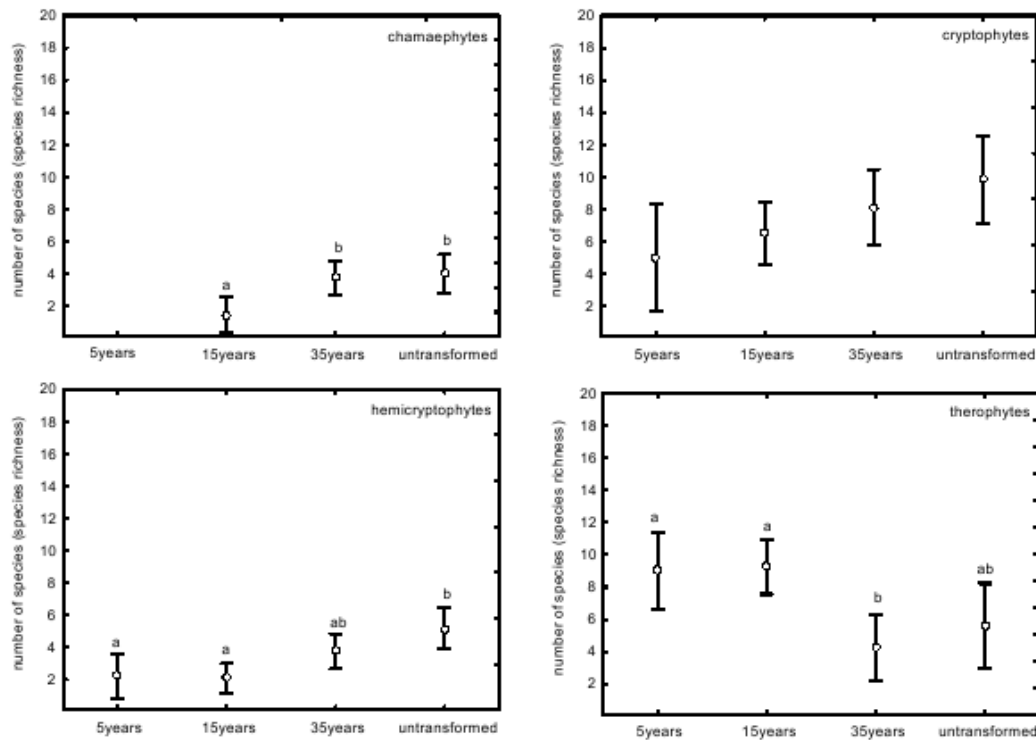
**Table A.2.:** Shannon-Wiener Diversity index H, variance of Shannon-Wiener Diversity index and upper and lower 95% confidence intervals for successional stage. Differing letters in the last column indicate significant differences in Shannon Diversity between successional stages. Data from Walton in prep.<sup>a</sup>

Recovery	H	Variance H	Lower 95%	Upper 95%	
natural	4.426	0.0039158	3.9671	4.19926	a
35years	4.0009	0.0037577	3.67916	3.90368	b
15years	3.9286	0.0035662	3.64186	3.87186	b
5years	3.3059	0.0062596	2.94297	3.23152	c

<sup>a</sup>Walton, B.A. (2005). Vegetation patterns and dynamics of Renosterveld at Agter-Groeneberg Conservancy, Western Cape, South Africa. Unpublished MSc thesis, University of Stellenbosch, South Africa.

and is highest in the untransformed areas. These differences in number of species is not significant, though (One-way ANOVA,  $F_{3,30}=2.304$ , NS). The pattern is still similar in the bunch grasses and restios (hemicryptophytes). The early and intermediate successional stages have a significantly lower species richness in hemicryptophytes than the late successional stage and the untransformed areas (One-way ANOVA,  $F_{3,31}=6.599$ ,  $p<0.01$ ). A different scenario shows with regard to the therophytes (annual grasses and forbs). Here, the number of species is significantly higher in the early and intermediate successional stages, and decreases with advance in succession (One-way ANOVA,  $F_{3,30}=6.184$ ,  $p<0.01$ ). Therefore, the number of shrubs, geophytes, bunch grasses and restios increases with an advance in secondary succession, while the number of annuals decreases. Species diversity follows a similar pattern similar to that of species richness (Table A.2). The Shannon-Wiener index for diversity is lowest in the early successional stage, and increases with an advance in secondary succession. Species diversity is the same for both intermediate and late successional stages, although species richness differs. Species diversity, like species richness, of the untransformed areas is considerably higher than for the late successional stage, indicating the recovery of these areas is not complete, or species are being lost due to the transformation by ploughing.

The pattern of mean percentage life form cover differs from that seen in species richness (Figure A.2). In the chamaephytes, no difference can be found in the percentage cover



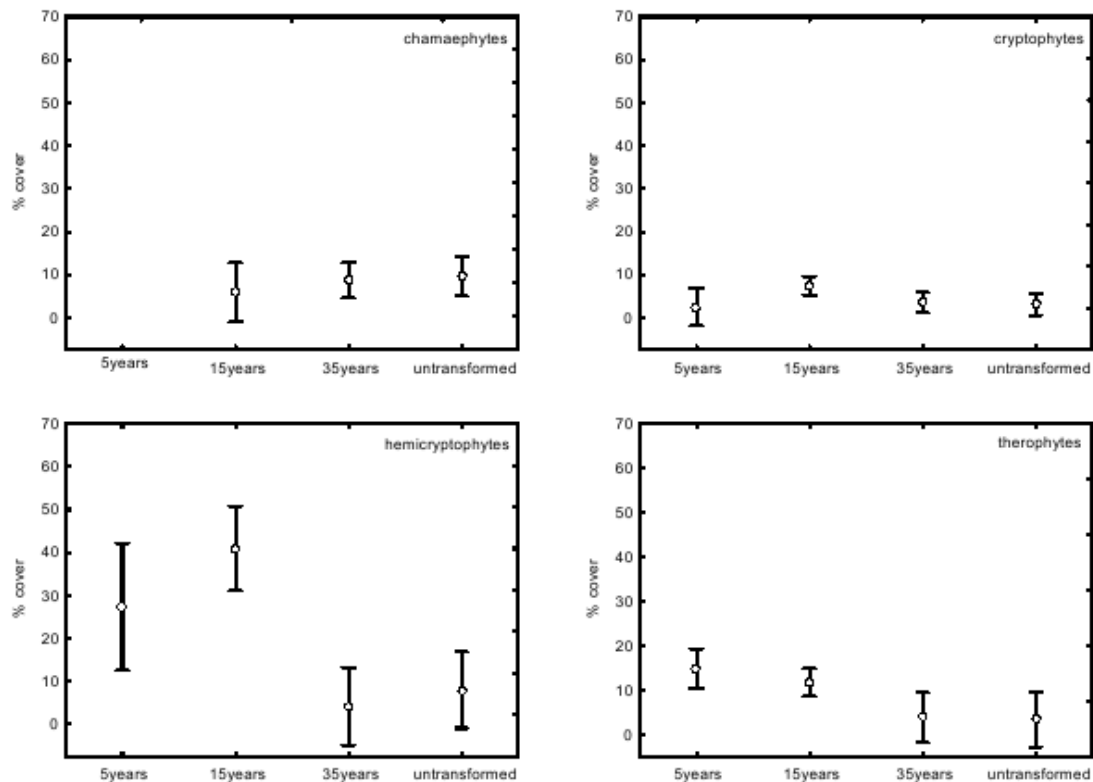
**Figure A.1.:** Species richness for four Raunkiaer life forms in plots of different recovery ages. Differing letters indicate significant differences in species richness between recovery ages (Scheffé post-hoc test). Data from Walton in prep.<sup>a</sup>

<sup>a</sup>Walton, B.A. (2005). Vegetation patterns and dynamics of Renosterveld at Agter-Groeneberg Conservancy, Western Cape, South Africa. Unpublished MSc thesis, University of Stellenbosch, South Africa.

values between the intermediate and late successional stages and untransformed areas (Resampling Stats,  $F_{2,130}=3.802$ , NS). While the species richness of cryptophytes increases with recovery time, the mean percentage cover actually decreases. Mean percentage cover of geophytes is significantly higher in the intermediate successional stage than in all other areas (Resampling Stats,  $F_{3,222}=7.680$ ,  $p<0.05$ ). A similar picture can be observed in the hemicryptophytes. Again, mean percentage cover is highest in the intermediate successional stage, and significantly lower in the late successional stage and untransformed areas (Resampling Stats,  $F_{3,97}=56.183$ ,  $p<0.001$ ). Mean percentage cover of annual species (therophytes) is significantly higher in the early and intermediate successional stages than in the late successional stage and untransformed areas (Resampling Stats,  $F_{3,227}=7.680$ ,  $p<0.001$ ).

The vegetation on the abandoned fields in the early successional stages is still dominated by alien pasture grasses and annual forbs, as well as a few geophyte species, like *Oxalis purpurea*, the latter occurring mainly in disturbed areas. With an advance in secondary succession, bunch grasses, shrubs and geophytes establish. The untransformed areas consist of a diverse species mix of shrubs and sub-shrubs, bunch grasses, restios and





**Figure A.2.:** Mean percentage cover of life form types in various successional stages. Data from Walton, in prep.<sup>a</sup>

<sup>a</sup>Walton, B.A. (2005). Vegetation patterns and dynamics of Renosterveld at Agter-Groeneberg Conservancy, Western Cape, South Africa. Unpublished MSc thesis, University of Stellenbosch, South Africa.

geophytes.

### A.3.2. Seed Dispersal

Main dispersal agents in West Coast Renosterveld are wind and animals (large herbivores)(Shiponeni, 2003). Seeds that are adapted to wind dispersal are characterised by wings or plumes, and are able to travel long distances. Both asteraceous shrubs and indigenous grasses show this adaptation. The main species dispersed by wind and trapped in the pit traps on the experimental site were alien as well as indigenous grasses and forbs, and three shrub species. Seed rain density of indigenous species was highest close to the natural vegetation, while seeds of alien species were found equally likely along the length of the three transects on the old field (Shiponeni, 2003). Seed density of *Elytropappus rhinocerotis* (Asteraceae) and *Tribolium hispidum* (Poaceae) was positively correlated with percentage plant cover, which was highest close to the natural vegetation. Seeds caught in the nursery trays were again dominated by seeds of both alien and indigenous grasses and forbs, but in contrast to the pit traps, geophyte seeds, which are hard and round and adapted to tumbling, formed a major component. Again, seed density of indigenous species was highest close to the natural vegetation, and decreased rapidly with

**Table A.3.:** Height of seedlings in the two competition treatments. Means  $\pm$  SD. Data from Iponga in prep.<sup>a</sup>

Species	Treatment		F-value	p-value	
	no competition	competition			
<i>Athanasia trifurcata</i>	24.31 $\pm$ 11.18	9.15 $\pm$ 3.38	15.165	0.000	***
<i>Relhania obtusifolia</i>	17.06 $\pm$ 6.59	9.50 $\pm$ 3.28	7.562	0.084	NS
<i>Salvia chamaelanga</i>	23.95 $\pm$ 14.41	9.30 $\pm$ 3.60	14.650	0.040	*
<i>Leucadendron corymbosum</i>	15.23 $\pm$ 2.94	9.61 $\pm$ 2.61	5.627	0.000	***
<i>Olea europea ssp. africana</i>	19.91 $\pm$ 10.35	17.34 $\pm$ 6.49	2.573	0.384	NS
<i>Crassula glomerata</i>	6.11 $\pm$ 2.41	6.88 $\pm$ 2.83	0.770	0.220	NS

<sup>a</sup>Midoko-Iponga, D. (2004). Renosterveld restoration : the role of competition, herbivory and other disturbances. Unpublished MSc thesis, University of Stellenbosch

distance from the edge (Shiponeni, 2003). Seeds dispersed by game species were mainly those of grasses and forbs, which form part of the diet of the animals. About two-thirds of the forbs and half of the grass species dispersed in this manner were indigenous. Seeds that are transported by animals are dispersed over long distances, enabling species to recolonise transformed areas further away. The highest number of geophytic species were found in the soil seed bank samples, although indigenous and alien forbs and grasses were again dominant (Shiponeni, 2003). Seed density of the geophytes was again higher closer to the natural vegetation. Seeds of some species were found across the field, but these species had already established on the old field. Results from the seed dispersal study indicate that very few species can cover long distances necessary to recolonise disturbed and transformed areas. Therefore, dispersal of indigenous species, especially geophytes, seems to limit the return of the natural vegetation.

### A.3.3. Establishment of Indigenous Species

Seedlings of the four shrub species were negatively affected by the grass competition (Table A.3). The height of the *Athanasia trifurcata*, *Salvia chamaelanga* and *Leucadendron corymbosum* seedlings was significantly lower on plots with grass competition than on plots where grass was removed. Seedlings of *Relhania obtusifolia* growing on plots with grass competition were also smaller than seedlings growing on plots without competition, but the difference was not significant.

The growth of the tree species, *Olea europea ssp. africana*, usually growing on nutrient rich underground termitaria, was not affected by grass competition. Similarly, the height of *Crassula glomerata* seedlings was also not influenced by grass competition.

