Assessing the invasion potential of *Eucalyptus grandis* in South Africa

by

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DECLARATION

I, the undersigned, certify that this is my original work which does not have any materials that have been accepted for the award of any degree in any university and, to the best of my knowledge has no materials that have been published previously or written by another person, expect where due reference has been made in the text.

Kudakwashe Musengi

8th of August 2014

ABSTRACT

Alien invasive species can have serious negative impacts on the biodiversity and functioning of ecosystems, but identifying invaders early, before they cause problems, can dramatically reduce the costs of controlling them. There is substantial research in identifying key attributes of invasive species, which can potentially be used in this regard. Many Eucalypts have formed the backbone of forestry in South Africa since the 1800s. While many other plantation species such as pines and legumes, have become serious invaders in many parts of the world, Eucalyptus species have been not been nearly as successful in invading alien environments. This is surprising considering that in their native habitat; members of this genus dominate almost all vegetation types. This project used available theory on the qualities that characterise invasive species to assess the invasive potential of one Eucalyptus species: *Eucalyptus grandis (rose gum)*. Many alien plants take a long time to establish naturalised populations and spread through new ecosystems and this research provides information on the likelihood that *E. grandis* will become a problem species in the future.

A field study was used to determine whether there is any indication that it is in fact, invading from plantations in Mpumalanga, and if so, which ecological processes affect invasion. Belt transects (5 by 50 metres) were used in sampling the populations growing near plantations. To determine whether frost is affecting the populations, one site was at high elevation where it is exposed to frost (near Graskop) and the other at a low elevation area with infrequent frost (near White river). Key reproductive traits such as generation time and seed viability which are known to affect invasion potential were also studied. Demographic data was used to determine the rates of establishment of *E. grandis* outside of plantations. The results showed that *E. grandis* had a short generation time and its seeds had a viability of 97%. Assessing the shape parameter (c) of the Weibull distribution function showed that both the Graskop (c=1) and White River (c=1) size class distributions had reverse j-shaped curves, characteristic of good rejuvenation. However, some Graskop sites had a monotonic function ($c < 1$) showing that frost is affecting the rejuvenation process. Generally the results show that rate of spread is low and this might suggest that the populations are on the establishing populations' invasion stage. However, there is no indication that there are any environmental or life history factors that would prevent *Eucalyptus* from becoming invasive in the future, and I would recommend strict monitoring of its rates of spread out of plantation forests in various parts of the country.

DEDICATION

To my Dad, Mum, Trevor and Tinashe

Thank you for all your love and support.

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TABLE OF CONTENTS **PAGE**

LIST OF ABRREVEATIONS

°C	Degrees Celsius
CAR	Conservation of Agricultural Resources
DAFF	Department of Agriculture, Forestry and Fisheries
GI	Germination Index
MAT	Mean Annual Temperature
NSW	New South Wales
SAPPI	South African Pulp and Paper Industries
pV	Proportion of Viable seeds
T_{50}	Time taken for 50% of the seeds to germinate

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION

1.1 Invasive alien species

The deliberate or unintentional introduction of new species by humans is a leading cause of the global biodiversity crisis (Wilcove *et al*., 1998). Invasive species are defined as naturalised alien plants outside their native range as a result of relocation and have the ability to produce very large numbers of offspring at considerable distances from parent plants (Richardson *et al*., 2000). The most aggressive invaders can spread far from parent plants and cover large areas. Up until the 19th century, formidable hindrance to immigration and emigration of species by mountains and oceans led ecosystems to evolve in relative isolation. Increased rates of human movement around the world saw the intentional introduction of alien species (Wilcove *et al*., 1998). Today's spread and global trade of species which are backbones of horticulture, agriculture and forestry act as constant sources of alien invasive species.

Invasive aliens include a variety of plants from aquatic weeds such as *Eichhornia crassipes* commonly known as the Water Hyacinth, to large trees from genera such as *Eucalyptus* and *Acacias*. Such plants in their own native ecosystems are constrained and of no harm but, when introduced into foreign habitats can cause enormous damage. Some invasive species termed "transformers" (Richardson *et al*., 2008) can create dramatic and unexpected shifts in the dynamics of ecosystems. The resemblance of some invaders to "ecosystem engineers" has been pointed out due to the devastating consequences they can have on ecosystem dynamics (Richardson *et al*., 2000). The negative impacts of invasive species have significant costs to economies. The worldwide total costs of damage created by invaders and subsequent control programmes is approximately USD$314 billion per year (Pimentel, 2002). In South Africa, at least 200 plants species are known to be serious or potentially serious invaders and this list of invaders continues to grow on a regular basis (Neil *et al*., 2004).

A considerable number of terms have been used to describe various aspects of biological invasions, sometimes leading to misuse and confusion. Many recent contributions have debated the relative merits of various terms in invasion biology (Richardson *et al.,* 2000). Invasive plants are defined as alien plants that yield large quantities of reproductive offspring at huge distances from parent plants whilst weeds are plants not necessarily aliens that grow in sites where they are not wanted usually having detectable economic and environmental effects (Richardson *et al*., 2000). According to Randall (1995) 'environmental weeds' are alien plant taxa that invade natural vegetation usually adversely affecting native biodiversity.

In South Africa the Conservation of Agricultural Resources (CAR) Act assesses alien plants in terms of how invasive they are using an invasiveness index which ranges from 1 (least invasive) to 5 (most invasive). This and other information (for example, the economic value of the plant) is then used to place aliens into one of three CAR categories which define of how they can be legally used and propagated. Category 1 plants should not be found on land or inland water surface other than in biological control reserves and may not be planted or propagated for any reason. Category 2 plants are invasive, but serve a commercial purpose so all reasonable steps must be taken to curtail the spread of these plants outside demarcated areas (Department of Agriculture, Forestry and Fisheries – DAFF, 2000).

Category 3 plants must not occur on any land or inland water surface except in a biological control reserve. However, plants already in existence at the time of commencement of the regulations may continue to exist, provided they are not within 30 metres of the 1:50 year flood line of any type of inland water. Table 1.1 below shows some of the major invasive trees in South Africa, the areas affected, their relative invasiveness, and the management category they fall into. The portion of plantation for each commercial plantation species is there for comparison purposes. To compare the effect of time on affected areas the year of introduction is also shown. Both *Pinus canariensis* and *Acacia mearnsii* are very serious invaders (Invasiveness index of 4) but because they are valuable economically, they fall into the same CAR category as *Eucalyptus grandis*, which is not considered a serious invader.

Table 1.1 *The degree of invasiveness of some selected alien trees in South Africa.*

Species	Area planted (ha)	Year introduced	Area invaded (ha)	Invasiveness index	CAR Category
Pinus canariensis	3 498	1878	unknown	4	2 Invader
Acacia mearnsii	106 687	unknown	2500 000	4	2 Invader
Eucalyptus grandis	280 823	1890	unknown	1	2 Invader
Eucalyptus lehmanni	unknown	1896	unknown	4	1 Weed

Indication of invasiveness: 5 = highly invasive; 1 = less invasive

CAR category: 2 = can be planted for economic use, 1 cannot be planted or propagated.
Sources: Duggan and Henderson, 1981; Dept. of Agriculture, Regulation No. 15, 2000.

1.2 Determinants of the 'invasive potential' of a species

One of the most fascinating questions in ecology that has been the focus of increased research efforts in the last 50 years is what controls invasiveness of alien species (Richardson and Pysek, 2008). Potential determinants of invasiveness that are frequently studied include introduction history, species traits, and ecological and evolutionary processes which are described below.

1.2.1 Residence time

Studies on introduction history ask, for example, whether invasiveness is associated with propagule pressure (the number of individuals introduced and the frequency of introduction events). The introduction of alien species in South Africa dates back to the middle of the seventeenth century. The invasion probability of a species is usually high if it was introduced a long a time ago (long residence time).

Residence time together with other stochastic factors determines the ability of a species to express its invasion potential and when it will invade (Rejmánek *et al*., 2005). Over 100 000 km^2 have been invaded by alien trees, which is more than 8% of South Africa's total area (van Wilgen *et al*., 2001).

1.2.2 Ecological and evolutionary processes

Invasive species show enhanced growth and vigour in the adventive range following introduction (Blossey, 1993). The most common explanation for this phenomenon is that the natural enemies that are found in the native range do not follow the migrating species hence the species will not be having enemies in their new range. This is known as the escape from biotic constraints hypothesis also known as the "escape from enemy" hypothesis. This hypothesis generally highlights that species in their native range are suppressed by natural enemies and immigrate leaving their enemies behind. However, alien success will depend on potential enemies in the new range. The *Chrysanthemoides* genus (a shrubby daisy found on the west coast) has a centre of diversity in South Africa with no problems of invasion but *Chrysanthemoides monilifera* is invasive in Australia because of few "enemies" in Australia (Richardson and Pysek, 2008).

1.2.3 Abiotic constraints

Species are sometimes introduced to environments that are not very similar to their native environments. This can hinder or help the invasive process: For example frost is an environmental barrier to distribution and limits the geographical range of many invasive species (Bruelheide, 2002). Population differences in frost resistance have been noted for invasive species such as *Buddleja davidii* (Ebeling *et al*., 2008). On the other hand, there are many examples of species from higher-resource environments invading into low-resource environments and dramatically altering ecosystem properties. The extent to which the abiotic environment limits alien spread appears to depend on particular circumstances, but many invasive species have a larger climatic niche than in their natural habitat.

A few studies have shown that in low-rainfall environments invasiveness is decreased (Alpert *et al*., 2000, Stohlgren *et al*., 2001) and it has been shown that nutrient enrichment strongly supports the spread of alien species in low fertility shrublands in south-eastern Australia

(Lake and Leishman, 2004). It has been agreed that invasive species' fitness can be enhanced more than native species by resources such as nutrients and light (Davis *et al*., 2000).

1.2.4 Species traits

There are many studies that aim to determine the particular functional traits that are associated with invasive species –such studies ask, for example, whether invasiveness is associated with fitness or dispersal-related characteristics. Many attempts have been made to construct lists of common traits shared by successful invaders. The hope behind such efforts is clear: detect a broad list of traits that, for example, invading insects, aquatic vascular plants, or birds share as a group, and then perhaps the identity of future invaders could be predicted from these taxonomic groups (Mack *et al*., 2000). Although there are exceptions, the common traits shared by many invasive species include the following: they thrive on disturbance; they do not have specific or narrow growth requirements (habitat generalists), they have short generation times and produce copious amounts of seeds which are viable.

1.3 The invasive potential of *Eucalyptus* in South Africa

South Africa has become the third largest and oldest plantation resource in the southern hemisphere (Swain and Gardner, 2003). The introduction into South Africa of exotic forest tree species with much faster growth rates than indigenous species brought an advantage to the timber industry, but the potential for these introduced plantation species to invade needs to be assessed and monitored. Approximately 149 *Eucalyptus* species had been established in South Africa by 1940 (Forsyth *et al*., 2004). Many species of *Eucalyptus* are fast growing and produce high value timber and they have been used by the South African forestry industry since the late 1800s. Despite this, they have not been nearly as successful in invading alien environments as other widely planted trees such as pines (Forsyth *et al*., 2004; Higgins *et al*., 1998) and legumes, many of which have become serious invaders in many parts of the world.