Although the survival rates of all shrub seedlings exposed to grass competition were lower than the survival rates of plants growing on plots without grass competition, the differences were not significant (Table A.4). Survival of seedlings of the annual species was also lower on the plots with grass competition. Seedlings of *Olea* were again not affected by grass competition and survival rates were equally low in both treatments. The observed negative influence of the competition by (alien) grasses on the establishment of indigenous

**Table A.4.:** Survival rates of species planted on experimental plots. Means  $\pm$  SD. Data from Iponga in prep.<sup>a</sup>

Species	Treatment		$\chi^2$ -value	p-value	
	no competition	competition			
<i>Athanasia trifurcata</i>	0.64 $\pm$ 0.34	0.34 $\pm$ 0.42	3.59	0.936	NS
<i>Relhania obtusifolia</i>	0.32 $\pm$ 0.43	0.06 $\pm$ 0.09	2.65	0.977	NS
<i>Salvia chamaelanga</i>	0.85 $\pm$ 0.34	0.50 $\pm$ 0.53	3.5	0.941	NS
<i>Leucadendron corymbosum</i>	0.88 $\pm$ 0.17	0.54 $\pm$ 0.19	1.8	0.994	NS
<i>Olea europea ssp. africana</i>	0.45 $\pm$ 0.28	0.40 $\pm$ 0.21	1.58	0.996	NS
<i>Crassula glomerata</i>	0.82 $\pm$ 0.20	0.58 $\pm$ 0.22	1.74	0.994	NS

<sup>a</sup>Midoko-Iponga, D. (2004). Renosterveld restoration : the role of competition, herbivory and other disturbances. Unpublished MSc thesis, University of Stellenbosch

**Table A.5.:** Species richness after restoration treatment. Means  $\pm$  SD.

Treatment	number of species/1m <sup>2</sup>
burn	30 $\pm$ 5.29
brush cut	29 $\pm$ 4.35
herbicide	26 $\pm$ 3.61
control	32 $\pm$ 1.73

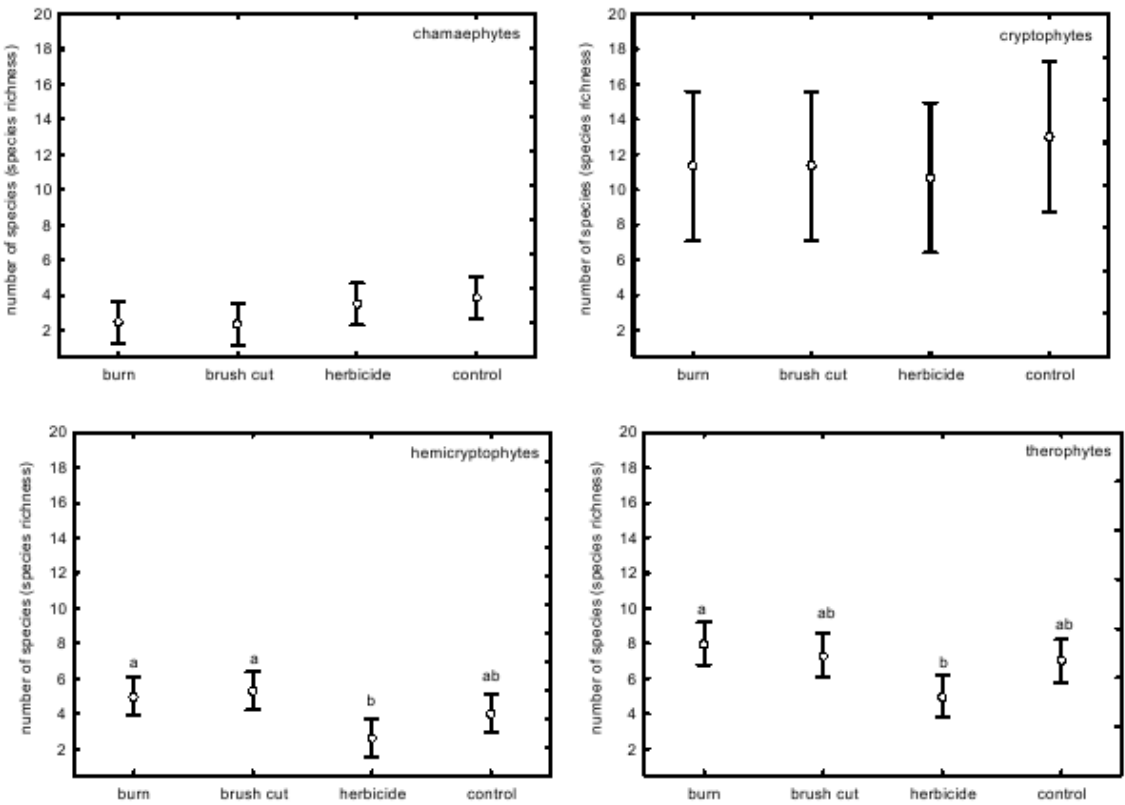
shrub species combined with the limited seed dispersal, impacts severely on the capacity of indigenous Renosterveld species to recolonise abandoned agricultural areas.

#### A.3.4. Restoration Experiments

As the restoration experiments are still ongoing, results are not yet conclusive. While species richness is lowest on those plots treated with herbicides, and higher on the other plots, differences between treatments are not significant (Table A.5, One-way ANOVA,  $F_{3,12}=1.191$ , NS).

Chamaephyte species richness on the herbicide treatment is as high as on the control plot (Figure A.3), while the number of shrubs is lower on the burnt and brush cut sites. None of these differences are significant (One-way ANOVA,  $F_{3,24}=1.666$ , NS). Difference in number of geophyte species is also not significant (One-way ANOVA,  $F_{3,12}=0.290$ , NS). Cryptophyte species richness is highest on the control site, and lowest on the site where herbicide was applied. The number of geophyte species is equally high on the burnt and brush cut sites. As the herbicide selected targets grass species, both the number of bunch grass and annual grass species is significantly lower in the herbicide treatment than on the other sites (hemicryptophytes: One-way ANOVA,  $F_{3,12}=6.458$ ,  $p<0.05$ ; therophytes: One-way ANOVA,  $F_{3,12}=6.000$ ,  $p<0.05$ ).

Species diversity on the treatment plots follows the pattern of species richness (Table A.6). Diversity, as calculated with the Shannon-Wiener diversity index, is highest on the control site. It is similar on the burnt and brush cut plots, and the plot treated with herbicide has the lowest species diversity.

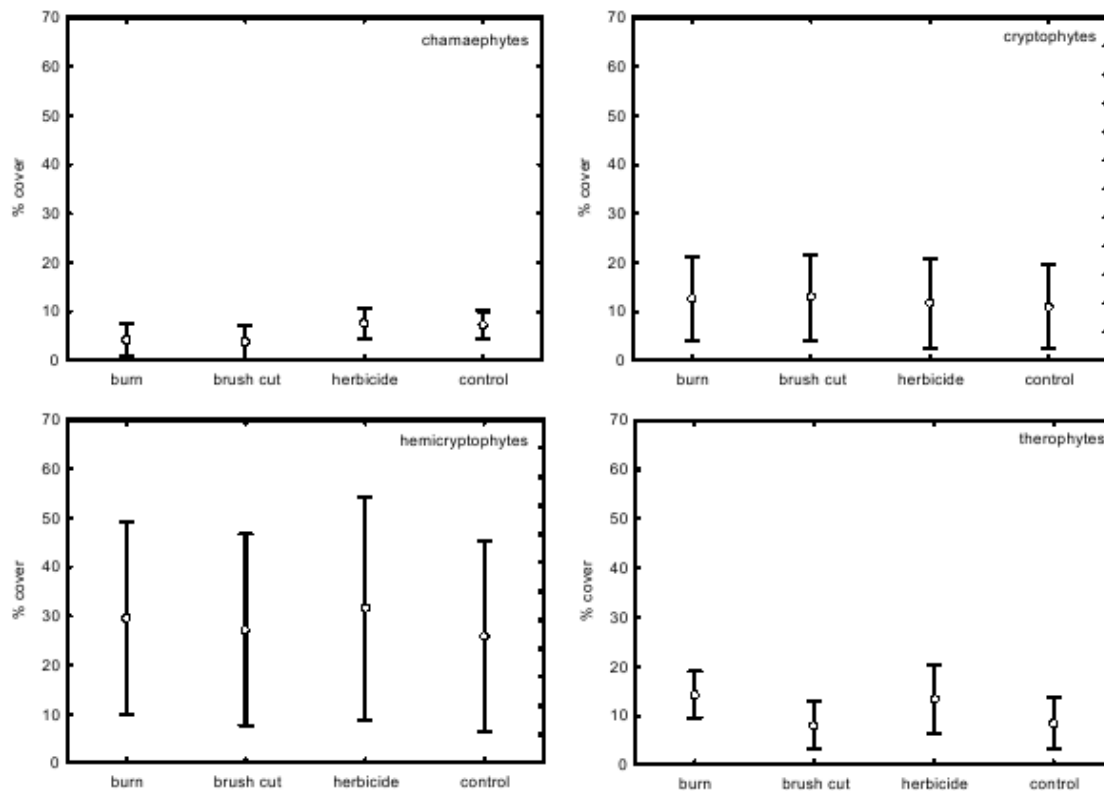


**Figure A.3.:** Species richness within life form types after restoration treatment. Differing letters indicate significant differences between treatments (Scheffé post-hoc test). Data from Iponga in prep.<sup>a</sup>

<sup>a</sup>Midoko-Iponga, D. (2004). Renosterveld restoration : the role of competition, herbivory and other disturbances. Unpublished MSc thesis, University of Stellenbosch

**Table A.6.:** Shannon Diversity Index H, Variance of H and upper and lower 95% confidence intervals obtained by bootstrapping of restoration treatments. Differing letters indicate significant differences between treatments. Data from Iponga in prep.

Six months after treatment, or eight months for the burn, respectively, mean percentage cover is similar on all treatments (Resampling Stats,  $F_{3,256}=7.144$ , NS). This is also reflected when mean percentage cover for each life form is regarded separately. While shrub cover is highest on the herbicide treatment, and lowest on the brush cut site, differences are not significant (Resampling Stats,  $F_{3,53}=7.767$ , NS). Cryptophyte cover is highest on the brush cut plot, but only slightly lower in the other treatments. Again, the differences between treatments are not significant (Resampling Stats,  $F_{3,54}=3.228$ , NS). Although species richness of hemicryptophytes is lowest in the herbicide treatment, these plots have the highest cover of bunch grasses. Cover on the burnt plots is slightly lower, and lowest on the brush cut and control treatments. The differences between treatments are again not significant (Resampling Stats,  $F_{3,41}=15.699$ , NS). A similar pattern presents itself in the therophytes. Annual grass cover is equally high in burn and herbicide treatments



**Figure A.4.:** Mean percentage life form cover on treatment plots. Data from Iponga in prep.<sup>a</sup>

<sup>a</sup>Midoko-Iponga, D. (2004). Renosterveld restoration : the role of competition, herbivory and other disturbances. Unpublished MSc thesis, University of Stellenbosch

and lower in the mowed and control plots. These differences in cover are again not significant (Resampling Stats,  $F_{3,58}=11.441$ , NS). The results above show that none of the treatments had a significant effect on species richness, species diversity or mean percentage cover. While herbicide application reduces the number of grass species, the cover of both bunch and annual grasses is still high on these plots. Treatments will need to be repeated and monitoring should continue for at least another growing season to be able to draw reliable conclusions on the suitability of the treatments.

## A.4. Conclusions

Monitoring of secondary succession has shown that even after thirty to forty years of recovery, species richness and species diversity are still lower than on the untransformed sites. While the number of shrub species has approached natural levels after 35 years of recovery, the number of geophytes, hemicryptophytes and annual species is still lower. Most of the geophyte species occurring in West Coast Renosterveld are endemic, and many of these become increasingly rare. The studies on seed dispersal illustrate why geophyte and hemicryptophyte species are unable to colonise transformed areas - the seeds are only

able to disperse over very short distances. Most of these seeds were only recorded close to patches of natural vegetation, and only a few meters away from natural vegetation (?). Seeds of most geophyte species are short-lived, losing viability after 2-3 years (Manning et al., 2002). Corms and bulbs may be more persistent than seeds however, particularly small corms that have hard protective casings. Some *Oxalis* spp. have become agricultural weeds because of the ability of the bulbils to survive cultivation (Preston et al., 2002). Others, such as *Micranthus* spp. survive in caches of thousands of corms maintained by mole-rats (Lovegrove and Jarvis, 1986). The shrub species, in contrast, are mainly wind dispersed, and are able to cover longer distances (Shiponeni and Krug in prep<sup>4</sup>). It is thus easier for these species to recolonise transformed areas. Once these seeds arrive on old lands, they face another obstacle: they need to establish in areas that are covered in (alien) annual plants. Growth and survival of the shrub seedling is negatively influenced by the competition of the annuals. Successful establishment of shrub seedlings can only happen in those areas where competition of grasses is low, be it patches where grass has been kept short due to grazing or where the grass cover has been removed completely (Midoko-Iponga et al., 2003). Digging sites of porcupines, for example, might create grass-free microsites, where these species can establish. As hand-weeding is too labour-intensive and too expensive to implement on a larger scale, the restoration trials initiated in an effort to find ways of facilitating natural recovery. So far the results of these experiments are not conclusive. As the main objective is to remove grass competition, herbicide application is the most efficient way. Overall species richness and diversity might be lower under this treatment than under the others, the dead grass forms a mulch layer that protects the species that are establishing (M. Gregor, pers.comm., Iponga in prep.<sup>5</sup>), and might thus be the favourable treatment. Both burning and brush cutting seem to favour grasses, and seem thus not to be suitable methods. Treatments on the restoration plots will be repeated, and development of the vegetation will be monitored further to prove which of these methods is the most suitable to facilitate restoration. In addition to these restoration experiments, farm-scale experiments are envisaged to establish the success and feasibility of these treatments for the farmer who wishes to facilitate the restoration of transformed areas. Senescent natural vegetation will be subjected to the same treatments to determine which of these methods is the best to rejuvenate the vegetation, and leads to the highest species diversity. Within this project, restoration of vegetation was the focal point. It is hoped that by restoring the vegetation small habitat patches, other components of biodiversity will re-colonise the restored areas, and serve as nuclei for the natural restoration of adjacent transformed areas.

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<sup>4</sup>Krug, R.M. (2007). Modelling seed dispersal for restoration and invasion. Unpublished PhD thesis, University of Stellenbosch

<sup>5</sup>Midoko-Iponga, D. (2004). Renosterveld restoration : the role of competition, herbivory and other disturbances. Unpublished MSc thesis, University of Stellenbosch

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## **B. Restoration of old fields in Renosterveld: A case study in a Mediterranean-type shrubland of South Africa.**

*This book chapter was authored by Cornelia B. Krug (University of Stellenbosch) and Rainer M. Krug, for inclusion in “Old field dynamics and restoration”, edited by Dr V. Cramer and Prof R.J. Hobbs, and to be published by Island Press / Society for Ecological Restoration International. The main author, Dr. Cornelia B. Krug, has agreed that this paper is included into my PhD as an appendix. The complete book manuscript is submitted for printing, and will be released in (boreal) autumn 2007. This appendix reflects the book chapter as accepted for publication, and no additional changes were made.*

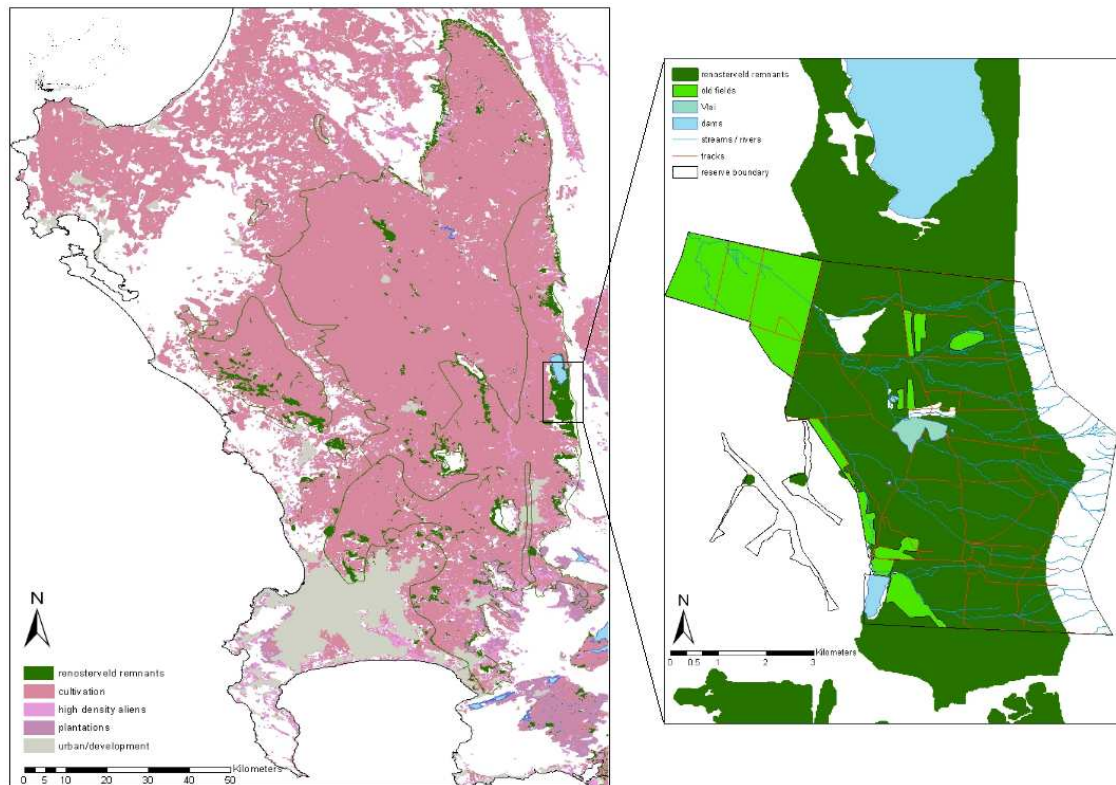
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### **B.1. Introduction**

Renosterveld is part of the Cape Floristic Region, the smallest and most species rich of the world's floristic regions, and is regarded as a biodiversity hotspot (sensu Myers et al., 2000). It can be classified as a Mediterranean-climate shrubland (sensu Di Castri, 1981), being associated with the relatively fertile shale and granite soils of the Cape lowlands (Low and Rebelo, 1998; Boucher and Moll, 1981) and occurring under a winter or year-round rainfall regime of 250mm to 600mm. The vegetation is dominated by low sclerophyllous shrubs, mostly belonging to the Asteraceae and Fabaceae, with an understorey of geophytic species from a range of families (e.g. Hyacinthaceae, Iridaceae, and Orchidaceae), graminoids (Poaceae and Cyperaceae), and some Restionaceae (Low and Rebelo, 1998; Low and Jones, 1995; Moll et al., 1984). About one-third of the plant species occurring in renosterveld are endemic to the Cape Floristic Region, although few of these are endemic to renosterveld alone (Low and Rebelo, 1998). The geometric tortoise (*Psammobates geometricus*), one of the rarest tortoise species in the world, only occurs in west coast renosterveld, and is severely threatened by habitat transformation and fragmentation (Baard, 1993). In the past, renosterveld supported large herds of game, like mountain zebra, quagga, blue antelope (a sister species of roan and sable), red hartebeest, eland, and bontebok (Low and





**Figure B.1.:** Remaining west coast (Boland / Swartland) renosterveld remnants as identified by von Hase et al. (2003), and location of old fields in the natural vegetation remnant on Elandsberg private nature reserve. Data for transformed habitats from Cape Conservation Unit (2003), geographic information for Elandsberg from CapeNature (2004)

Rebello, 1998). Blue antelope and bontebok are renosterveld endemics, whereas the quagga also occurred in the Karoo, a semi-arid grassy shrubland (Skinner and Smithers, 1990). Large species like elephant, black rhinoceros and buffalo were also common, as were large carnivores (lion, cheetah, wild dog, spotted hyena and leopard) (Low and Rebello, 1998). An interesting feature of renosterveld are underground termitaria (termite mounds), which were formed about 30 000 years ago (during the Pleistocene) when the climate was cooler and wetter than today (Midgley et al., 2002). The vegetation on those nutrient enriched patches is related to thick vegetation, and dominated by fleshy-fruited trees and shrubs (e.g. *Olea*, *Rhus* and *Euclea*), and maintained by the deposition of bird-dispersed seeds.

Today, renosterveld has been transformed into agricultural and urban areas, the remaining natural habitat is highly fragmented, and most of the large animal species are extinct in the region. Of the original extent of west coast (Boland/Swartland) renosterveld, once covering 668 026ha, only 42 726ha (6.21%) remains as natural vegetation, in 1 175 remnants (von Hase et al., 2003). More than two-thirds of these remnants are less than 5ha in size, less than 5% are fragments larger than 100 ha, and only seven habitat remnants are larger than 1 000 ha (von Hase et al., 2003, Figure 1). The vegetation within the remnants itself is transformed, and mostly dominated by Renosterbos, *Dicerothamnus rhinocerotis*, an asteraceous shrub.



As most of the remnants are too small and/or too isolated to carry viable plant and animal populations, it becomes essential to consider options for the restoration of this vegetation type to ensure its survival. Successful restoration however, depends on an understanding of the ecological processes shaping an ecosystem, and knowledge of past and present land uses. We cannot base our understanding solely on the processes in existing fragments, but we have to include information on historic and prehistoric changes of the vegetation, why and when they occurred and how they can be related to anthropogenic influence.

### B.1.1. Prehistoric and Historic Land Use

Similar to other Mediterranean-climate ecosystems, renosterveld has been influenced by human activity over thousands of years, although the impacts were not as severe as in the Mediterranean Basin (Newton, 2006). Here we consider three phases in which considerable changes due to human activity took place: Khoi herders (2000 ybp until 1700s), European settlement (1652 - early 1900s) and modern agriculture (early 1900s until today).

#### Pre-history: Khoi-San hunter-gatherers, indigenous large herbivores and fire

From around 10 000 ybp, the climate in the western and south-western Cape became more similar to today's climate (Newton, 2006), favoring a vegetation dominated by shrubs. The presence of shrub species was likely controlled by a range of factors, such as water and nutrient availability, soil type and fertility, palatability of the species and grazing pressure. Composition of the large herbivore fauna, as described by Skead (1980), Klein (1974) and du Plessis (1969), suggests a mixed shrub - grass vegetation. Most species were either mixed feeders like eland and red hartebeest, or pure browsers (e.g. black rhinoceros), with mountain zebra being the only pure grazer occurring in the area (Skinner and Smithers, 1990). Shrub patches were likely interspersed with more or less extensive grassy areas, consisting mainly of bunch grasses like *Ehrharta*, *Pentaschistis*, *Merxmüllera*, *Tribolium*, *Cymbopogon* and *Eragrostis* species and locally abundant *Themeda triandra* and *Cymbopogon marginatus* (Low and Rebelo, 1998). Geophytes formed an abundant understorey under shrubs and among the grasses.

Anthropogenic influence at that time was relatively low as only nomadic Khoi-San hunter-gatherers, inhabited the region. Geophytes formed an important part of their diet (Deacon, 1992; Parkington, 1977) and the Khoi used small-scale burns to increase the growth and abundance of these plants, but also to attract and snare antelope (Deacon, 1992). In addition to these small scale anthropogenic fires, larger-scale fires occurred naturally in renosterveld. These fires most likely originated in the fire-prone fynbos vegetation bordering on renosterveld. Burning favors grasses (Cowling et al., 1986), and some geophyte species only germinate after fire (Manning et al., 2002). This attracts game species to freshly burned areas (Luyt, 2005; Nicola Farley, pers.comm.).

### **Prehistory: Khoi herders, the introduction of livestock and fire management**

At around 2000 ybp, the lifestyle of the Khoi-San changed from hunter-gatherer to herder of domestic livestock, first with goats and sheep, and later with cattle (Klein, 1986; Schweitzer, 1979; Schweitzer and Scott, 1973). This lifestyle change impacted directly on the vegetation, as the Khoi used fire to promote the growth of grasses for grazing their livestock (Thom, 1952). After a period of intense browsing and grazing the Khoi burned the vegetation and moved on, returning after one to four years to complete a cycle (Thom, 1952, 1954). Through short burning intervals and short but intense grazing pressure, shrub cover was reduced, leading to a substantial increase in grass cover.

The presence of the indigenous large herbivore fauna was not impacted upon by these practices, as hunting pressure by the Khoi was rather low (Klein, 1974), and game species profited from the freshly burned areas. The activities of the Khoi (burning and intensive grazing) coupled with the activity of the large herbivores (browsing and grazing) led to large tracts of grassland (Thom, 1952), though parts of renosterveld remained relatively undisturbed.

### **European Settlement: introduction of cropping and habitat transformation**

In 1652, Jan van Riebeck established a provisioning station for the Dutch East India Company in Table Bay, Cape Town, with fruit and vegetable gardens as well as livestock compounds. Twenty years later, the Cape was purchased from the Khoi (Newton, 2006) and the expansion inland began a few years later, setting the scene for the transformation of renosterveld into agricultural lands for crop and livestock farming. Cereal crops and vines were planted on the nutrient-rich renosterveld soils to the north and east, cattle were grazed in natural vegetation and fallow fields. A hundred-and-fifty years after van Riebeck's arrival, grapes were the main crop of the Boland (Paarl / Stellenbosch / Somerset West areas), while cereals, mostly wheat, were planted extensively in the Swartland (Wellington / Malmesbury areas) (Newton, 2006). By this time, the land was already severely degraded, and erosion of the topsoil was common (Newton, 2006; Thom, 1958) as even steep slopes were ploughed and planted.

The settlers farmed mainly cattle and sheep traded from the Khoi (Thom, 1952, 1954, 1958; Leibbrandt, 1901, 1902) or brought in from Europe. In contrast to the nomadic Khoi, these livestock herds were not moved, but remained on the same pastures, usually on less fertile, poorer soils of the farms, throughout the year. To encourage the growth of grasses, the vegetation was burnt, and immediately grazed again. However, veld burning was prohibited by law as early as 1687 to prevent excessive burning and runaway fires and to protect crops and live stock (Newton, 2006), and thus, naturally occurring fires were suppressed.

The Europeans also hunted the abundant game birds and large game mammals of the renosterveld, often on a large scale, for domestic consumption (Thom, 1958). The large herds of game were quickly diminished, and two species became extinct: Bluebock (Hippo-

tragus leucophaeus) around 1800 (Skinner and Smithers, 1990) and quagga (*Equus quagga*) by 1875 (Skinner and Smithers, 1990). The other indigenous large herbivores disappeared from the Western Cape before the turn of the 20th century.

### Modern Agriculture: transformation and fragmentation

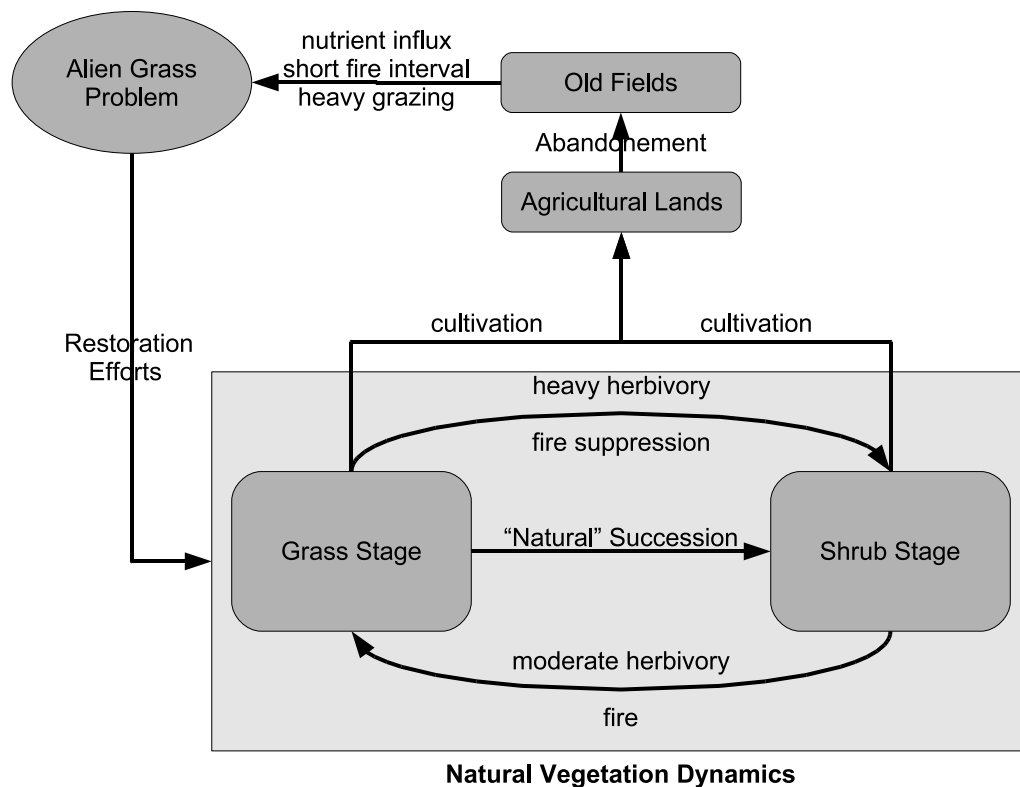
The discovery of gold and diamonds in the north of the country at the beginning of the 19th century, coupled with the development of an efficient transport system, led to the mechanization and intensification of agriculture in the fertile regions of the Western Cape, mostly within renosterveld (Talbot, 1947). This led to the extreme fragmentation present today. Larger areas were planted, including marginal lands, and rest periods were shortened, leading to severe soil exposure, compaction and erosion by the 1950s (Newton, 2006). Only thirty years later was farming regulated to control erosion. Ploughing of the marginal areas and steep slopes was abandoned, however, no special care was taken of small remnants and they received the same treatment as the field, for example, were sprayed and fertilized (Donaldson et al., 2002). This had negative effects on species composition and diversity in the remnant, and encouraged the invasion by alien species, especially grasses (Musil et al., 2005).

#### B.1.2. Change in Ecological Processes

We have used a state and transition model (Figure 2) to illustrate the pattern and dynamics of renosterveld, and how this has changed with human impact. We consider renosterveld as a mosaic of grass and shrub patches, with herbivory and fire as the main processes driving the shift between states. We do not include thicket patches in the model. The changes occurring during European settlement, through the removal of large herbivores and the suppression of fire, had a considerable impact on ecosystem processes in renosterveld, and led to the dominance of a single species, *Dicerotheramnus rhinocerotis*, in many west coast renosterveld remnants.

The role of large herbivores in renosterveld is threefold: they disperse seeds of grasses and some geophytes over long distances Shiponeni (2003); Shiponeni and Milton (2006); create gaps in shrubby patches through browsing and trampling, thus enabling germination and establishment of geophytes and grasses; and reduce grass cover through grazing, facilitating shrub establishment (Midoko-Iponga et al., 2005; Midoko-Iponga, 2004). The removal of large herbivores restricted the long-distance spread of dung-dispersed species. Without large browsers, fewer gaps were created in the shrub patches, restricting the establishment of shade-intolerant species and favoring longer-lived shrub species (Boucher, 1983). Overgrazing of the natural vegetation by cattle, coupled with the suppression of fires, resulted in monospecific stands of renosterbos (*Dicerotheramnus rhinocerotis*), a long-lived, wind-dispersed unpalatable asteraceous shrub.