Although most *Eucalyptus* are not currently highly problematic invaders in South Africa they are still listed as potential invaders in many national and international lists (Richardson *et al*., 1994; Dept. of Agriculture, Regulation No. 15, 2001) and have been targeted for invasive alien plant clearing programme for the past 15 years in South Africa. In Australia, members of the genus *Eucalyptus* dominate in nearly all environments – from forests, to arid

shrub lands (Forsyth *et al*., 2004; Crisp *et al*., 2012). About 90% of the whole complex of the Australian vegetation is dominated by the genus *Eucalyptus* (Jacobs, 1976). Being the dominant canopy trees they have impacted the functional and structural ecology of Australia and they have several characteristics that make them particularly capable of becoming canopy dominants – rapid growth rates and vigorous response to injury. Just from looking at their functional dominance in Australia one might expect these species to be vigorously invasive in many places around the world. There is a weak, but significant correlation between the number of plantations of 57 *Eucalyptus* species plantations in southern Africa and the numbers of records of spontaneous occurrence outside plantations (Poynton, 1979; Rejmanek, 2000). The more frequently cultivated a species is the greater chance it has to become invasive.

The study assessed invasion potential of *Eucalyptus grandis* (Rose gum) in Mpumalanga. Historically, *Eucalyptus grandis* has been the most important hardwood for the South African forestry industry. *Eucalyptus grandis* was brought to South Africa in 1890, and by 1973 it represented about 75% of all *Eucalyptus* species planted in South Africa (DAFF, 2000). It was also introduced to a lot of other countries in Africa from 1890-1920 (Jacobs, 1976). *Eucalyptus grandis* flowers most of the times and generally gives little honey surpluses. Large quantities of its wood have been used for general construction and for the building of boats. The fibre is used for manufacturing sulphate pulp.

Interactions between range condition and invasion susceptibility, including drivers of vegetation pattern, degradation and invasion, are poorly understood, but remain very important for conservation and the sustained utilisation of rangelands. Untangling the complex determinants of *Eucalyptus grandis* invasive success in South Africa is useful for improving our understanding of plant invasions. When looking at aspects of invasions, it is useful to conceptualize processes that limit or facilitate invasions as an invader negotiating a series of barriers (Kruger *et al*., 1986, Richardson *et al*., 2000). This study aims to find out why *Eucalyptus grandis*, has not expressed its invasion potential in South Africa. Their low performance as invaders is puzzling.

1.4 Objectives

In this project I used available theory on the qualities that characterise invasive species to assess the invasive potential of *Eucalyptus grandis*. Following from this I used a field study to determine whether there is any indication that it is in fact, invading from plantations in Mpumalanga, and if so, which ecological processes affect this invasion potential. This study focused on the following environmental factors: frost and pests to assess the impact these factors could be having on the invasive potential of *Eucalyptus grandis.*

- Objective 1: Use the theory of invasiveness introduced above (and see Table 1.2) to test whether theory would expect *E. grandis* to become a serious invader.

- Objective 2: Quantify the rate of spread of *E. grandis* into neighbouring vegetation from plantations under various environmental conditions in Mpumalanga.

Table 1.2 *Summary of our understanding of the drivers of invasion, and what is known about E. grandis in this regard.*

Driver of Invasion	**Theory**	**What is known about *E. grandis***	**What was done in this project**
Invasive species traits	High reproductive Potential	Not known	Seed germination study
	High regeneration and recruitment levels	Not known	Studied generation times and size-class distributions
Environmental suitability for invasion	Thrive in new environments that do not have biotic constraints	Attacked by snout beetles and *Leptocybe invasa* (Oballa *et al*.,2010)	Checked the presence of pests
	Thrive in environments with similar abiotic conditions to native range	Sensitive to frost (SAPPI, 2006)	Studied the impact of frost
Invasion history	Long residence time Should be usually more than 50 years	Was introduced in 1890 (Dept. of Agriculture, 2000)	Due to long invasion history this was not tested

Hypotheses

- Hypothesis 1: *Eucalyptus grandis* is not a serious invader because its seeds have low vigour and or it has long generation times.
- Hypothesis 2: The rate of spread of *Eucalyptus grandis* is low because it is grown in areas which are not environmentally optimal.

1.5 Structure of the Research report

This chapter was the general introduction to the Research report giving some theoretical background of the research. The research is written up as a series of chapters which address different components. Chapter 2 focuses on the invasive species traits addressing hypothesis two and Chapter 3 is about environmental suitability addressing the first hypothesis. The study sites and methods are described in detail in each data chapter, so there is inevitably some repetition in the material and methods section of Chapter 2 and 3 because of how this research paper is structured. Chapter 4 has the overall conclusions of the research but Chapter 2 and 3 have their own conclusions.

CHAPTER 2

ASSESSING INVASIVE SPECIES TRAITS

ABSTRACT

Reproductive potential plays a vital role in the invasion success of plants species. A germination study in the lab was done to assess the vigour of *Eucalyptus grandis* seeds. The seeds were collected from trees in Graskop and White River. The seeds from different trees at each site were mixed together and twenty seeds were placed on a petri dish (5 replicates for each location). The numbers of seedlings germinating were counted at 24hr intervals and the proportion of viable seeds (pV), germination index –GI and the time taken for 50% of the seeds to have germinated (T_{50}) were calculated. Generation time was also studied as one of the reproductive potential factors. During a demographic study we also noted whether there are any signs of flowers/fruits on each tree, so as to have an idea of the size when *E. grandis* starts to become reproductively mature. A multiple logistic regression analysis was performed in R where flowering state (yes/no) was predicted by the two explanatory variables (height and location). Interactions between height and location, to see whether size of first flowering was influenced by the environmental conditions of the site were also assessed. The explanatory power of three different logistic models: one that only considered height, one that considered height and location (Graskop/White River) and one that considered an interaction between height and location were compared. The Bayesian Information Criterion (BIC) was used to compare the models. For each site I determined the height when 80% of the trees were reproductively mature, and using literature on growth rates of *E. grandis* at the two locations I converted this height to an estimated generation time. *Eucalyptus grandis* is expected to be a serious invader as evidenced by the high seed viability (97%) and short juvenile periods (50% of individuals mature within 3 years)

2.1 Reproductive potential: Germination and generation time

Many studies have established that attributes related to reproductive capacity and vegetative reproduction are important associates of invasiveness (Richardson and Cowling, 1992; Crawley *et al*., 1996). In particular, the production of copious amounts of viable seeds is one of the common traits shared by invasive species (Richardson and Rejmánek, 1996). Large quantities of viable seeds increase the chances of germination and dispersal to new environments thus increasing population growth of the species. Similarly, age at first reproduction has vital consequences for rates of population growth (Inouye *et al*., 1980). A short generation time (age at first reproduction) results in high rates of population increase and will also influence how easy it is for an alien species to spread into a new environment (dispersal rates).

Many Eucalyptus species produce large quantities of seeds (Williams *et al*., 1997) and this makes their failure as invaders surprising. It is possible that these seeds are not particularly viable in the new environment –introduced Eucalyptus species are often propagated from cuttings (AFTD, Agro-Forestry-Tree Database 2012) so their seed viability might not be very high. Similarly, although Eucalypts have high growth rates there is no information available on how quickly new saplings become reproductively mature, and whether this is influenced by environmental conditions.

Aims of this chapter

A germination study was undertaken to assess the vigour of *Eucalyptus grandis* seeds. The aim was to test how quickly Eucalyptus seeds germinate, and what proportion of their seeds is viable. I also tested for differences in seed viability between the two populations in my study, although I did not expect to find this because presumably the genetic material in this plantation species is not very variable. Height of first flowering was used to assess generation time in the *E.grandis* populations. By linking this to growth rate data I aimed to quantify generation time for this species, as well as to determine whether flowering age varied between the two populations in my study.

2.2 Materials and methods

2.2.1 Study Area

The Highveld region of South Africa contains large expanses of plantation forestry. My study took place in Mpumalanga province, South Africa, near the towns of Graskop and White River (Figure 2.1). The sites in Graskop (24 ° 55' S, 30 ° 46' E) are generally at high altitudes (1600 m a.s.l) compared to those in White River (25 ° 09' S, 31 ° 02' E) – 953 m a.s.l, and are more frequently exposed to cold temperatures. Sites at Graskop experience "heavy" frost (See Chapter 3- Figure 3.3) in more than 80% of years, whereas in White River severe frost occurs less than 20% of the time (Schulze and Maharaj, 2007).

At each location I identified five replicate study sites – areas adjacent to a mature plantation that have not been cleared or managed for at least 8 years. These sites were chosen to be as similar as possible in terms of management history and plantation age except that I tried to sample the full range of landscape features (i.e. some sites running from the plantation edge down into the valley, and some sites running from the plantation edge out into the crest). This is because from driving around it appeared that *E. grandis* spread more easily out of plantations into the river than into the grassy crests.

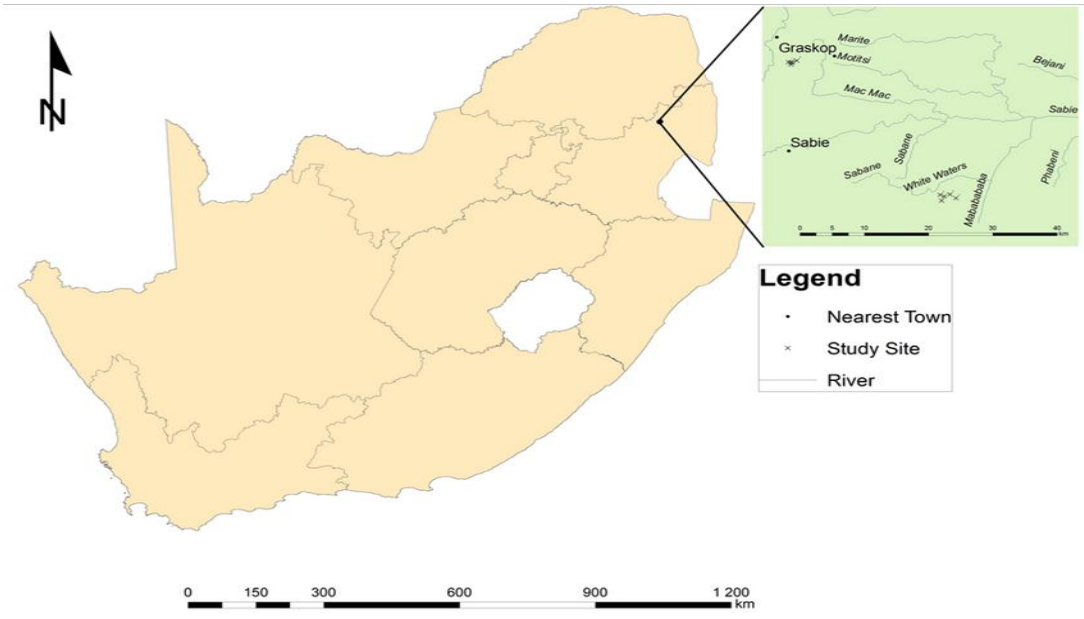


Figure 2.1 *Site map showing sampling locations and the nearby tributaries.*

2.2.2 Seed viability

Seeds of *Eucalyptus grandis* were harvested from mature fruits of a random selection of 5 trees in Graskop and White River to be germinated in the lab to assess their viability. The seeds from different trees at each site were mixed together. The counting process of the seeds was tiring as the seeds are very small. Twenty seeds were placed on a petri dish (5 replicates for each location). Two 90mm sheets of filter papers were placed in the lid of the 90mm petri dishes; the seeds were placed in the lid and moistened with distilled water. A third sheet of filter paper was used to cover and the base of the petri dish was used to seal. Incubation of the seeds was done at 25°C.