Fire reduces shrub cover and leads to the establishment of grasses (Cowling et al., 1986), and encourages the germination of geophytes. Some geophyte species occurring in



**Figure B.2.:** Conceptual state and transition model for renosterveld vegetation dynamics.

renosterveld, e.g. Amaryllids, are only able to germinate after fire (Manning et al., 2002). Increased fire occurrence and frequency lead to the development of vast grasslands in the Western Cape. Remaining shrubby patches allowed for the regeneration of longer-lived shrub species. Heavy grazing by livestock immediately after burning lead to an increase in unpalatable species, especially *Dicerothamnus rhinocerotis* (Levyens, 1956), a reduction of the grass component and limited germination of geophyte species dependent on fire.

Fragmentation also affected ecological processes in the renosterveld remnants. Many very small fragments were (and are still) treated as part of the surrounding fields, and were sprayed with fertilisers and pesticides (Donaldson et al., 2002), and burnt with the harvested wheat fields. In addition, many of these small fragments were used for grazing livestock and were often oversown with legumes or grasses to increase the fodder value. Nutrient enrichment, especially of nitrogen and potassium, favors introduced grasses over indigenous species (Orlander et al., 1996). Overgrazing and frequent burning increases the proportion of introduced grass species occurring in a remnant and exacerbates the invasion problem (van Rooyen, 2004). To a lesser extent, woody introduced species are also a threat to vegetation remnants. Rouget et al. (2003) estimate that about 5% of west coast renosterveld remnants are invaded to a level of 75% cover or more.

Survival of populations of indigenous plant species within the vegetation remnants is also threatened by the limited reproductive potential of many indigenous species. The movement of pollinators across a fragmented landscape may be restricted, and some taxa that

are important pollinators in renosterveld, (e.g. monkey beetles) are sensitive to changes in habitat characteristics (Donaldson et al., 2002). The abundance of pollinators may be affected by fragment size (Donaldson et al., 2002). Some of the orchid species occurring in renosterveld have been documented to be pollinator-limited (Donaldson et al., 2002) as their pollinators, such as oil-collecting bees, have very specific habitat requirements (Pauw, 2004). However, Kemper et al. (1999) have shown that pollinator resources (i.e. geophyte density) do not decline with decreasing fragment size, and a diversity of insect pollinators can be maintained (Donaldson et al., 2002). Species composition changes with fragment size (Donaldson et al., 2002) or degree of isolation (Vrdoljak and Samways, 2005), and fragment size and isolation of a remnant influences seed or fruit set (Donaldson et al., 2002). Transformation also has an effect on seed dispersal (Kemper et al. 1999), and species with short dispersal ranges are not able to colonize distant fragments (Shiponeni, 2003).

### B.1.3. Incentives for Restoration

Due to the highly transformed state of renosterveld, all remaining remnants have been declared 100% irreplaceable in relation to conservation targets (von Hase et al., 2003; Cowling, 2001). In theory, this should prevent any further transformation of the vegetation for agricultural or development purposes. However, to successfully implement the fine-scale conservation plans for the Cape Floristic Region, and to maintain ecological processes across the landscape, the restoration of abandoned fields and degraded habitat remnants is required. Restoration of old fields can contribute to increasing the area under conservation, providing habitat for rare or endangered species (e.g. the geometric tortoise), creating corridors or stepping stones linking fragments and buffer zones between transformed and natural areas. Restored sites can also play an important role by serving as propagule sources for future restoration or natural expansion of habitat (Musil et al., 2005).

Wheat cropping was heavily subsidized during the 20th century in South Africa (Newton, 2006). With the removal of these subsidies (Donaldson, 2002), an increase in labor costs due to improved labor laws in post-apartheid South Africa, and taxation of all land, the feasibility of dryland agriculture is more difficult. Dryland cropping of cereals is being abandoned, and farmers are searching for alternative crops, for example olives, wine grapes or canola (Fairbanks et al., 2004). However, increased interest in the conservation of native vegetation (Winter and Esler, 2005; Winter, 2003), and the provision of financial incentives to set aside land for conservation (Botha, 2001), has led to a search for alternative use and income strategies from natural renosterveld vegetation, based upon activities such as game farming or ecotourism. For example, CapeNature, the provincial nature conservation agency, has created the Stewardship Program, where land is set-aside for conservation under contract. The Biodiversity and Wine Initiative supported by South African Wine and Brandy, markets products whose production is coupled with the conservation of biodiversity. These programs assist land owners to conserve natural vegetation, and farmers contribute in-kind by clearing aliens, restoring abandoned land, and conducting erosion

control.

As the incentives for restoration differ, so do the purposes of the sites to be restored. At the onset of restoration, a goal needs to be established on what is to be achieved with the restoration of an abandoned field, and what the land will be used for. Is it to increase the area of natural habitat, e.g. for game farming, to increase the proportion of suitable habitat for a species, to return bulb species to an area where they occurred before, e.g. to attract tourists to visit a site? Or will the restored sites act as corridors of stepping stones, linking larger fragments and thus allowing for dispersal and thus gene flow between populations? Each of these goals needs a different approach. As renosterveld is a shrubland with a bulb and grass component, the primary aim for the restoration of a site should be to establish a mix of shrubs, grasses, and bulb species. When the site is to be used for game farming, the grass and shrub component should be rather high, to provide graze and browse for the antelope species. Bulb species provide an important food source for grazers. On the other hand, when bulb species are the main focus of restoration, their proportion needs to be larger. Most bulb and grass species need open areas between shrubs, so disturbances, e.g. small scale fires, are necessary to create open patches within the vegetation.

## B.2. Old Field Restoration in Renosterveld: Underlying Vegetation Dynamics and Ecological Processes

### B.2.1. Study Site

The focus of the Renosterveld Restoration Project were abandoned agricultural fields at the Elandsberg Private Nature Reserve on the Farm Bartholomeus Klip ( $19^{\circ}03' E$ ,  $33^{\circ}27' S$ ), near Hermon in the Western Cape, South Africa (Figure B.1). About half of the property (approx. 3500 ha) is a working sheep and wheat farm, while the other half was proclaimed a private nature reserve in 1973 to protect the geometric tortoise, *Psammobates geometricus*. Since then, a number of indigenous game species have been re-introduced. The vegetation in the low-lying areas of the reserve is classified as Alluvium Sand Fynbos and Swartland Shale Renosterveld (Mucina and Rutherford, 2004), with Mountain Fynbos on the mountain slopes. The lowland portion of the reserve is about 1000 ha in size. Elandsberg is part of the largest remaining renosterveld vegetation complex in the Western Cape (Newton, 2006; von Hase et al., 2003)

A number of abandoned agricultural fields of different ages are incorporated into the reserve. All of these fields were ploughed and planted with oats (*Avena sativa*) in the 1960s and 1970s. The fields were classified into different successional stages according to age class: last ploughed before 1997 (5 years of recovery), before 1987 (15 years) and before 1967 (35 years). The youngest abandoned fields, which were oversown with European grasses after oat planting was discontinued, serve as grazing grounds for the re-introduced game species and act as buffers between the natural vegetation and the agricultural fields (Figure B.1).



The old field used for experimental studies was abandoned and incorporated into the reserve in 1987. Until 1985, oats were the main crop on the field; the field was over-sown with European grasses (*Briza* sp., *Lolium* sp. and *Vulpia* sp.) and used for sheep grazing (Mike Gregor, pers. com). Although the field is directly adjacent to an extensive patch of natural vegetation, introduced grasses still dominate the vegetation. Little indigenous vegetation is present, with the exception of *Dicerothamnus rhinocerotis*, *Athanasia* sp., *Relhania* sp. and *Asphalatus* sp. that have established at the edge of the field that borders the natural vegetation. Some geophytes, mostly weedy *Oxalis* species that are adapted to disturbances, have also established on the old field. Game species regularly grazing the sites are bontebok, burchell's zebra, black wildebeest, eland and springbok.

### B.2.2. Underlying Vegetation Dynamics and Processes

A study on secondary succession in old fields at Elandsberg has shown that although the structure of vegetation within the remnants and the oldest old fields is similar, species richness and species diversity are lower in the old fields (Walton, 2005; Krug et al., 2004a). This is due to fewer understorey species (forbs, geophytes and grasses) in the old fields. While structural recovery appears complete, a number of species are either not able to re-colonize after disturbance or have been lost from the seed bank.

The re-colonization ability of a species depends upon its seed dispersal properties and the successful establishment of its seedlings, which is determined by the competitive ability of the species and resource availability (light, nutrients, moisture) at the site. In a fragmented landscape, seed dispersal is limited (Bakker and Berendse, 1999), and the chance of seeds being dispersed to abandoned sites is very low. The main seed dispersal agents in renosterveld are wind and large herbivores, with about 41% of the species reaching the old fields dispersed by wind, and the same proportion dispersed in the dung of game species. The remaining species reached the site through other methods, mostly through tumbling (Shiponeni and Milton, 2006; Shiponeni, 2003; Krug et al., 2004b). The seed density of indigenous species was closely related to distance from natural vegetation (Krug, 2007; Shiponeni, 2003), indicating that very few seeds of most species are dispersed over large distances. Seed rain was dominated by introduced grasses, and only two indigenous species, the shrub *Dicerothamnus rhinocerotis* and the grass *Tribolium hispidum*, contributed significantly to the seed rain (Shiponeni, 2003). No seeds of geophyte species present in the natural vegetation were found in the old field. Corms of geophytes are dispersed by porcupines; however, these distances are usually rather short. Large herbivores transport mostly seeds of grasses and annuals. These were however mainly species occurring on the old fields, and introduced grass species dominated the samples (Krug, 2007; Shiponeni, 2003). Although the large herbivores dispersed a large number of seeds and species, they contributed very little to movement of species from the natural vegetation to the old field. The results indicate that the re-colonization of old fields by native species in renosterveld is partly dispersal-limited.

Even though the seeds of indigenous species are dispersed, very few seedlings are ob-

served in the old fields. Germination of seeds is inhibited by the existing vegetation (Grace, 1999; Thompson et al., 1977). Grasses, particularly introduced grasses, are known to interfere with the survival and growth of woody species and forbs (Davies, 1985). Herbivory also influences species establishment, either through seedling removal or by trampling, and the maintenance of grazing lawns by game species inhibits the recolonization of indigenous shrubs. Competition and herbivory are known to negatively affect species establishment (Bonser and Reader, 1995). In recent experiments, grass competition had a greater effect on seedling growth and survival than herbivory (Midoko-Iponga et al., 2005; Midoko-Iponga, 2004). The negative influence of competition from alien grasses on the establishment of indigenous shrub species, combined with limited seed dispersal, impacts severely on the capacity of indigenous renosterveld species to recolonize abandoned agricultural areas.

### B.2.3. Implications for Successful Restoration Interventions

To facilitate the return of indigenous species to these old fields, introduced grass species must be removed and seeds of indigenous species broadcast on the cleared sites. Ideally, large herbivores (game and live stock) should be prevented from entering the area to be restored, to prevent seedling losses from grazing or trampling and to prevent dispersal of introduced grasses onto the site.

Abandoned fields set aside for restoration are often adjacent to fields that are still being worked and are thus subjected to an influx of nutrients through fertilizers. In addition, agricultural fields are ploughed along contour lines, and drainage lines are established, changing the surface water flow and soil hydrology. High nutrient levels in the soil favor alien grasses (Milton, 2004; Orlander et al., 1996), while the changes in soil hydrology might prevent the establishment of indigenous species (Andrej Rozanov, pers. comm.). The drift of herbicides and pesticides may also have a negative impact on restored plant and animal (particularly pollinator) communities on the site. In a highly fragmented landscape, local species pools are often diminished. Due to geographical and topographical variability of the landscape, suitable ecotypes of species might not be available. As very few large fragments still exist, sourcing of seeds in the quantities required for restoration may pose a problem.

The highly fragmented nature of the ecosystem may have considerable negative impacts on the persistence of indigenous species and the survival of the populations after restoration. The restoration of plant communities does not necessarily imply that other taxa will follow. For example, the specific habitat requirements of specialized pollinators might not be met within restored sites or adjacent small fragments, due to subtle differences in microclimate, soil type or soil structure, or the availability of host plants for larvae. The dispersal ranges of animals are limited by the connectivity of their habitat, and the availability of corridors or stepping stones between fragments (Beier and Noss, 1998). The extent at which ecosystem processes can be recreated and maintained on restored sites, and the landscape within a mosaic of different vegetation fragments, needs to be con-



sidered. In the case of renosterveld, where a high degree of transformation took place over a relatively short time period, it is nearly impossible to restore the original vegetation. Therefore, restoration efforts should focus on a specific goal (see above) rather than aiming to re-create a vegetation type that has been largely transformed.

### B.3. Old Field Restoration of Renosterveld: Application and Methodology

Our recommendations for the restoration of renosterveld are largely based on our current understanding of ecological processes. Although preliminary field-trials have been conducted (Midoko-Iponga, 2004; Midoko-Iponga and Krug, unpublished), the methods suggested need to be tested in large-scale field trials, some of which are underway.

#### B.3.1. Methods for Renosterveld Restoration

Current restoration efforts in renosterveld aim to reduce the cover of introduced grasses while at the same time maintaining or even increasing species richness and diversity of indigenous target species (geophytes, indigenous grasses and shrubs). Below we detail some of these restoration experiments conducted in the renosterveld. Midoko-Iponga (2004) compared the effectiveness of brush cutting, burning and herbicide (grass-specific, post-emergence) application on the removal of introduced grasses. The plots were treated once, in autumn, and were then monitored over a 12 month period (Midoko-Iponga, 2004), to determine the effects of the treatments on species richness and diversity and cover abundance of target species. The plots were monitored again 24 and 30 months after treatment to determine longer-term vegetation changes after a once-off treatment (Midoko-Iponga and Krug, unpublished). In addition, seeds of an indigenous grass, *Ehrharta calycina* (Poaceae), and an indigenous shrub, *Eriocephalus africanus* (Asteraceae) were sown onto the treatment plots, and the survival and growth of the emerging seedlings was monitored.

Herbicide application and burning proved equally effective in reducing the cover of introduced grasses (Figure B.3). However, indigenous species richness and diversity was lowest after burning (Table B.1 and Table B.2). A year after treatment, introduced grass cover was similar in all treatments, and gradually declined over the next year and half (Figure B.3). Thirty months after the treatment, richness and diversity of indigenous species across all treatments was very similar (Table B.2). Musil et al. (2005) found that herbicide application, and a combination of a light burn with a subsequent herbicide application, were most effective methods to control introduced grasses while at the same time maintaining a high diversity of indigenous species, especially geophytes.

Based on our understanding of the ecological processes, and on the results of the preliminary field-trials, we recommend for successful restoration of abandoned old fields in renosterveld the application of a grass-specific herbicide at the onset of winter, preceded

**Table B.1.:** Species richness  $\pm$  SD of indigenous species six, twelve, twenty-four and thirty months after treatment.

Treatment	Control		Burn		BrushCut		Herbicide		F-value	p-value	
	mean	SD	mean	SD	mean	SD	mean	SD			
6 mths	11.00	1.00	7.67	1.53	10.00	1.00	10.00	1.73	3.27	0.080	<i>ns</i>
12 mths	4.67	1.53	3.33	2.08	2.67	1.53	3.67	1.53	0.74	0.560	<i>ns</i>
24 mths	7.33	1.53	7.67	0.58	7.33	1.15	7.67	0.58	0.10	0.956	<i>ns</i>
30 mths	8.67	1.53	10.00	1.00	8.33	2.52	9.00	1.00	0.58	0.642	<i>ns</i>

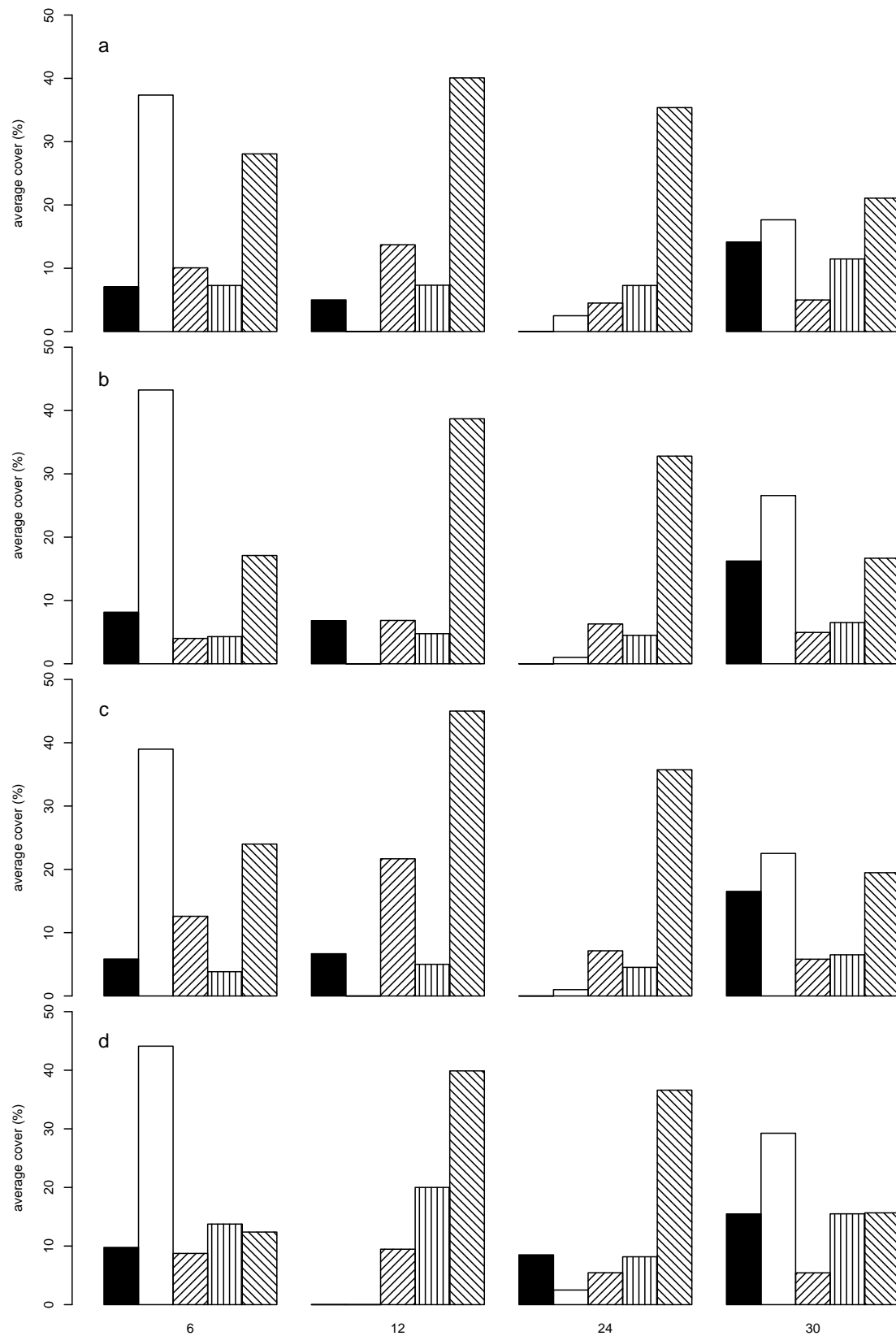
**Table B.2.:** Simpson diversity index D and Simpson equity index E of indigenous species (forbs, geophytes, shrub and grasses) six, twelve, twenty-four and thirty months after treatment.

Treatment		Control	Burn	BrushCut	Herbicide
6 mths	Diversity	4.93	2.69	4.55	4.74
	Equity	0.45	0.35	0.46	0.47
12 mths	Diversity	2.47	2.91	2.32	2.69
	Equity	0.60	0.90	0.91	0.77
24 mths	Diversity	4.67	4.33	3.81	4.27
	Equity	0.65	0.57	0.52	0.55
30 mths	Diversity	6.13	5.51	4.69	5.23
	Equity	0.71	0.55	0.58	0.58

by an autumn burn to achieve a flush of the target alien grasses. We further recommend a repeat application of a grass-specific herbicide to control the recruitment of alien grasses. However, herbicides need to be applied with caution, as they can damage the roots of indigenous vegetation even at low concentrations (Cornish and Burgin, 2005). Oversewing with a mix of indigenous species should be considered, especially in those areas with limited seed sources. Sowing times of the species used is dependent on their time of flowering and seed set, usually before, during and after the winter rains, or between March and October. Indigenous grasses should not be sown too early after herbicide application, as the seedlings are destroyed and resources are wasted. However, both Midoko-Iponga (2004) and Musil et al. (2005) found that herbicide application was the most expensive treatment method, costing about R 36 100/ha (US\$ 6 000/ha) and R13 380/ha (US\$ 2 230/ha) respectively. Therefore, Musil et al. (2005) recommend mowing grass before seed set, and removing the cut grass for fodder to offset costs, as the most feasible method for clearing introduced grasses in renosterveld. This strategy however, as the repeat application of grass-specific herbicide, affects the recruitment of indigenous grasses, which are an integral part of renosterveld vegetation. As we have only conducted research on old fields covered with introduced grasses, no recommendations can be made on how to restore sites dominated by introduced annual dicots.

### B.3.2. Problems and Potential Solutions

Although suitable restoration strategies for west coast renosterveld could be identified within this project, a number of problems and pitfalls still remain. Seeds of indigenous



**Figure B.3.:** Average cover in percent of forbs (closed), geophytes (open), shrubs (upward diagonally hatched), indigenous grasses (vertically hatched) and introduced grasses (downward diagonally hatched) six, twelve, twenty-four and thirty months after treatment (a: control, b: autumn burn, c: autumn brush cut, d: autumn herbicide application).

species are not easily available and need to be collected by hand, adding to the total cost of the restoration. Natural vegetation remnants that can be used as seed sources are often small and have a diminished species pool. As topography, microclimate and soil are highly variable, particular ecotypes might not be suitable for the area to be restored. Phenology of species also differs, species flower and set seed before, during or after the winter rain fall period, which determines the time of seed collection and seed broadcasting. It might therefore be necessary to oversow the restoration site repeatedly after treatment. Many of the introduced grasses are now resistant to the herbicides most commonly available (Mike Gregor, pers.comm.). The state of the land surrounding a restored site will also have an impact on the success of restoration. Restored sites that are adjacent to, or surrounded by, active agricultural fields are more likely to have a persistent alien cover of introduced grasses, than sites adjacent to natural remnants. Heavy grazing and frequent burning also leads to an increase in introduced grasses, and the timing and severity of these two disturbances needs to be carefully considered.

## B.4. Conclusions

Renosterveld is a highly transformed and fragmented ecosystem. Very little is known on the original ecosystem processes, and we can only speculate about the role large herbivores and fire played in the system before transformation by European settlers. Renosterveld was most likely a mixed shrub - grassland, with a large geophyte component. Very few large renosterveld fragments remain, and all vegetation remnants are considered irreplaceable. Vegetation on abandoned fields, and in small remnants, is dominated by introduced grasses. Restoration of renosterveld can serve a number of needs, be it to create buffer zones between natural and agricultural areas, to create “nuclei” for further restoration of large tracts of lands, to create stepping stones and corridors connecting fragments, and at the same time, can be used as an alternative to traditional land use of cropping.

Currently the most suitable method for the restoration of renosterveld is the repeat application of a grass-specific herbicide, coupled with a light burn, to reduce the cover of introduced grasses while at the same time maintaining a high richness and diversity of indigenous species. We are currently investigating soil hydrology and soil nutrient status in abandoned agricultural fields, and how these affect the persistence of introduced grasses and the establishment of indigenous vegetation, with the aim to better understand the drivers of vegetation dynamics on old fields, and to improve our restoration guidelines.

## B.5. Acknowledgements

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### **C. Graphs showing the spread over time for different seed productions**