The number of seedlings germinating were counted at 24hr intervals and continued until there was no change in germination percentage for ten days. A seed was considered germinated if it had radicle longer than 1mm. The proportion of viable seeds (pV), germination index –GI (Zanjan *et al*., 2012) and the time taken for 50% of the seeds to have germinated to 50% (T_{50}) germination were computed by using the following formulas:

$$pV = N/S$$

Where N is the final number of germinated seeds and S is the total number of seeds placed in each dish.

$$GI = \Sigma (T_i \times N_i) / S$$

Where, T_i is the number of days after planting, N_i is the number of seeds germinated on day I, and S is the total number of seeds placed in each dish (Zanjan *et al*., 2012).

$$T_{50} = t_i + (0.5\ N - n_i)\ (t_i - t_j) / n_i - n_j$$

Where, N is the final number of germinated seeds, n_i and n_j cumulative number of seeds germinated by adjacent counts at times t_i and t_j when, ni < 0.5N and < nj > 0.5 N. The GI is a measure of viability and seed vigour that incorporates both rate and amount of germination (Seednet, 2014). Seed lots with greater germination indices and which take short time to germinate are considered to be more vigorous. These data were compared with information in the literature on the viability of seeds from similar environments, and on the viability of

typical invasive species. The data were submitted to Mann-Whitney U test using R statistical package to determine if any of the measured parameters differed statistically between the Graskop and White River populations.

2.2.3 Generation time

During the demographic study (see Chapter 3 for details) we also noted whether there are any signs of flowers/fruits on each tree, so as to have an idea of the size when *E.grandis* starts to become reproductively mature. As we recorded this as a yes/no variable it was assessed using a logistic model using the generalised linear modelling function in R (glm). A multiple logistic regression analysis was performed where flowering state (yes/no) was predicted by the two explanatory variables (height and location). I also looked for interactions between height and location, to see whether size of first flowering was influenced by the environmental conditions of the site.

I compared the explanatory power of three different logistic models: one that only considered height, one that considered height and location (Graskop/White River) and one that considered an interaction between height and location. The Bayesian Information Criterion (BIC) was used to compare the models (Burnham and Anderson, 2004). For each site I determined the height when 80% of the trees were reproductively mature, and using literature on growth rates of *E. grandis* at the two locations I converted this height to an estimated generation time. This was then compared with information on the typical generation times of species in similar environments, and of typical invasive species.

2.3 Results

2.3.1 Seed germination

Of all the *E. grandis* seeds harvested 97% were viable and there was no significant difference between the proportion of viable seeds between the sites, Graskop and White River. There was also no significant difference between the germination indices (Figure 2.2a and 2.2b) in Graskop and White River population (Mann-Whitney U test: P= 0.29).

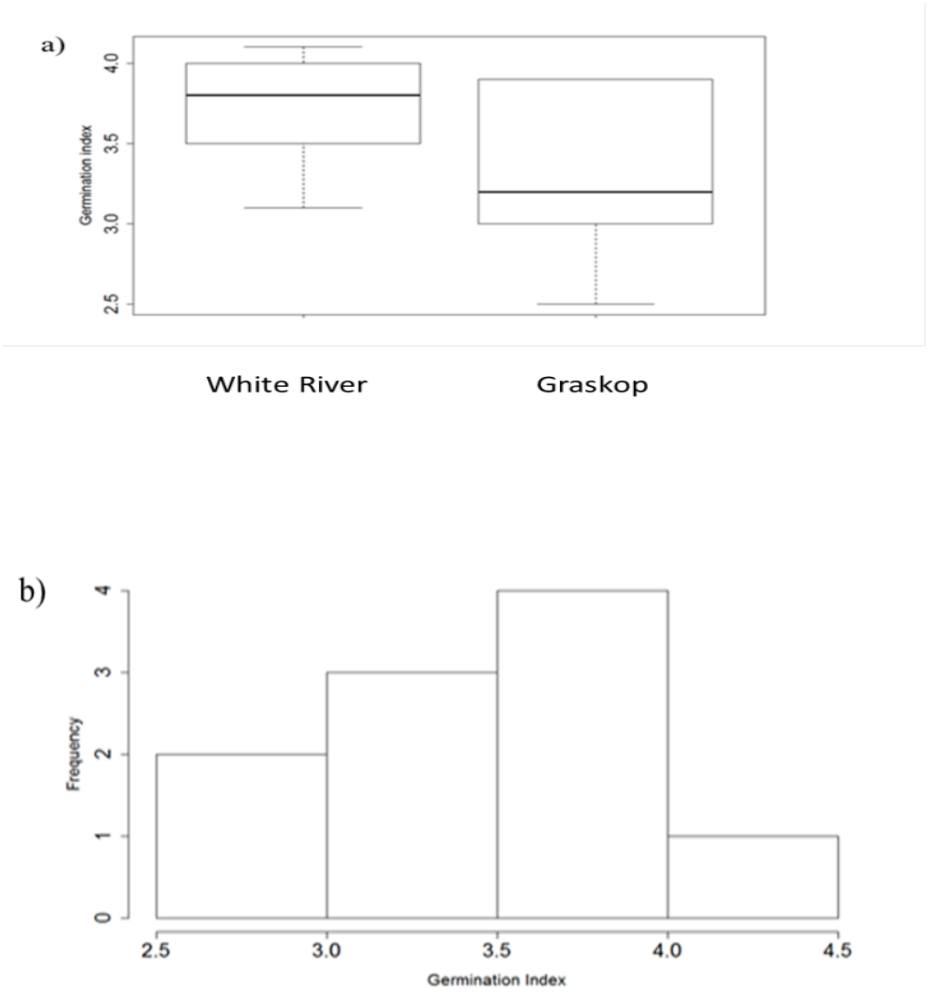


Figure 2.2 *a) Boxplots showing germination indices of Graskop and White River seeds; b) Histogram showing the range of germination indices recorded in the 10 replicate samples (both White River and Graskop are included here as there was no difference between sites).*

The time taken for 50% of the seeds to germinate ranged from 1.83 to 4 days (Figure 2.3b), but again there was no significant difference between the germination rates between the two sites (Mann-Whitney U test: P= 0.141 – Figure 2.3a).

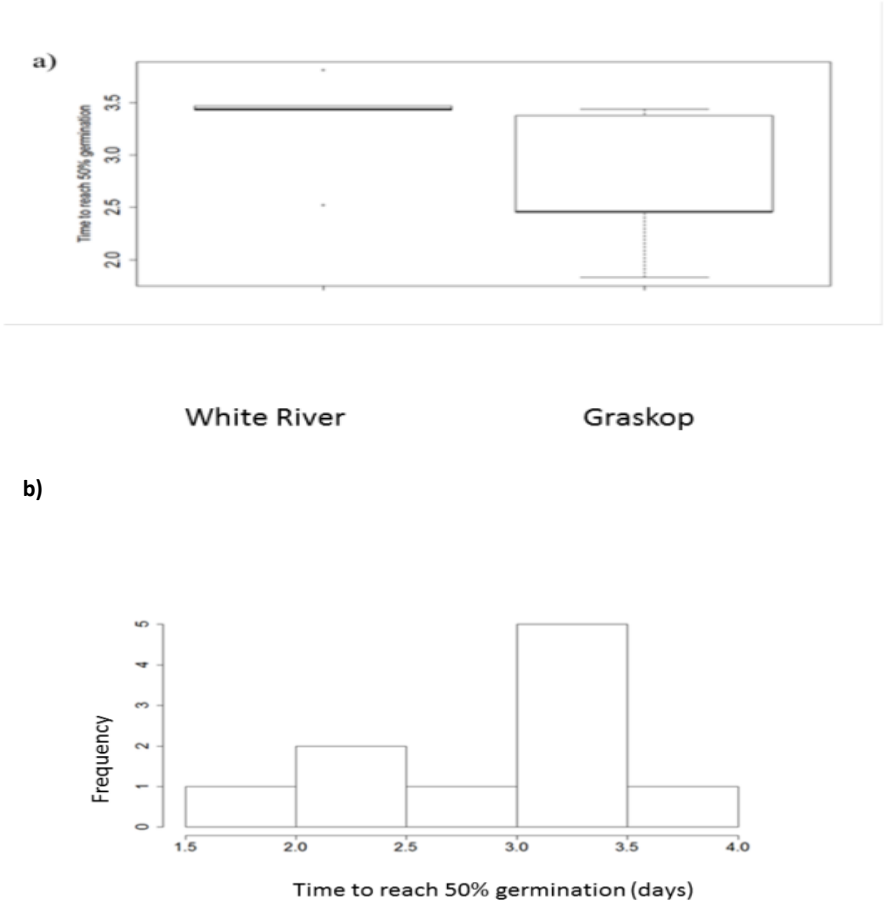


Figure 2.3 *a) Boxplots showing times to reach 50% germination; b**)** Histogram of the time taken to reach 50% germination.*

The germination parameters of *Eucalyptus grandis* are similar to those of known invasive species (Table 2.1).

Table 2.1 *Comparison of the germination of E. grandis seeds to other known invasive species seeds.*

Species	Mean (sd) GI	Mean (sd) T_{50} (days)	Mean (sd) Viability (%)
E. grandis	3.5 (0.53)	3 (0.65)	97% (0.06)
Acacia saligna	unknown	4	84%
Clausena excavata	unknown	4	98% (Vieira *et al*., 2010)
Mikania micrantha	2.4	unknown	90% (Yang *et al*., 2005)

2.3.2 Generation time

There was quite a bit of variability in flowering height in the populations – some very small individuals (< 2m) did have flowers/fruit, but other individuals greater than 20m showed no signs of being reproductively active (Figure 2.4). For every one metre increase in height the odds of having flowered increase by 1.18 times (exp (0.16934)). Increase in the height of the trees leads to greater probability of having flowers.

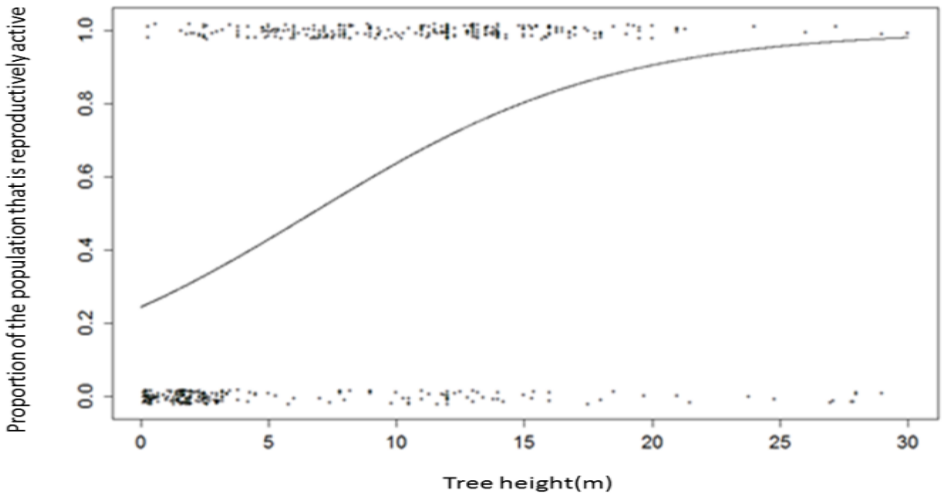


Figure 2.4 *Showing a logistic model fit to the relationship between tree height and whether a tree is flowering or not. Data are presented for both locations. The point data has been slightly adjusted on the Y axis (using the R function "jitter") so as to show the individual points.*

Of the three logistic models considered the one with the highest explanatory power included an interaction between height and location (i.e. the effect of height on flowering varied between Graskop and White River). This model (F~H+LOC+H*LOC) model had a BIC of 515 (Table 2.2) which was a great improvement on a model with height alone (BIC 594). Location independent of height was not significant and had no effect on the explanatory power. Therefore, although the average number of flowering trees in each location is similar, the height at which they start flowering at each site varies significantly (Figure 2.5).