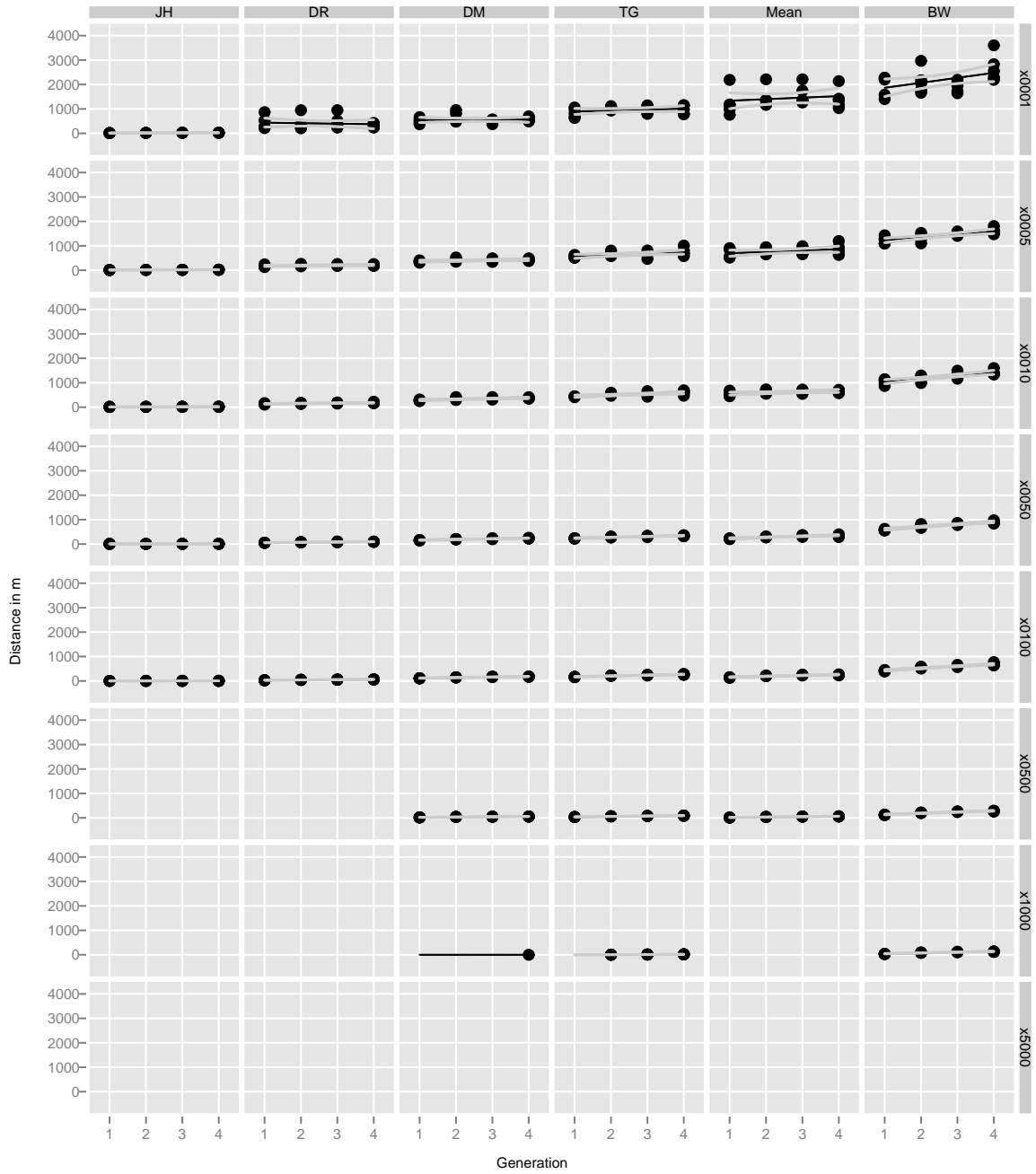


Figure C.1.: Seed Production 25

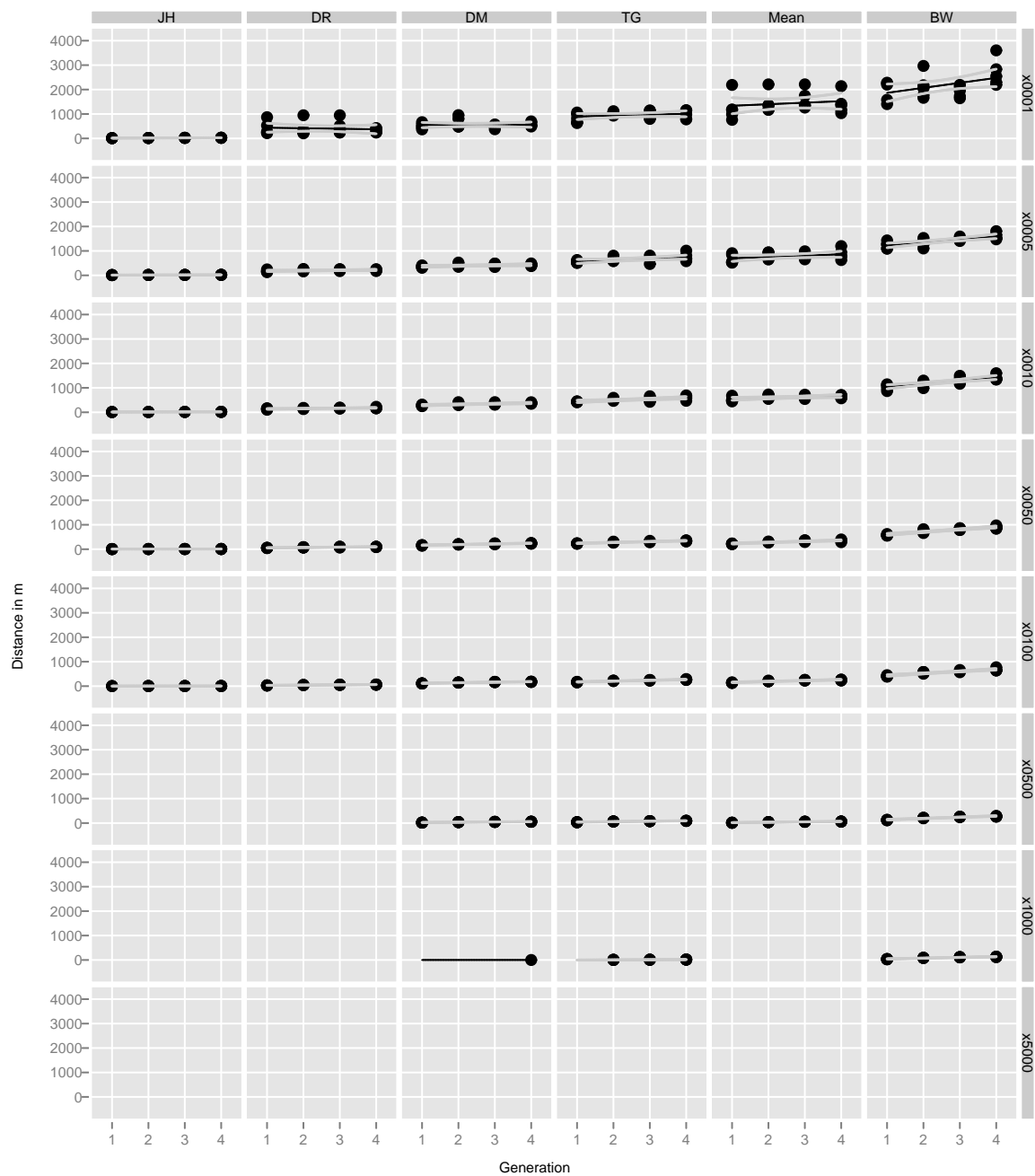


Figure C.2.: Seed Production 25

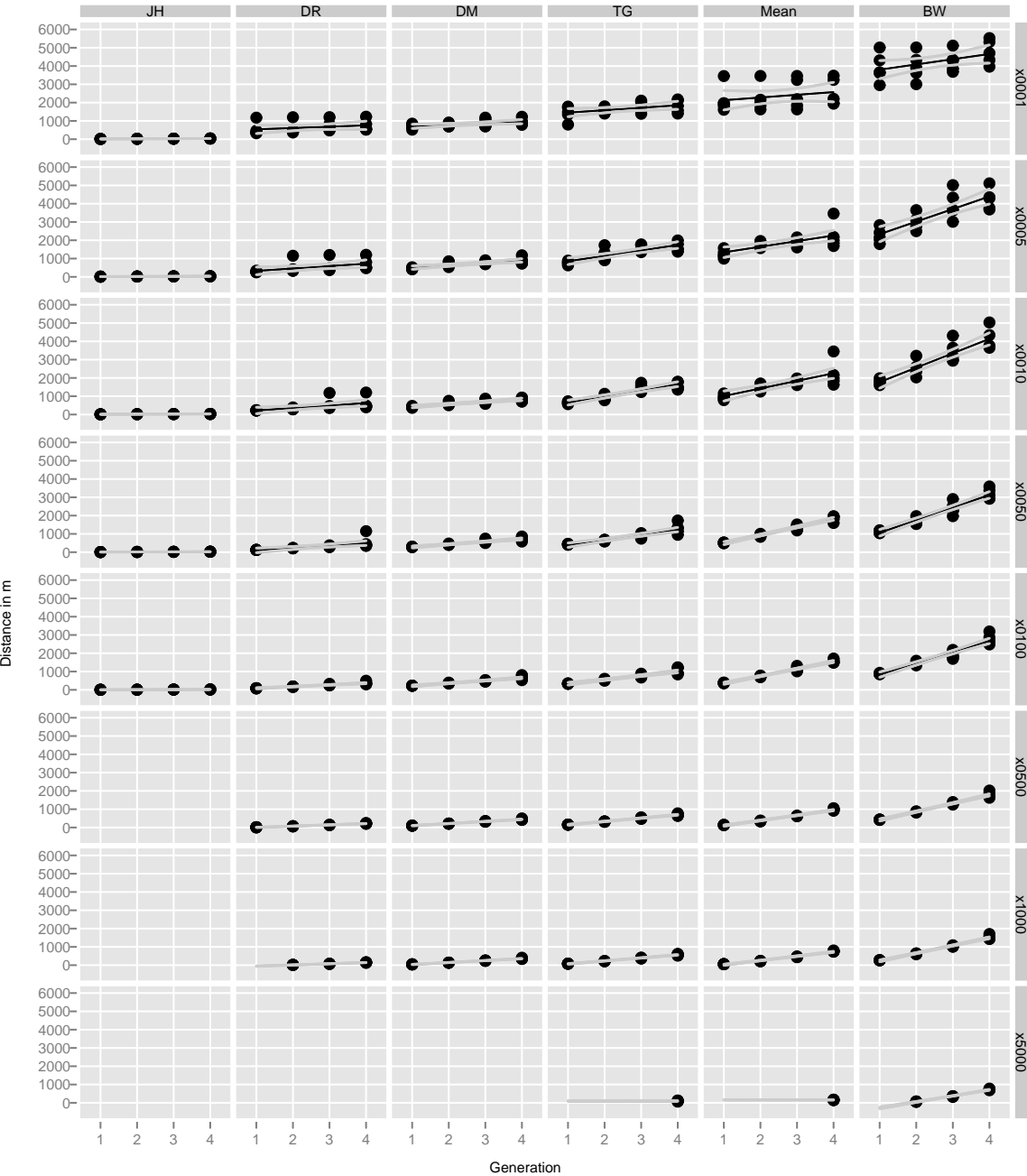


Figure C.3.: Seed Production 143



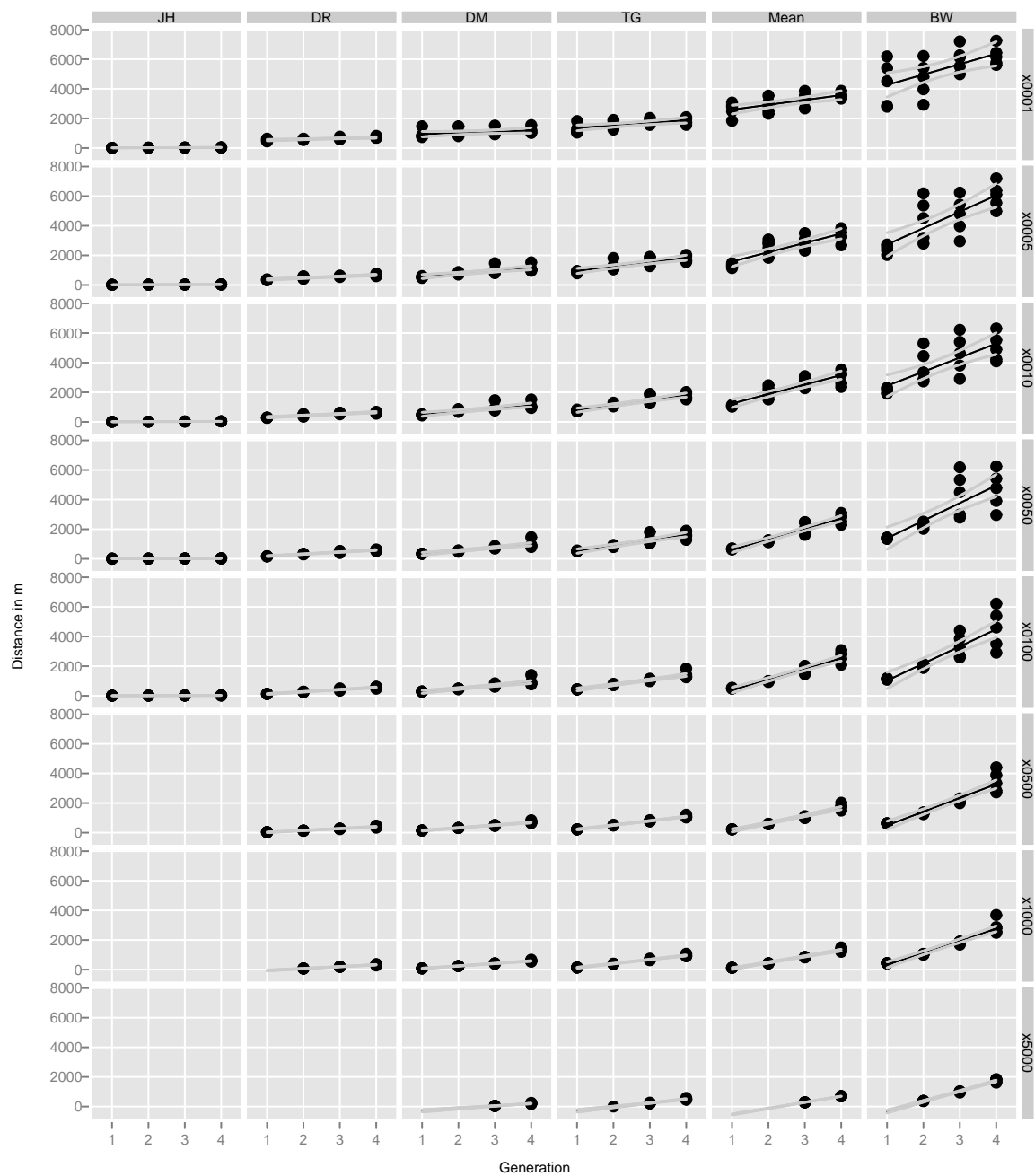


Figure C.4.: Seed Production 308

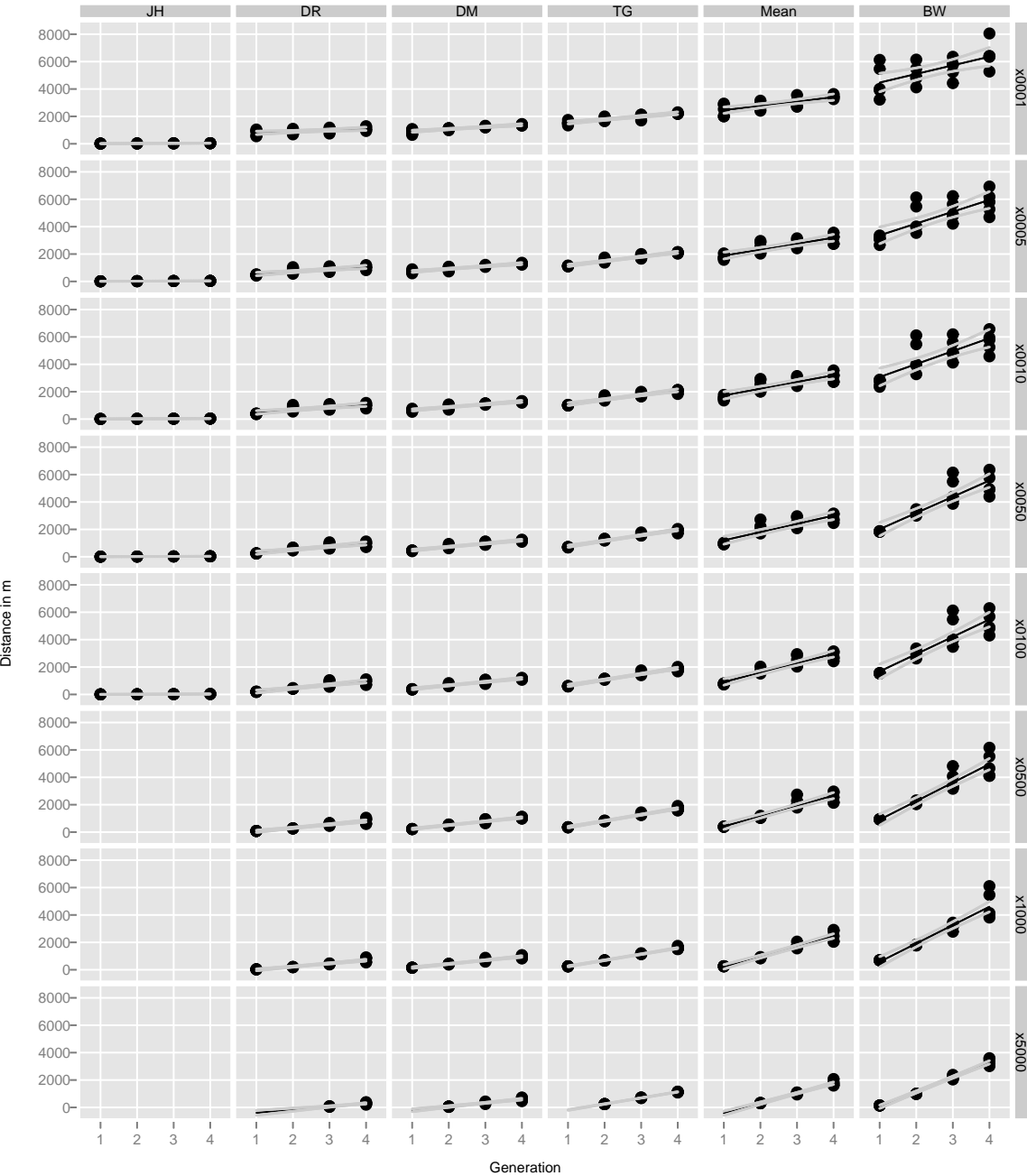


Figure C.5.: Seed Production 880

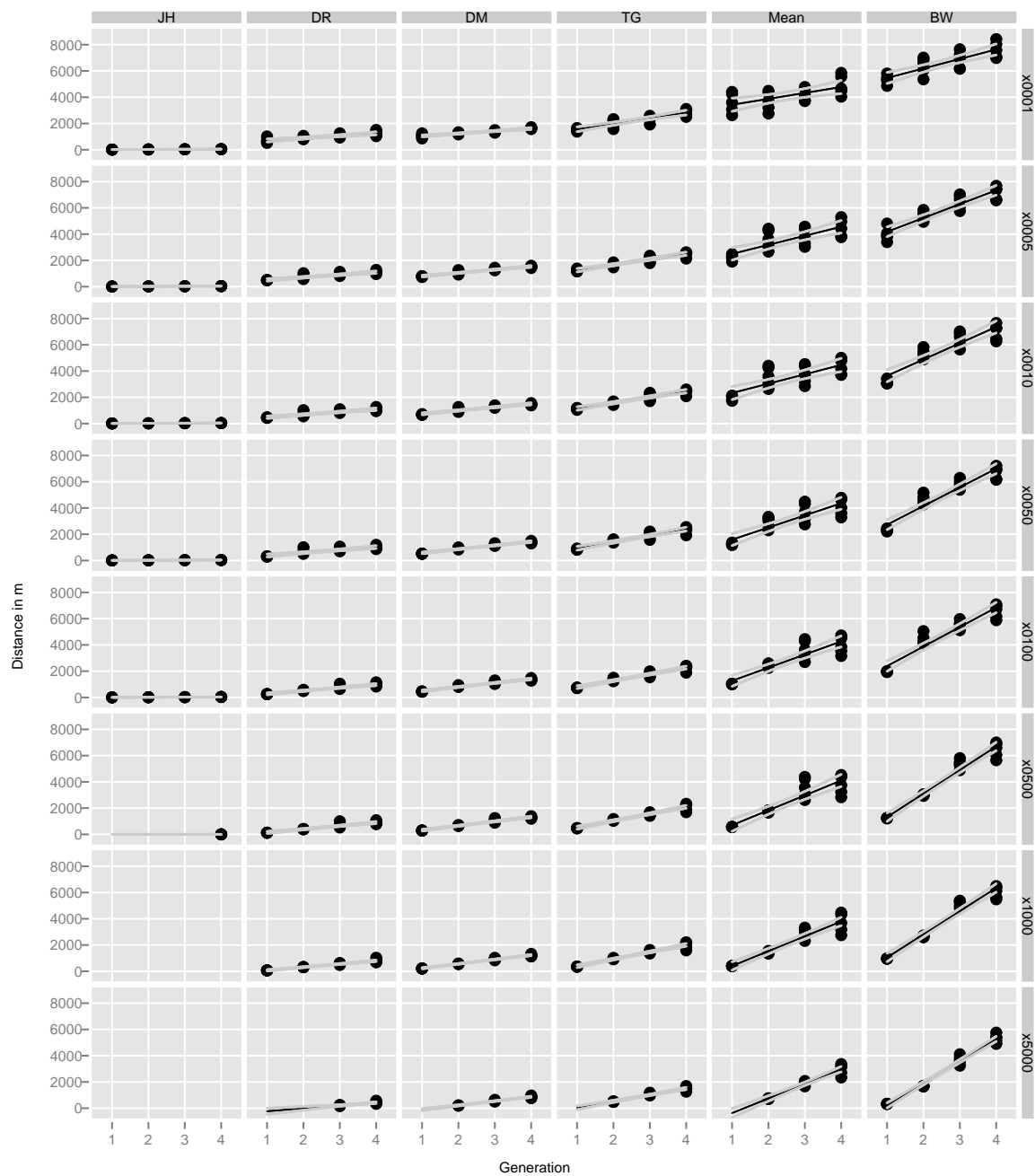


Figure C.6.: Seed Production 2134

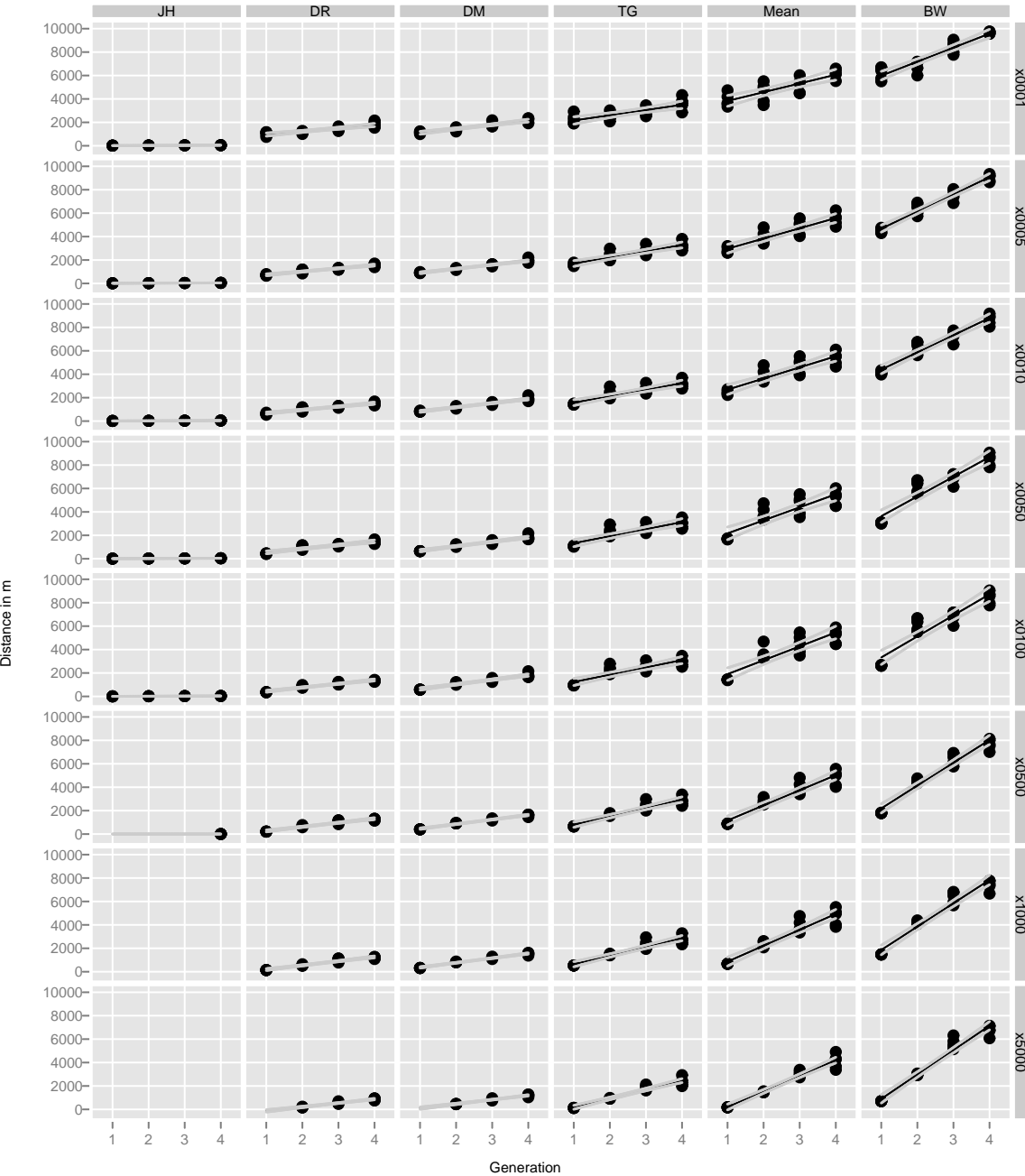
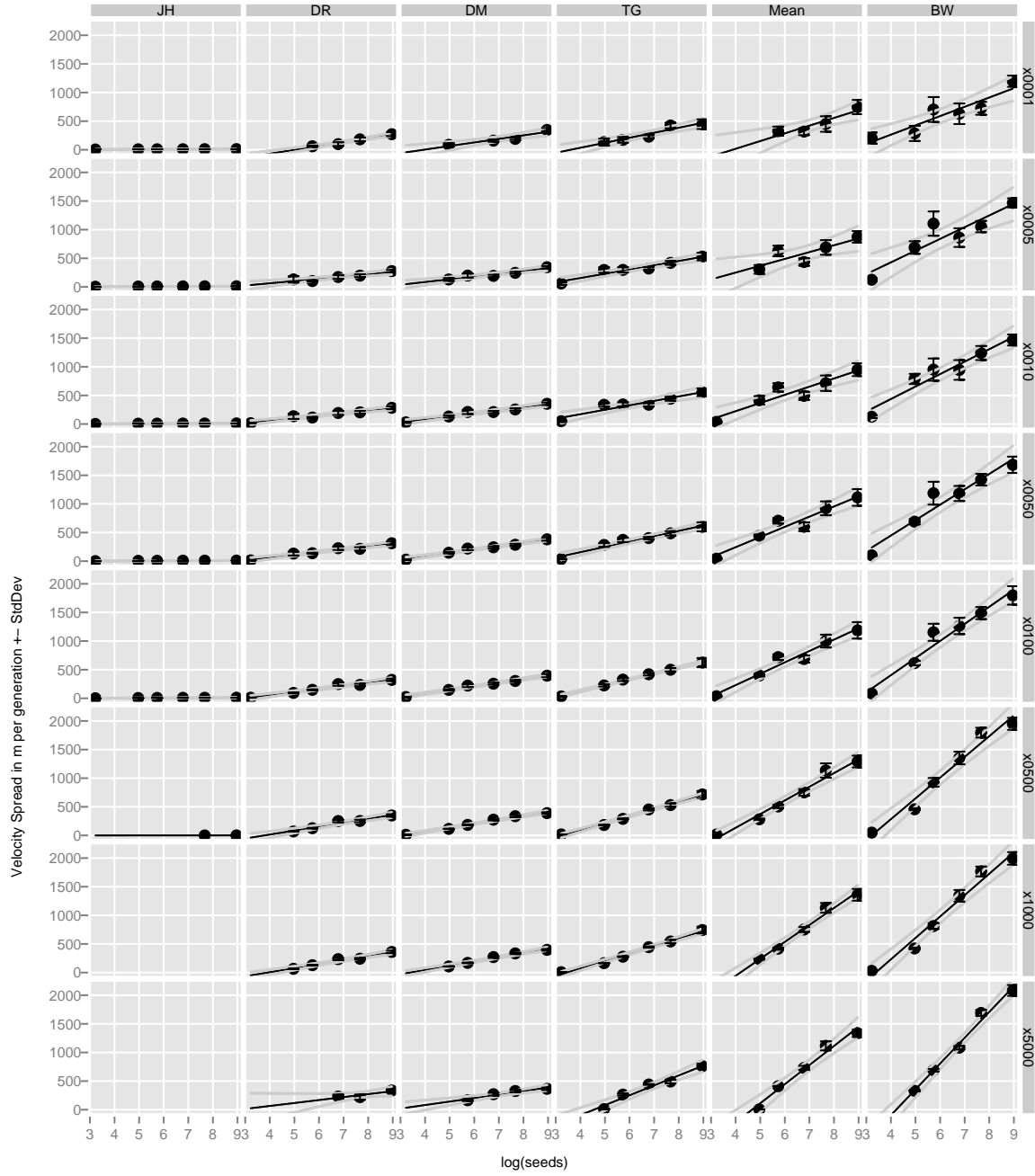


Figure C.7.: Seed Production 7777