Table 2.2 *Summary comparing the three logistic models.*

Model	% Variance	BIC	ΔBIC	Intercept	Height	Location	Height*Location
F~H	84	594	79	-1.1***	0.16***	-	-
F~H+LOC	84	597	82	-1.0***	0.17***	-0.33 ^{ns}	-
F~H+LOC+H*LOC	71	515	0	-2.8***	0.58***	2.62***	-0.53***

It appears that reproductive maturity occurs more quickly at White River than Graskop (Figure 2.5) with individuals ~ 6m tall having an 80% probability of being reproductively mature, whereas at Graskop it took until ~15m for 80% of the individuals to be reproductively mature. On the other hand, at Graskop a significant proportion (~20%) of the very small trees (<3m) were already flowering.

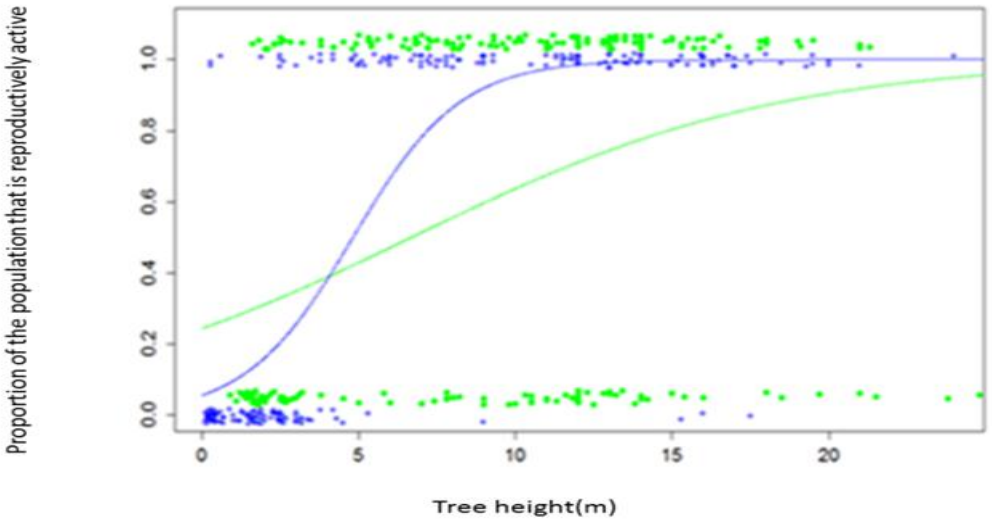


Figure 2.5 *Height at first flowering of Graskop sites (green) and White River sites (blue). The Graskop data has been shifted up slightly (using the R function "jitter") to make the comparison clear.*

The generation time of *E. grandis* reported the literature is 2-3 years (NSW Department of primary industry, 2010). Given that *E. grandis* can grow several meters a year (Oballa *et al*., 2010) the generation times measured in this study at White River are in line with other data and for Graskop slightly longer. Importantly, these generation times are in the same range of other known invasive species which causing a lot of problems, for example, the black wattle in South Africa (Table 2.3).

Table 2.3 *Comparison of the height at first flowering of E. grandis to other known invasive species.*

Invasive species	Generation Time
Eucalyptus grandis	2-3 years (NSW Department of primary industry, 2010)
Eucalyptus camaldulensis Dehnh	3 years (CAB International, 2000)
Pinus patula	2 years (Barrett and Mullin, 1968)
Acacia mearnsii (Black wattle)	20 months (FAO, 2014)

2.4 Discussion

Overall the findings presented here suggest that *Eucalyptus grandis* has some factors that potentially make it highly invasive. *Eucalyptus grandis* seeds are highly viable (>98%) and have shown to have high vigour as they reached 50% germination within four days. This is in line with the vigour found in known invasive species such as *Acacia saligna* and *Mikania micrantha* and indicates that seed vigour is definitely not a factor limiting the expansion of *E.grandis* into natural vegetation outside plantations. This is despite the fact that most *E. grandis* material planted in South Africa is grown from cuttings (AFTD, 2012) so the high vigour of the seeds must be a characteristic of the original *E. grandis* stock that was brought to the country, rather than something that has been selected for by breeding.

The height of *Eucalyptus grandis* plants had a significant impact on flowering and the results suggest that *Eucalyptus grandis* has a short generation time as > 50% of the populations were flowering by the time they were 5 metres tall (i.e. generation times of 2-3 years). Interestingly, we found a significant difference in the generation times between the two locations – with plants in White River flowering at smaller sizes overall than plants in Graskop. This implies that the Graskop populations delay allocating resources to reproduction for longer than populations in White River – perhaps because when they are small they need to allocate resources to carbon storage and recovery from damage by frost. On the other hand, the fact that some very small trees at Graskop were already flowering

might demonstrate that age, and not height, is a driver of flowering ability in these species, and that even very short resprouting trees can flower if they are old enough.
To understand this better requires that we investigate the population dynamics of the species (See Chapter 3).

Either way, the generation times implied by these flowering heights are similar, if not shorter than the generation times found in other woody invasive species (Table 2.3) indicating that this is also not a barrier to the spread of *E. grandis* into native environments. The high reproductive potential and short generation time of *Eucalyptus grandis* that we found in this study indicate that these reproductive traits should be no barrier to *E. grandis* becoming invasive (Richardson and Pysek, 2008). This raises the potential that currently non problematic *E. grandis* plants that have been sometimes categorized as 'sleeper weeds' could be more invasive in the future. Invasive species pose a big threat to protected ecosystems and were considered as one of the main threats to ecosystem integrity in the 2005 Millennium ecosystem assessment**.** Therefore if *E.grandis* has conditions that facilitate it to reach its full invasion potential it is most likely to cause major problems in ecosystems.

One limitation of this study was that it did not consider viability and germination in the field. A further study could sample soil close to and far away from the plantation edge and perform some germination studies to look at the seed bank of *E. grandis* and the viability of *E. grandis* seeds in situ. Similarly as *E. grandis* plantations in Mpumalanga are usually in grasslands, it might be useful to consider the ability of *E. grandis* seeds to germinate and establish within a grass sward. As *E. grandis* is able to occur in savanna environments in Australia, competition with grass is likely to be something that the seedlings are able to survive, but it should still be studied.

2.5 Conclusion

This chapter assessed the reproductive traits of *E. grandis* and compared these traits to known invasive species. The traits assessed were: viability of the seeds, the time needed to germinate and time needed by *E. grandis* individuals to be reproductively mature. The results showed that *E. grandis* is expected to be a serious invader as evidenced by the high viability of the seeds (97%) and the short time needed to be reproductively mature (50% of individuals mature within 3 years). The germination study conducted in this chapter could have been

improved by collecting seeds from individual trees and testing the population-level variability in the viability and germination rates of seeds. A further study on germination eco-physiology of potential invasive species is necessary where light exposure, temperature and soil depth can be considered.

CHAPTER 3

ENVIRONMENTAL SUITABILITY

ABSTRACT

Abiotic factors can also play a pivotal role in the invasion potential of a species. The population dynamics of *Eucalyptus grandis* was assessed on two locations that are exposed to frost differently, Graskop and White River. I assessed the rate of spread of *E. grandis* into neighbouring vegetation from plantations in Graskop and White River. Belt transects (5 by 50 metres) were laid out from the edge of the plantation into the natural veld in each of the naturalized populations that are next to the plantations. On each transect the height, distance along the transect, and stem diameter at 30 cm above the ground of all the *E. grandis* individuals encountered within 2.5 metres either side of the transect was measured and recorded. During the transect walks, the number of resprouting individuals and those with affected with pests were recorded. Mann-Whitney U-test was used to analyse the difference in diameters, number of resprouting trees, number of trees affected by pests and densities between the locations, Graskop and White River. Comparison between the size class distributions in Graskop and White River was made using the Kolmogorov-Smirnov test. To give a quantitative basis for comparison of population size structures, the Weibull function was fitted to diameter frequency distribution at each site using the fBasics package in R. The results showed that there is recruitment at both locations (c=1). The rate of spread of individuals at Graskop is slower than at White River as evidenced by the high numbers of individuals which are not reproductively mature in Graskop (44%) compared to those in White River (19%). Frost is one environmental factor that is probably negatively affecting the recruitment of populations as shown by the high number of resprouts in Graskop (46 %) compared to those in White River (11.6 %). Generally the results show the rate of spread is low.

3.1 Introduction

When an alien species is introduced into an environment that is similar to its native environmental niche, one would expect that biotic interactions would be the only factors controlling its spread and potential to be invasive. However, if it is introduced into an environment different from its native niche, abiotic factors might also limit its potential to spread. For example, *Eucalytus grandis* covers a much wider range of climates in South Africa than it does in Australia. However, it should be noted that in 1948 a map of silvicultural zones was developed as a basis for the rational interpretation of the results of many planting trials (Poynton, 1979). Trees were planted in carefully selected climate regions that would suit them and this increased their chances of becoming invasive. In South Africa, *Eucalyptus grandis* is found in altitudes that are higher and temperatures that are lower so this could possibly stop it from spreading. However, alien species have sometimes invaded habitats that are totally different from their native habitats; for example, the latitudinal ranges of naturalized Gramineae species are 15-20^0 wider than their natural ranges (Rejmánek, 2000) so understanding abiotic limits of invasion potential is complicated.

3.1.1 Climatic conditions of the native range of *E. grandis*

The natural occurrence of *Eucalyptus grandis* is from Newcastle, New South Wales and north to around Bundaberg, Queensland (Figure 3.1) on low slopes of fertile valleys and is usually found in open woodlands/grasslands fringing rainforests. The altitude is mainly from sea level to 600m, but up to 1100m in the tropical north (NSW Department of primary industries, 2010). The mean maximum temperature of the hottest month ranges from 24-30°C (Table 3.3) and mean minimum of the coldest month around 7.3-19.4°C.

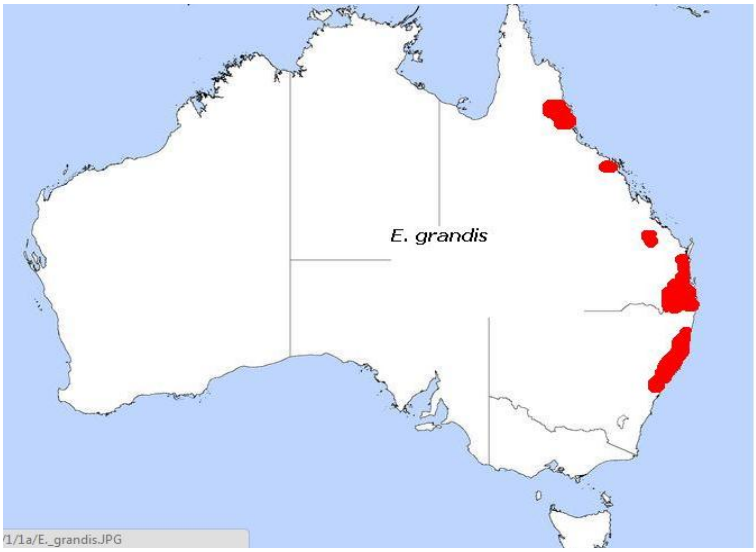


Figure 3.1 *Distribution of Eucalyptus grandis in Australia (Florabank, 2013).*

Adults of *E .grandis* are known to be frost sensitive (see Table 3.1 below) but can endure moderate frost up to 20 times a year (NSW Department of primary industries, 2010). Most eucalypts evolved in their native range in Australia where there are shortages of water for substantial parts of the year and have thus adapted to drought stress.

Table 3.1 *Tolerance of E.grandis to frost (NSW Department of primary industries, 2010).*

Frost	**minimum temperature (°C)**	***E. grandis* reaction**
Light	> 2	Tolerates
Medium	2 to -2	Tolerates
Heavy	-2 to 6	Avoid
Extreme	> -6	-

3.1.2 Climatic conditions where *E.grandis* is found in South Africa

South Africa's *Eucalyptus* plantations cover a broad range of environments, particularly in the subtropical and the humid warmer temperate regions (Otim, 2008). Comparing the distribution maps below (Figure 3.2), it can be clearly seen that plantation areas fall into high rainfall zones. The fast growth rate of *Eucalyptus grandis* has resulted in *E. grandis* being the most extensively planted hardwood in these regions. However, the increased demand for

hardwoods has resulted in the expansion of hardwoods into sites that are colder and drier, or warmer and drier, than the conditions *E. grandis* evolved in in Australia (Table 3.2). The total area of potential afforested land is also expected to increase due to climate change (Schulze and Kunz, 2010).