## **D. Dependence of velocity on seed production**



**Figure D.1.:** Raw data of velocity  $V_x$  of spread in dependence of  $\ln(\text{SeedProduction})$ . Lines are linear regressions. Details can be found in Table D.1

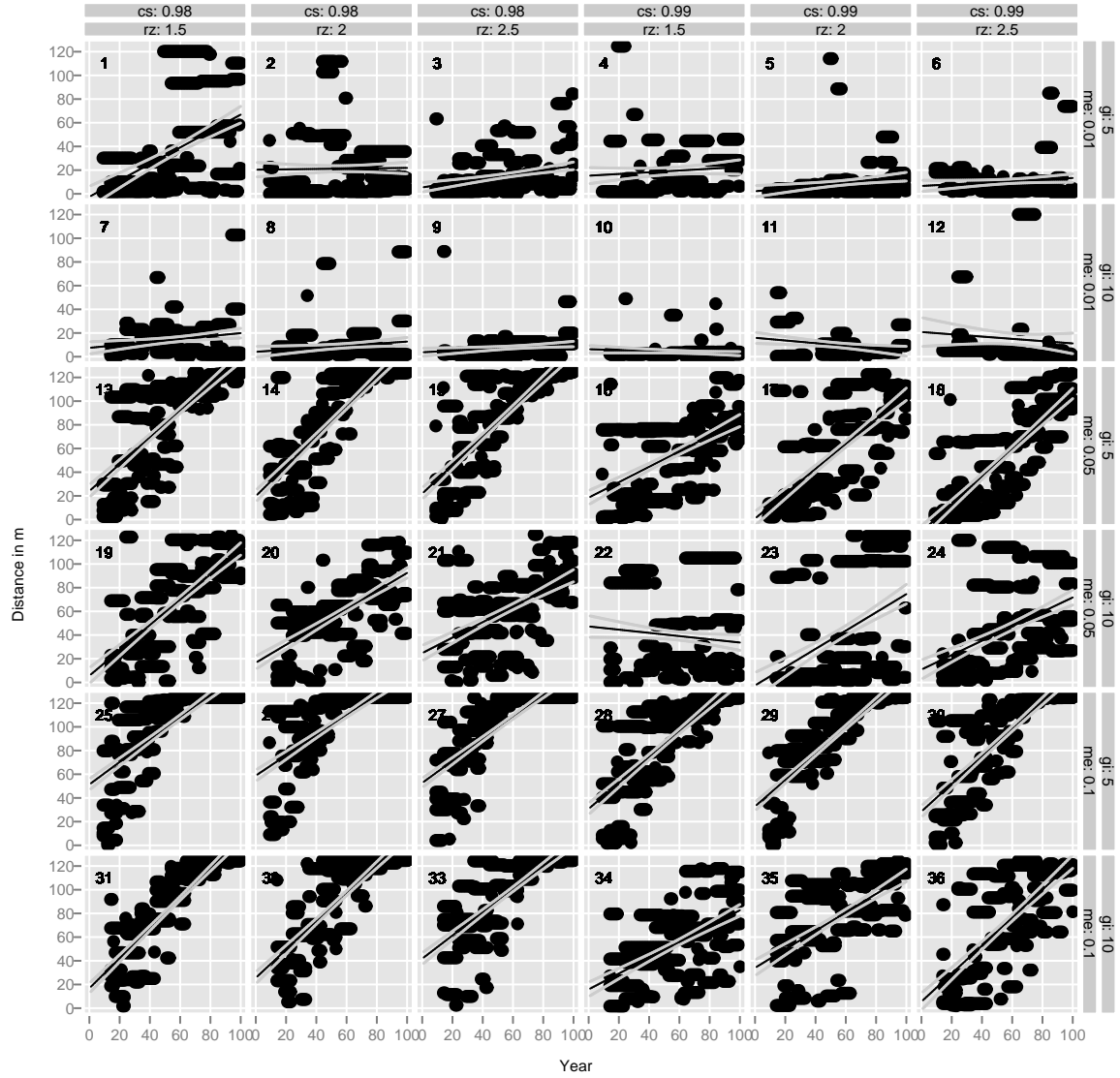
**Table D.1.:** Results of the linear regressions of the impact of the seed production on the velocities  $V_x$ . Slopes significantly different from zero are represented by p-values in bold and  $R^2$  values larger than 0.8 are also indicated in bold.  $V = m \cdot \ln(\text{SeedProduction}) + b$ , where  $m = \text{intercept}$  and  $b = \text{slope}$

Expert	Measure	intercept	slope	$R^2$	F	df <sub>2</sub>	p
JH	x0001	$1.831 \pm 1.409$	$1.10 \pm 0.22$	<b>0.961</b>	99.25	4	<b>0.000570</b>
	x0005	$-0.002 \pm 2.501$	$1.31 \pm 0.39$	<b>0.918</b>	44.61	4	<b>0.002613</b>
	x0010	$-1.058 \pm 2.643$	$1.42 \pm 0.41$	<b>0.921</b>	46.67	4	<b>0.002401</b>
	x0050	$-3.277 \pm 3.084$	$1.67 \pm 0.48$	<b>0.922</b>	47.36	4	<b>0.002337</b>
	x0100	$-3.632 \pm 2.544$	$1.70 \pm 0.39$	<b>0.948</b>	72.45	4	<b>0.001045</b>
DR	x0001	$-340.124 \pm 109.126$	$67.74 \pm 14.79$	<b>0.976</b>	80.61	2	<b>0.012180</b>
	x0005	$-95.897 \pm 118.815$	$39.80 \pm 17.06$	<b>0.874</b>	20.90	3	<b>0.019637</b>
	x0010	$-115.029 \pm 65.904$	$43.79 \pm 10.15$	<b>0.947</b>	71.45	4	<b>0.001073</b>
	x0050	$-132.627 \pm 65.650$	$49.19 \pm 10.11$	<b>0.958</b>	90.88	4	<b>0.000676</b>
	x0100	$-164.217 \pm 68.672$	$54.74 \pm 10.58$	<b>0.963</b>	102.84	4	<b>0.000532</b>
	x0500	$-259.969 \pm 125.400$	$68.88 \pm 18.01$	<b>0.949</b>	56.20	3	<b>0.004918</b>
	x1000	$-277.089 \pm 101.839$	$70.90 \pm 14.62$	<b>0.968</b>	90.29	3	<b>0.002471</b>
DM	x5000	$-141.328 \pm 432.851$	$51.67 \pm 55.12$	0.771	3.38	1	0.317312
	x0001	$-244.532 \pm 211.044$	$62.04 \pm 29.15$	<b>0.897</b>	17.40	2	0.052951
	x0005	$-107.769 \pm 117.876$	$48.32 \pm 16.93$	<b>0.913</b>	31.30	3	<b>0.011281</b>
	x0010	$-130.973 \pm 69.370$	$52.94 \pm 10.69$	<b>0.959</b>	94.26	4	<b>0.000630</b>
	x0050	$-149.503 \pm 54.804$	$59.01 \pm 8.44$	<b>0.979</b>	187.67	4	<b>0.000164</b>
	x0100	$-167.137 \pm 47.661$	$62.88 \pm 7.34$	<b>0.986</b>	281.71	4	<b>0.000074</b>
	x0500	$-212.880 \pm 48.607$	$69.39 \pm 7.49$	<b>0.988</b>	329.89	4	<b>0.000054</b>
TG	x1000	$-251.566 \pm 80.943$	$74.35 \pm 11.62$	<b>0.981</b>	157.18	3	<b>0.001094</b>
	x5000	$-162.854 \pm 177.783$	$61.04 \pm 24.09$	<b>0.925</b>	24.66	2	<b>0.038239</b>
	x0001	$-315.058 \pm 224.372$	$87.43 \pm 32.22$	<b>0.904</b>	28.29	3	<b>0.012985</b>
	x0005	$-142.945 \pm 126.643$	$74.49 \pm 19.51$	<b>0.933</b>	56.00	4	<b>0.001705</b>
	x0010	$-139.338 \pm 176.771$	$77.66 \pm 27.23$	<b>0.886</b>	31.24	4	<b>0.005027</b>
	x0050	$-215.110 \pm 119.368$	$93.01 \pm 18.39$	<b>0.961</b>	98.27	4	<b>0.000581</b>
	x0100	$-282.909 \pm 42.095$	$102.48 \pm 6.48$	<b>0.996</b>	959.35	4	<b>0.000006</b>
Mean	x0500	$-402.687 \pm 66.655$	$123.44 \pm 10.27$	<b>0.993</b>	555.10	4	<b>0.000019</b>
	x1000	$-449.390 \pm 83.559$	$130.62 \pm 12.87$	<b>0.990</b>	395.54	4	<b>0.000038</b>
	x5000	$-587.481 \pm 277.373$	$147.83 \pm 37.59$	<b>0.967</b>	59.42	2	<b>0.016416</b>
	x0001	$-522.369 \pm 590.380$	$134.82 \pm 80.00$	0.845	10.91	2	0.080720
	x0005	$-226.946 \pm 587.844$	$119.26 \pm 84.42$	0.719	7.67	3	<b>0.069635</b>
	x0010	$-346.960 \pm 327.460$	$142.83 \pm 50.45$	<b>0.885</b>	30.79	4	<b>0.005159</b>
	x0050	$-467.365 \pm 307.685$	$177.83 \pm 47.40$	<b>0.931</b>	54.07	4	<b>0.001822</b>
BW	x0100	$-565.169 \pm 261.383$	$198.76 \pm 40.27$	<b>0.959</b>	93.59	4	<b>0.000639</b>
	x0500	$-821.736 \pm 249.862$	$238.81 \pm 38.49$	<b>0.974</b>	147.87	4	<b>0.000262</b>
	x1000	$-1241.162 \pm 306.295$	$296.17 \pm 43.99$	<b>0.983</b>	174.16	3	<b>0.000940</b>
	x5000	$-1250.719 \pm 534.615$	$295.00 \pm 72.45$	<b>0.970</b>	63.70	2	<b>0.015339</b>
	x0001	$-385.409 \pm 418.752$	$162.28 \pm 64.51$	<b>0.859</b>	24.31	4	<b>0.007870</b>
	x0005	$-391.114 \pm 565.269$	$204.94 \pm 87.08$	<b>0.842</b>	21.28	4	<b>0.009937</b>
	x0010	$-432.928 \pm 369.842$	$217.51 \pm 56.98$	<b>0.933</b>	55.99	4	<b>0.001706</b>
	x0050	$-628.941 \pm 449.478$	$269.14 \pm 69.24$	<b>0.936</b>	58.04	4	<b>0.001594</b>
	x0100	$-791.450 \pm 385.043$	$298.78 \pm 59.32$	<b>0.961</b>	97.46	4	<b>0.000591</b>
	x0500	$-1166.914 \pm 415.461$	$362.68 \pm 64.00$	<b>0.969</b>	123.35	4	<b>0.000374</b>
	x1000	$-1264.290 \pm 399.973$	$373.90 \pm 61.62$	<b>0.972</b>	141.45	4	<b>0.000286</b>
	x5000	$-1900.499 \pm 409.790$	$451.04 \pm 58.85$	<b>0.987</b>	225.67	3	<b>0.000640</b>

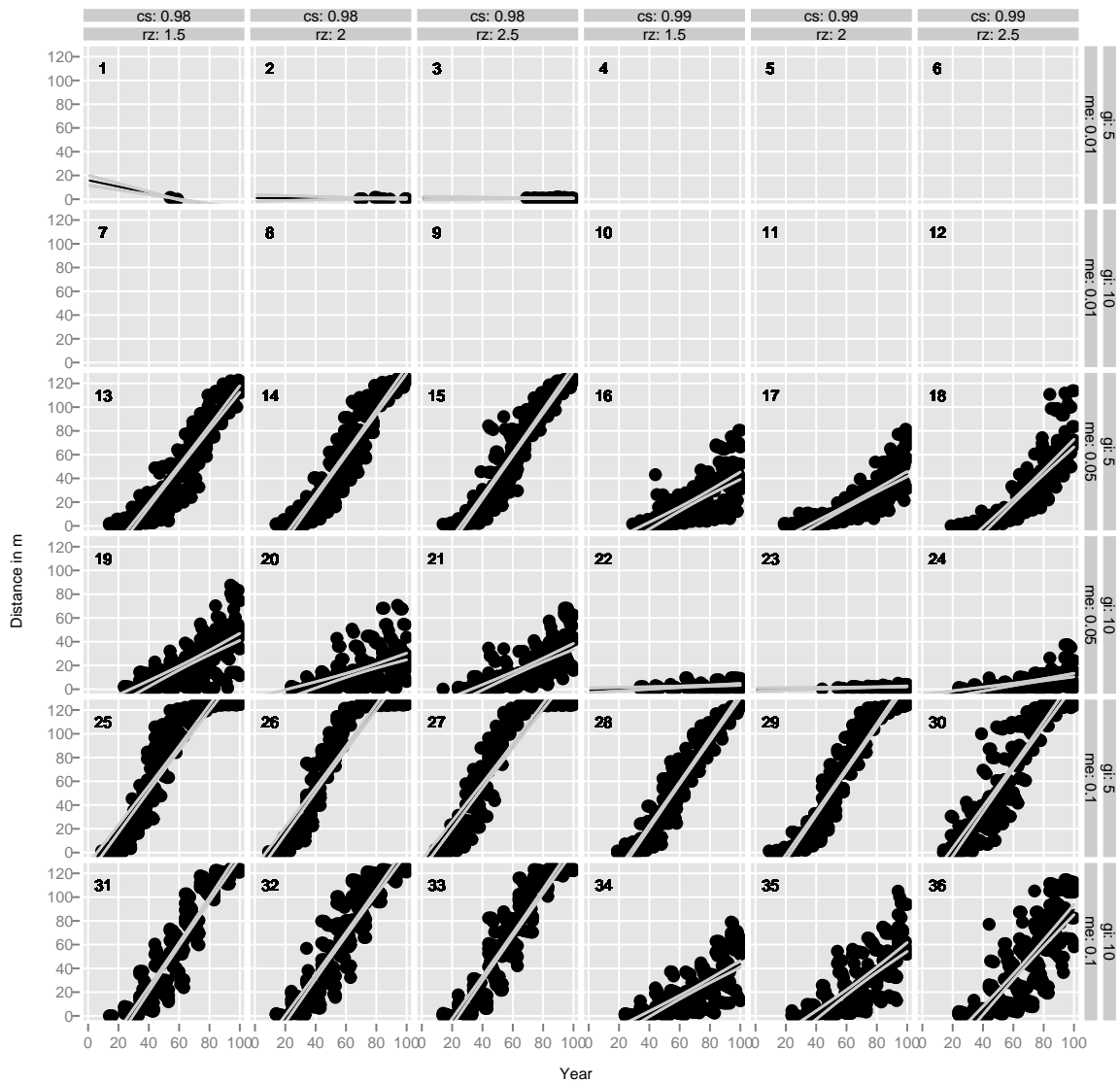




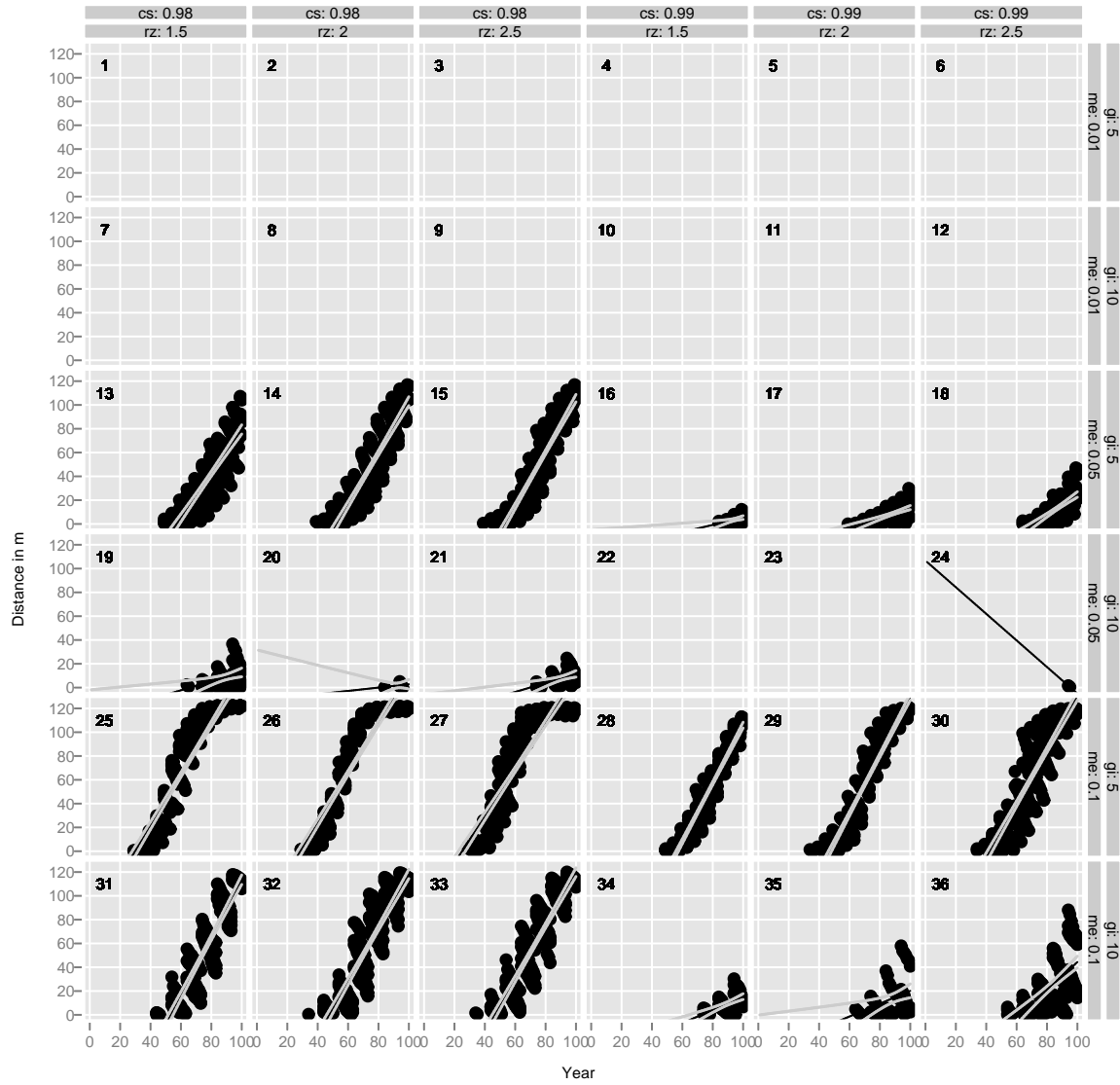
## **E. Spread pattern with plants older than 4 years**



**Figure E.1.:** Distance of the furthest plant from the initial seed source (measure x1), only taking plants older or equal than five years into consideration. Linear regression lines indicate the expected velocity. Data is combined from all simulations. Numbers in the upper left corners indicate the number of the scenario.



**Figure E.2.:** Distance of the 10<sup>th</sup> furthest plant from the initial seed source (measure x0010), only taking plants older or equal than five years into consideration. Linear regression lines indicate the expected velocity. Data is combined from all simulations. Numbers in the upper left corners indicate the number of the scenario.



**Figure E.3.:** Distance of the 100<sup>th</sup> furthest plant from the initial seed source (measure x100), only taking plants older or equal than five years into consideration. Linear regression lines indicate the expected velocity. Data is combined from all simulations. Numbers in the upper left corners indicate the number of the scenario.