Table 3.2 *Occurrence of frost in the native range of E. grandis and where is it is found in South Africa (Otim, 2008).*

Location	Frost Occurrence
New South Wales (Australia)	Infrequent
Newcastle (Australia)	Infrequent
Queensland (Australia)	Infrequent
Limpopo (South Africa)	Infrequent
KwaZulu-Natal (Africa)	Frequent
Mpumalanga (South Africa)	Infrequent: White River Frequent: Graskop

Table 3.3 below compares the climatic conditions of where *E. grandis* is found in Australia and South Africa.

Table 3.3 *Comparisons of climatic data for the native range of Eucalyptus grandis and where it is found in South Africa.*

Climatic condition	Australia	South Africa
Altitude (m a.s.l)	0 – 1100	900 – 1700
Mean monthly maximum Temperature (°C)	24 – 30	25- 27
Mean monthly minimum Temperature (°C)	7.3 – 19.4	5- 6
Mean Annual Temperature (°C)	19 –23.3	17–22
Rainfall (mm)	725–3750	900 – 1270

Sources: SAPPI, 2006; NSW department of primary industries, 2010; Australian Government Bureau of Metrology, 2014.

According to Swain and Gardner (2003) the Mean Annual Temperatures (MATs) that are below 18°C and altitudes ranging from 1050m to 1300m are not suited for planting *Eucalyptus grandis.* Cold tolerant species such as *Eucalyptus nitens* are generally suited to sites above 1200m which are prone to frost and frequent snowfalls. Frost is the occurrence of ice crystals either when dew freeze or water vapour changes into ice. It is also defined as surface temperature of less than 0°C (Snyder and de Melo-Abreu, 2005). The frequent frosts in the Highveld of South Africa might be a barrier to the spread of *E. grandis* because seedlings and saplings are "top killed" by frosts. Most of this frost damage occurs in winter in the form of tip scorching or total scorching, depending on the severity and frequency of the frost (Otim, 2008). Scorch forms on the leaves as an irregular browning, yellowing, or bronzing of tissues along the margins and tips of leaves (Integrated Pest Management, 1997). If the frost is severe the affected leaves will wither and the shoots may die back.

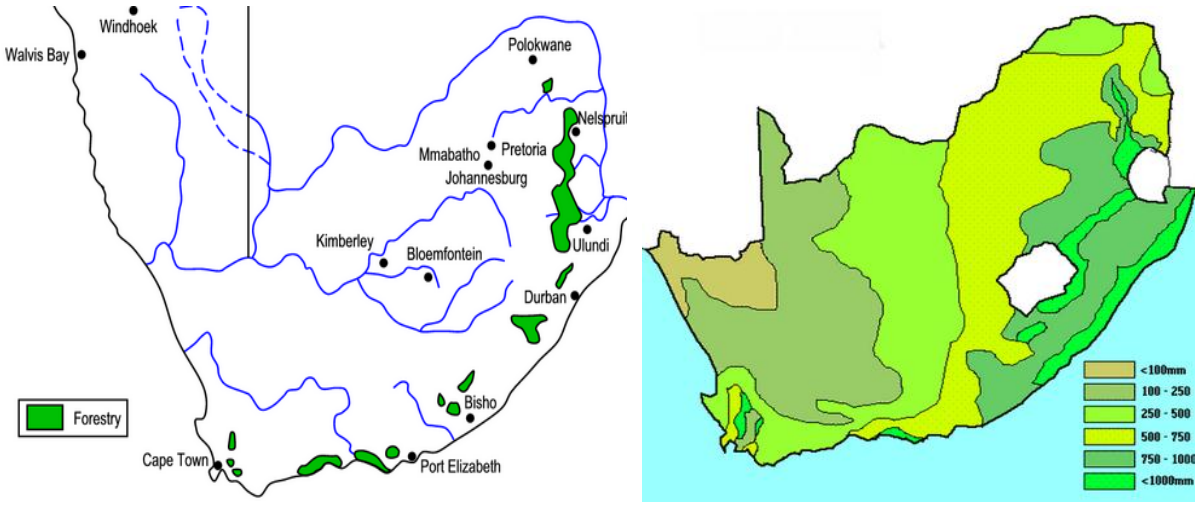


Figure 3.2 *Distribution of plantations in South Africa and the rainfall distribution map (Department of Agriculture, Forestry and Fisheries, 2000).*

The summer rainfall regions where most of the eucalypt plantations are found has three recognised climatic zones corresponding to: general snow and frost risk across the landscape (cool temperate), frost risk confined to low lying areas only (warm temperate) and frost free areas (sub-tropical) (Smith *et al*., 2005). The majority of these commercial plantations of eucalypts are found in the sub-tropical regions which usually has light frost at elevations over 600m and with annual rainfall over 800mm.

The Highveld of Mpumalanga and some areas in KwaZulu-Natal experience frost damage especially in the valleys and drainage areas (Figure 3.3). Most frost damage occurs in winter in the form of tip scorching or total scorching depending on the severity and frequency of the frost (SAPPI, 2006). Snow damaged plantations are more vulnerable to fires and are prone to consequential damage through pest or disease attacks. Low temperatures, severe frost, occasional snow and unique high altitude pests are known to be associated with high altitude sites where plantations are found (Swain and Gardner, 2003). Four major snow events in the forestry areas of South Africa have occurred in the past 30 years, on average a frequency of one event every 7.5 years (SAPPI, 2006).

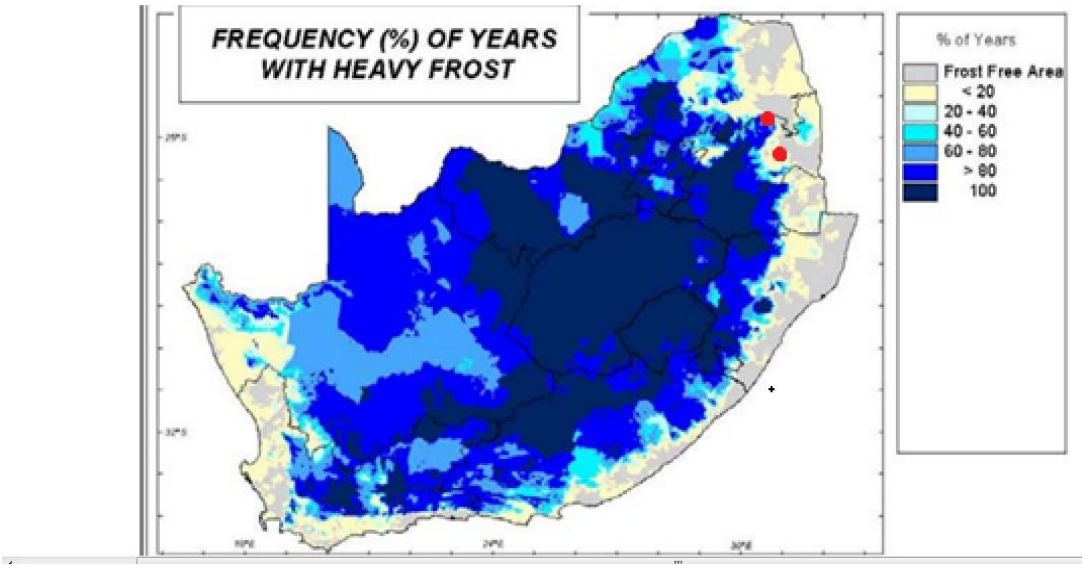


Figure 3.3 *Frost map showing the frequency of years with heavy frost and the study sites in red colour ("Heavy" frost is when the temperature of* $\leq 0^0$ *c is recorded on a Stevenson Screen assuming that the temperature on the ground would be even lower- Schulze and Maharaj, 2007).*

3.1.3 Fire and frost impact on *E .grandis*

I would expect recruitment and mortality rates of *E. grandis* to vary depending on factors such as fire and frost. Both fire and frost can damage above-ground biomass of small trees ('top-kill'), and therefore act to prevent trees from growing to adults. Seedlings of *E. grandis* are more sensitive to frost and fire than adults as these seedlings would not have attained a size that enables them to escape the most damaging impacts of frost and fire.

E. grandis is well adapted to fire – it resprouts vigorously and maintains a seed bank in its canopy for recruiting after fire. This means it probably would be able to withstand frost also, even though it is not exposed to it in its natural environment. In Queensland (Northern Australia) where *Eucalyptus grandis* is native, fire is a recurring element where most of the landscape is burnt every year. In South Africa, *Eucalyptus grandis* is also exposed to fire at pretty much the same frequency as in Northern Australia. The study sites for this project were located in grasslands where the fire return period is about 2-4 years (Figure 3.4), but managers try to keep fire out of plantations and will protect the areas around the plantations from fire.

Eucalyptus grandis is able to resprout after being affected by frost and fire, so these disturbances are unlikely to kill any but the smallest seedlings. According to Grady and Hoffman (2012) if a species has the ability to resprout then fire (or frost) decreases the plant size by killing the aerial biomass (topkill) and this may take years to return back to original form, so this could still slow rates of recruitment and spread of a species – particularly if they only reproduce when they have reached a certain size. Resprouts may remain in a suppressed state for a long time (Higgins *et al*., 2007), ensnared in a "fire trap" of persistent topkill and resprouting (Bond and Midgley, 2001). I would therefore expect to see some indication that frost/fire is slowing the spread of *E. grandis* – and more so in Graskop than White River as frost frequency depends on altitude – so would be higher at Graskop than White River.

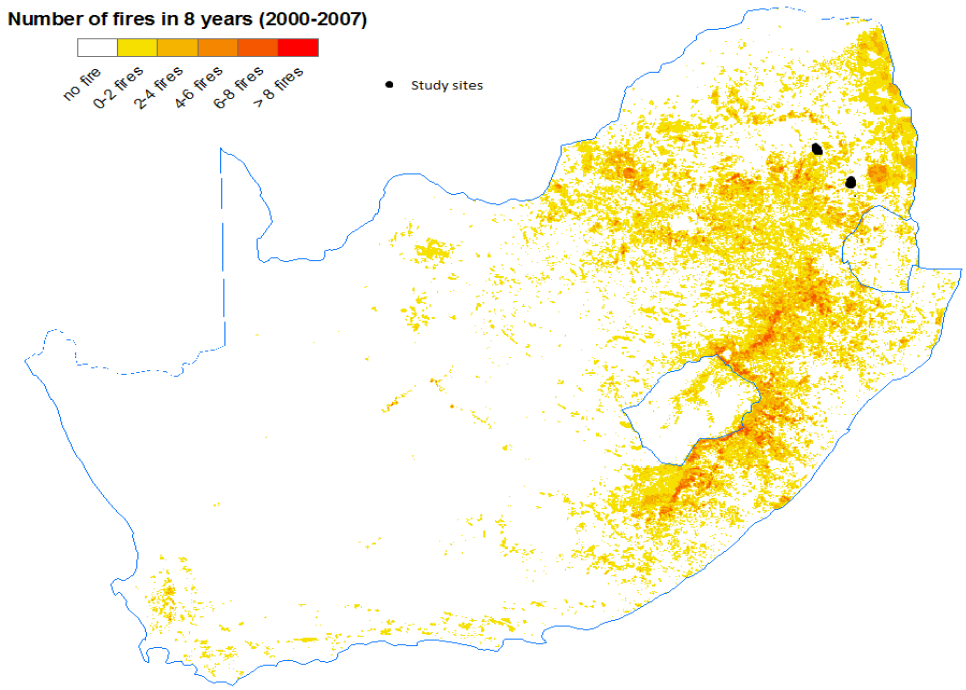


Figure 3.4 *Location of the study sites on a map of fire frequencies (Archibald et al., 2010).*

3.1.4 Population dynamics as a clue to identifying constraints on invasive species

According to Williamson (2006) the chances of moving from one phase of invasion to another is usually small. Many factors affect the chances of moving from one stage to another, propagule pressure and whether the introduction is intentional are two of the main factors (Williamson, 2006). There is disagreement about how to name the stages of invasion but there is some agreement on differentiating five main ones: bringing (import) into a country, release or escape in to the wild, establishing a population, spreading from an established population and becoming a problem that needs to be dealt with (Williamson, 2006). The stage between the arrival of a species in a new environment and its spread (i.e. post-introduction but pre-spread) has been considered differently by the invasion frameworks set out by Williamson *et al*., (2006) and Richardson *et al*., (2000).

Williamson-based schemes are implicitly population based; with the establishment stage focusing on the problems of small population viability whilst the Richardson scheme is individual based and deals with barriers that would hinder an individual from arriving at a new location (Blackburn *et al*., 2011).

In the establishment stage of invasion, bio-geographical and ecological factors come into effect and when it is the spreading stage there is need to consider both ecological and evolutionary factors. The invasion process is a succession of phases but the phases oftenly combine with one another. For example, there is a continuous extend between 'casual' (non-sustained populations) and 'established' (self-sustaining populations). Despite this, it does appear that invasion follows certain patterns, one after the other in succession (Williamson 1996, 1999, 2000; Richardson *et al*., 2000; Lockwood *et al*., 2005) and the invasion can be prevented at any stage in this process.

The rate of spread and pattern of non-indigenous species cannot be pinned on ecological factors alone; consideration should also be given to socio-economic factors (Williamson *et al*., 2003; Williamson *et al*., 2006). All of the factors that potentially influence invasion potential integrate at various levels and the most accepted factor of invasion is the 'fluctuating resources theory of invasibility' (Davis *et al*., 2000). This theory assumes that if an invader has access to resources and does not have fierce competition from native species for these resources then success of the invader is inevitable.

The size and age structure of a population is determined by the recruitment (or "birth") rates, growth rate and death rate (Prior, 2010). Identifying factors that influence population dynamics of species is important and plant populations can be seen as "spatial mosaics of structural phases which are always changing over time" (Everard *et al*., 1995). Size-class distributions give information on the proportion of a population that is at different stages of growth and can give insights into regeneration levels and recruitment bottlenecks of a population. In terms of invasive species, they could give insights into which stage of invasion a population is at, and what is preventing them invading. An inverse J-shaped curve - with more juveniles than adults and a smoothly declining function (Figure 3.5 below) is expected in a healthy recruiting population, because it allows for mortality and competitive effects on the probability of progressing to the next size class.

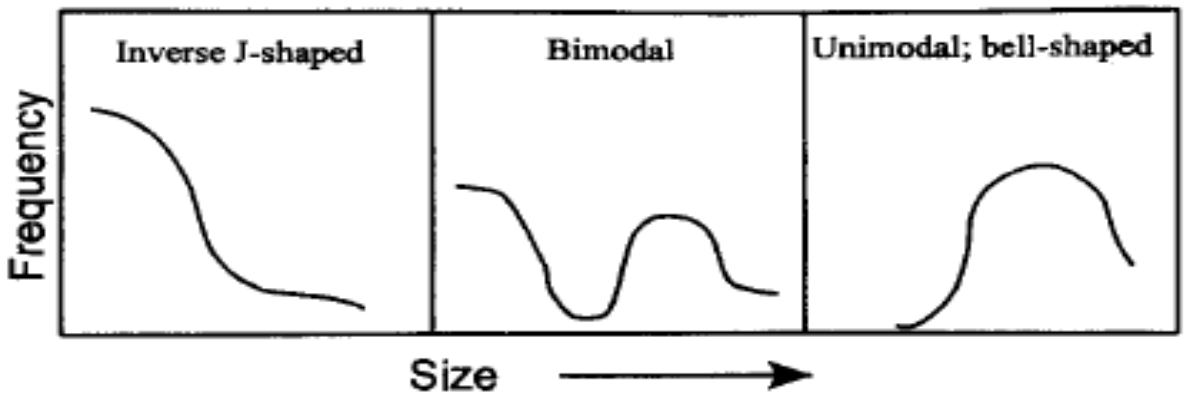


Figure 3.5 *Three possible curve shapes for size-class distributions (Everard et al., 1995).*

Demographic bottlenecks are usually deduced when there is a very steep slope between classes, indicating that something is preventing transition from one class to the next. These demographic bottlenecks can also result in bimodal or unimodal (Figure 3.5) size class distributions among plant populations (Lehmann *et al*., 2009) when the bottleneck is temporarily released. A u-shaped (bimodal) curve has got slightly more juveniles than adults indicating some form of recruitment but there is a sharp decline in the frequency of the middle aged class. This could indicate "cohort" recruitment – where the probability of moving between size classes depends on particular environmental conditions that happen seldom. The unimodal curve above shows the absence of juveniles indicating that there is no recruitment at all. This can be a special case of cohort recruitment, where something is preventing seedling establishment. If a population does not have any individuals in the smaller classes then it becomes difficult to maintain a relatively constant population.

Aims of this chapter

The previous chapter assessed the reproductive traits of *E. grandis* to test if it has the potential to become a serious invader. This chapter looks at the role of the environment in the invasion potential of *E. grandis*. The main aim of this chapter is to assess the rate of spread of *E. grandis* into neighbouring vegetation from plantations under various environmental conditions in Mpumalanga. Given that *E. grandis* plantations appear to occupy environments that are fairly similar to those in which it is found in Australia we wanted to test whether there was any indication that environmental conditions were limiting its spread in South Africa. In particular, as mentioned in the introduction, the main difference in environmental

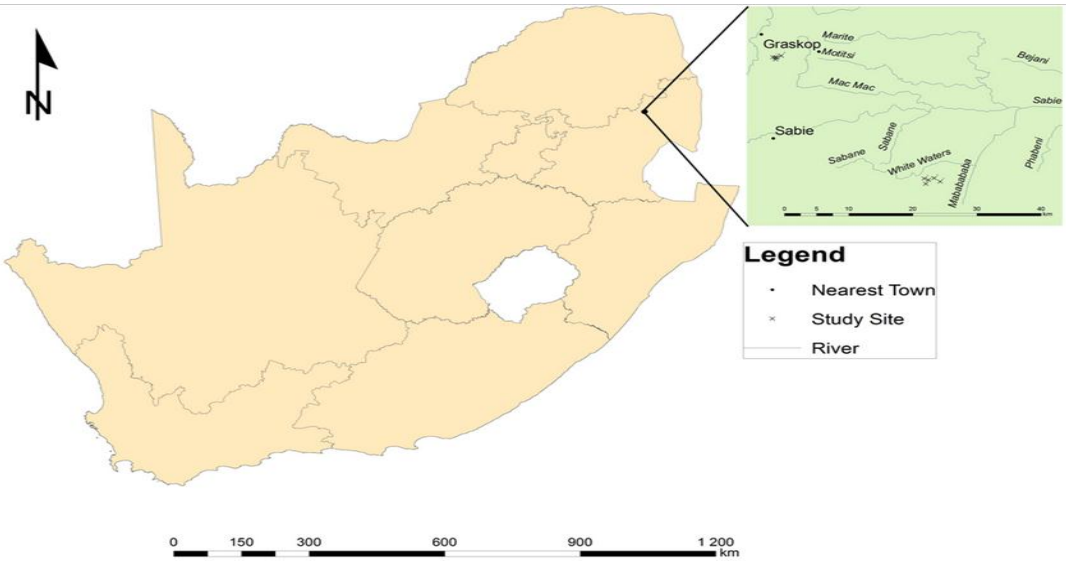
conditions between its native range in Australia and its planted range in South Africa is its exposure to frost. We therefore designed our research to test what impact frost has on the rate of spread and invasion potential of the species.

Looking at the size-class distributions of *E. grandis* individuals that have spread into the natural veld around the plantation edge is a way of assessing this. Size-class distributions can also tell us the recruitment and regeneration levels of *E. grandis*; high regeneration and recruitment levels are known to be associated with invasive species as shown in the first chapter. We expected that if there were no signs of any individuals spreading from the populations, then *E. grandis* was at the introduction stage of invasion where they have not been able to spread into other environments probably because of some environmental factor which may be limiting its ability to spread. On the other hand, if they were recruiting (i.e. had reached the establishing a population invasion stage) – they would have an inverse J-shaped distribution. If they were reproducing, but some other factor was stopping their spread then size class distributions can show us that something is hindering the spread.

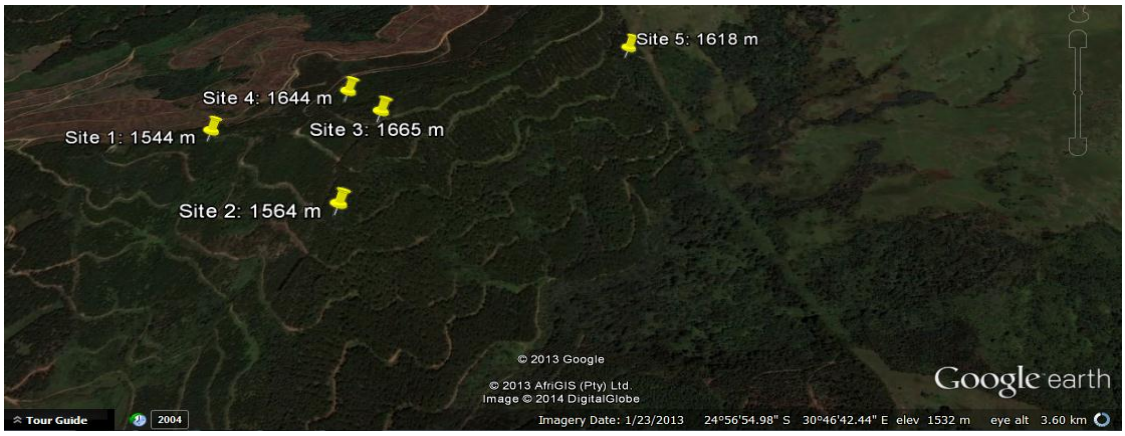
3.2 Material and methods

3.2.1 Study Area

My research took place in Mpumalanga, South Africa. I had sites in two different locations: Graskop and White River (Figure 3.6). The populations I studied are owned by York Timbers and Hard Rock Timbers. The sites in Graskop (24 ° 55’ S, 30 ° 46’ E) are generally at high altitudes (1600 m a.s.l) compared to those in White River (25 ° 09’ S, 31 ° 02’ E) -953 m a.s.l. Graskop usually receives about 1142 mm of rain per year, with most of the rain occurring in mid-summer and it often experiences severe frost with a mean annual temperature of 16.2 ^{0}C. Sites at Graskop experience “heavy” frost (Figure 3.3) in more than 80% of years, whereas in White River severe frost occurs less than 20% of the time (Schulze and Maharaj, 2007). White River receives about 722 mm of rain per year is mostly frost-free with mean annual temperature of 18.7 ^{0}C.



(a)



(b)

(c)

Figure 3.6 *Site map showing: a) Sampling locations in Mpumalanga province; b) Sampling sites in Graskop; c) Sampling sites in White River.*

Five sites were at high altitudes where there is exposure to frost in Graskop and the other five were at low altitudes where there is infrequent frost in White River. To test specifically for the role of frost in preventing *E. grandis* invasion I chose sites that were similar in terms of their fire regimes, but were exposed to very different frost frequencies. Plantations are usually protected from wild fires by annual firebreaks to protect the plantations from grassland fires and this would probably have the added benefit of preventing saplings invading into the grasslands. However, the sites that I worked on had not been actively managed for at least 8 years, and were therefore exposed to the natural fires that are usually associated with grasslands. From Figure 3.4, it is apparent that fires occur naturally at both sites with return times of 3-4 years. I sampled five different populations at each location to account for variability related to topographic position and plantation age. The sampling was done over a period of 17 days, the first field work was done from the 7th to the 14th of June 2013 and the second one was on the 19th to the 29th of November 2013.

Table 3.4 *Description of the sites sampled. The locations of these sites are shown in Fig 3.6.*

Location	Site	Altitude(m)	Site conditions
Graskop	1	1544	Dense area with a lot of small and mature trees. A small river between the trees.
Graskop	2	1564	Lots of mature trees and few small ones. Some pine trees in-between.
Graskop	3	1665	Plenty of resprouts mainly small trees. Few scattered mature trees.
Graskop	4	1644	Lots of resprouting for both young and mature trees.
Graskop	5	1618	Population on steep slope hillside. Dense population dominated by pine trees.
White River	1	923	Few small trees and many mature trees.
White River	2	925	Young trees covering most of the space.
White River	3	917	Trees of almost the same age, mostly young trees, few resprouts and close to Da Gama dam.
White River	4	970	Very dense place, a lot of old and small trees, Mixture with some other tree species, population near Da Gama dam.
White River	5	1031	Few mature trees and lots of seedlings and young trees.

3.2.2 Lay out of transects

In order to assess how invasive *E. grandis* is, and the stage of invasion of *E. grandis*, I set up my sampling sites on the edge of various *E. grandis* plantations. Belt transects (5 by 50 metres) were laid out from the edge of the plantation into the natural veld in each of the naturalized populations that are next to the plantations (Figure 3.7). I tried to control for management by only sampling areas that have had not been cleared for the past 8 years. I also ensured that I sampled pure *E. grandis* stands – not hybrid stands – as hybrids of *E. grandis* and *Eucalyptus dunnii* are often used in colder parts of the country (K. Padayachee Pers. comm. 2013).

Figure 3.7 *Population growing next to the plantation near White River, Mpumalanga Province.*

Transects were run from the edge of the plantation out into the natural vegetation. The number of transects between the sites varied from one to three depending on the population density of a site because I aimed to sample a certain minimum number of trees at each site. To determine this minimum number I did a preliminary study in June 2013 where I assessed how many individuals were necessary to get a reasonable size-class distribution (Figure 3.8).

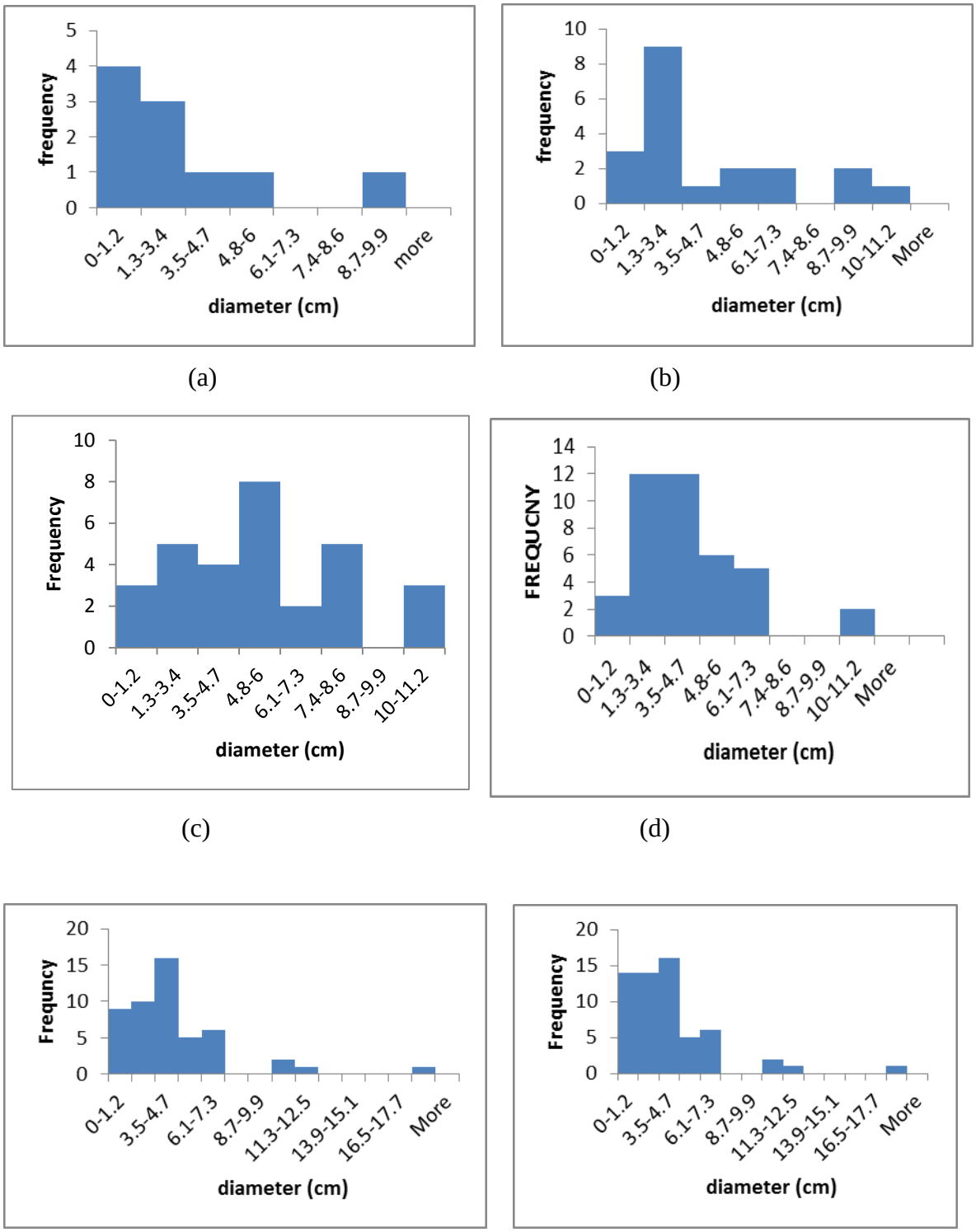


Figure 3.8 *Histograms showing the size-class distributions: a) first ten individuals; b) first twenty individuals; c) first thirty individuals; d) first forty individuals; e) first fifty individuals; f) first sixty individuals.*

So I aimed at assessing 50 trees per site because there was still some change going on at 60 trees but not substantially: the main pattern of a typical reverse J with slightly reduced recruitment in the very small size classes persists. On each transect the height, distance along the transect, and stem diameter at 30 cm above the ground of all the *E.grandis* individuals encountered within 2.5 metres either side of the transect was measured and recorded. Tree calipers were used to measure the stem diameters, and a 2.5m pole was used to visually help estimate the tree heights.

For tall trees the pole was placed beside a tree and I would walk away from the tree whilst holding a pen at arm's length and would stop when the pen covers the 2.5m pole. The pen would be moved up counting the number of times the pen can be fitted until the very top of the tree. The number of times the pen is required to reach the very top of the tree was then be multiplied by 2.5 m to get the height of the tree. For trees that have multiple stems the diameter for all the living stems was noted and the average basal area was calculated and converted back to average stem diameter ((basal area = sum(pi × r^2)) ÷ (total number of stems)).

3.2.3 Target tree population densities

I assessed 50 trees on each site and the loci starting and end points of all transects were recorded in the field on a handheld GPS. The distances of the *E. grandis* individuals along the transects were also noted which allowed me to calculate the population density at the site (number of trees / (transect length × transect diameter). The population densities were submitted to Mann-Whitney U test using R statistical package to determine if they differed statistically between the Graskop and White River populations.

3.2.4 Resprouts and pests

On each tree we recorded the presence or absence of insect pests like ants and termites and different types of caterpillars on the leaves and branches which usually affect *Eucalyptus* plantations. The trees were also checked to see whether they have resprouted or not. The noting of any young plants regenerating was done and we tried to establish their methods of establishment. The number of resprouts and trees with any form of infection were compared between the sites.

3.2.5 Assessment of size structures of the populations

Size structure studies in tree communities mostly focus on DBH (diameter at breast height) or basal diameter (Baker *et al*., 2005; Coomes and Allen 2007; Wang *et al*., 2009), or tree height (Lehmann, 2009; Helm and Witkowski, 2012). These are usually strongly correlated with each other but in a situation where there is a great deal of top-kill they could sometimes vary. I assessed size structure both in terms of basal diameter (diameter at 30cm) and tree height, so as to gain maximum insight from my data. The number of sapling and adult individuals was determined. Saplings were defined as those individuals less than 3m in height – which is generally considered the cut-off height for when saplings have escaped the fire trap (Bond and Midgley, 1995).

3.2.6 Statistical analysis

Statistical modelling was done using the software R (version 3.0.2). The data were not normally distributed so we used the non-parametric Mann-Whitney U-test to analyse the difference in diameters, number of resprouting trees, number of trees affected by pests and densities between the locations, Graskop and White River. Comparison between the size class distributions of the *E. grandis* populations in Graskop and White River was made using the Kolmogorov-Smirnov test. Variations in the population structures were also analysed for each site by calculating the median, minimum and maximum diameter for each diameter class. To give a quantitative basis for comparison of population size structures, the Weibull function was fitted to diameter frequency distribution at each site using the fBasics package in R. This Weibull distribution has been frequently used to characterize tree size distributions (Baker *et al*., 2005) because it can have a variety of different shapes (defined by the shape parameter) and can indicate the degree to which a distribution fits an inverse-J shape.

The Bayesian framework was used to fit the Weibull model to diameter data from each site. The parameterization which was used for the probability density of the Weibull distribution is as follows: $f(d) = cd^{c-1}/b^{c} \exp(-(d/b)^{c})$

Where diameter $d > 0$, $b > 0$ and $c \geq 0$

The scale parameter (b) gives an indication of the characteristic diameter/height size of the population (it represents 63.2 quantile). The shape parameter (c) defines the shape of the frequency distribution. When the value of c < 1, the function is falling sharply (monotonic function) showing that there are fewer juveniles than adults in the population; when near or equal to 1 (c = 1) it is a negative exponential distribution (Figure 3.9) representing a healthy recruiting population with more juveniles than adults.

When c > 1, the function is unimodal and it shows lack of recruitment. When 1< c< 3.6 the distribution will be having a positive skew (Baker *et al*., 2005).

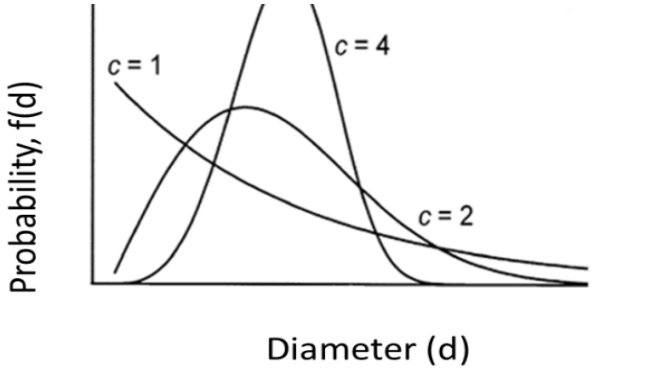


Figure 3.9 *Probabilty density function showing different possible shapes of the Weibull distribution defined by the shape parameter c (from Moritz, 2003).*

3.3 Results

3.3.1 Target tree population densities

The population densities in the study sites ranged from 1000 stems / ha to 3378 stems / ha (Figure 4). There was no significant difference between the population densities in Graskop and White River (Mann-Whitney U test: P= 0.64).

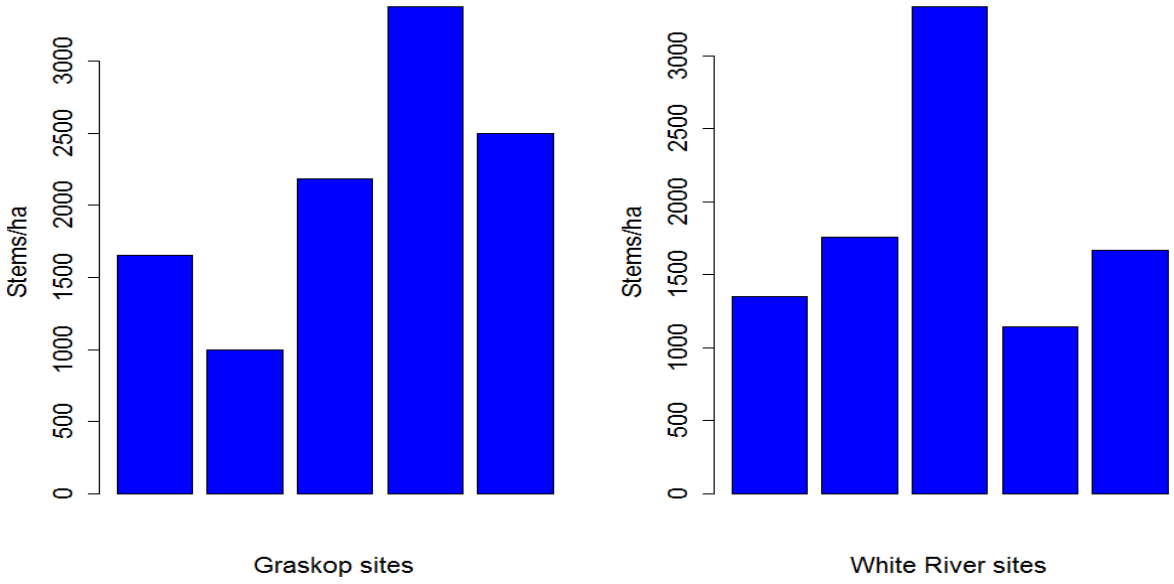


Figure 4 *Bar charts showing the range of population densities recorded in the 10 replicate sites.*

3.3.2 Pests and Resprouts

Both populations were infected with pests (Figure 4.1) but there was no detectable difference between the two populations (Mann-Whitney U test: P= 0.46). Of the 500 plants that were sampled in this study, only 10% were infected with pests.

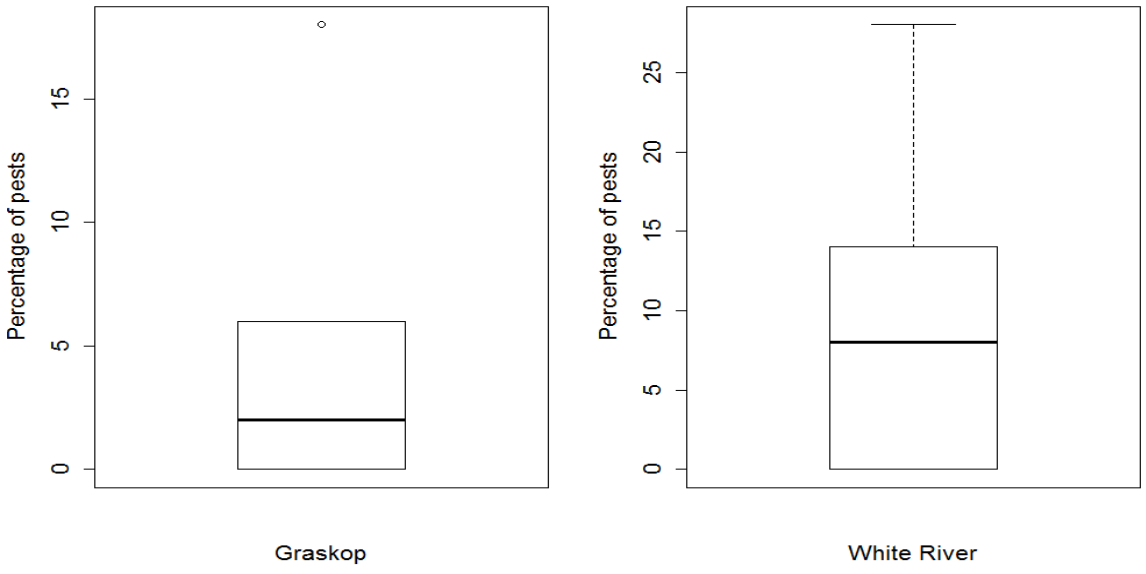


Figure 4.1 *Boxplots showing the proportions of infected trees with pests.*

There was a significant difference in the number of trees that were resprouting between the Graskop and White River populations (Mann-Whitney U test: P= 0.02). There was a lot of resprouting in Graskop compared to White River (Figure 4.2 a). In Graskop, resprouts accounted about 46 % of the trees whilst in White River only 11.6 % were resprouts. Generally, resprouting increased with increasing altitudes (Figure 4.2 b).

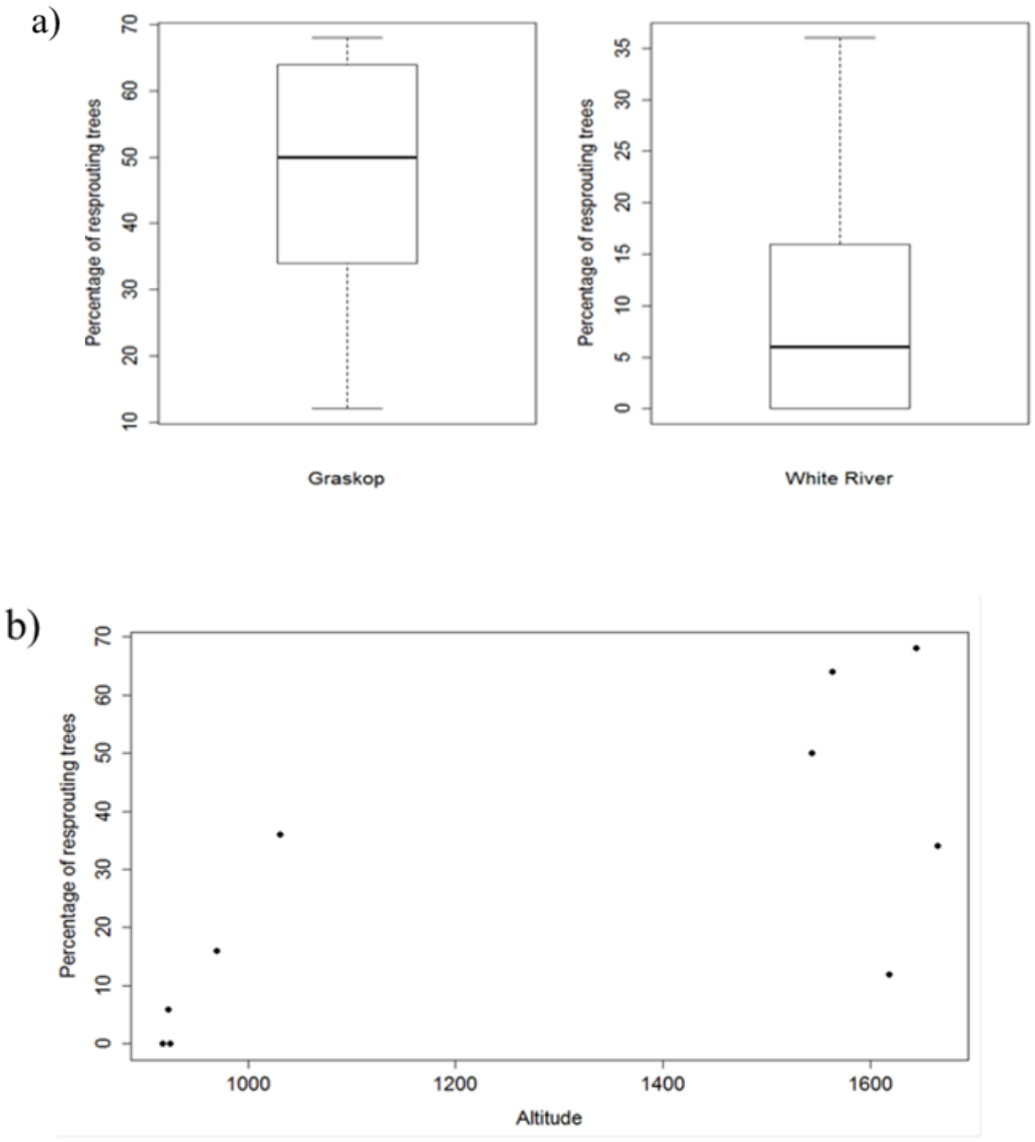


Figure 4.2 *a) Boxplots showing the percentage of resprouts across the sites in Graskop and White River; b) Relationship between altitude and percentage of resprouts.*

3.3.3 Size structures

Using diameters to assess size-class distributions showed that Graskop and White River populations both had large numbers of individuals in the smallest classes which follow the reverse-J curve, characteristic of good rejuvenation (Figure 4.3). The proportion of small individuals (diameter < 5 cm) was much higher at Graskop – 67% than White River- 46%. However, the rate of exponential decrease was higher in Graskop compared to that of White River. This rate of exponential decrease in Graskop started to increase from diameters of at least 5 cm (Figure 4.3). Graskop had fewer old trees (diameter > 20 cm) in the "adults" class compared to White River.

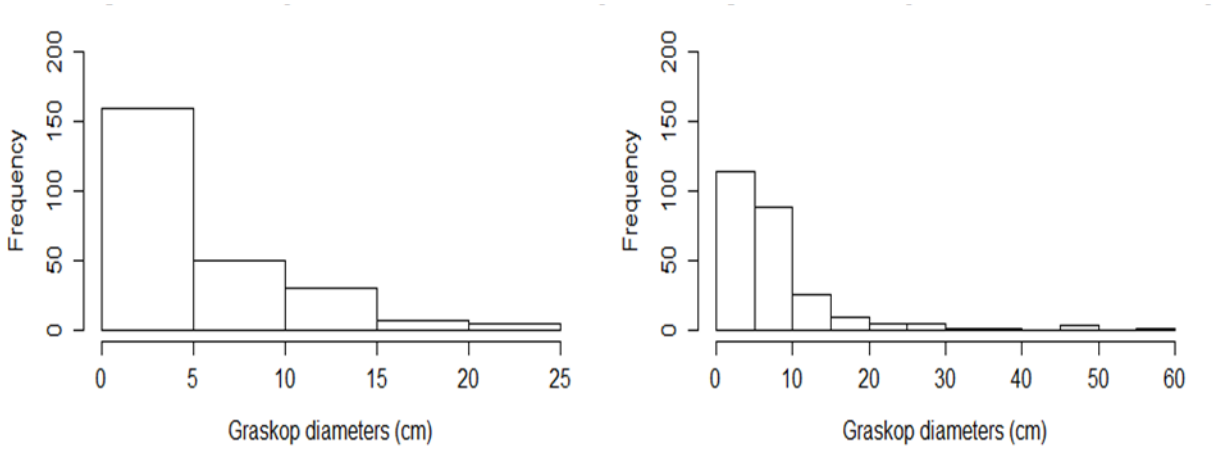


Figure 4.3 *Diameter size class distributions of all the populations in Graskop and White River.*

On average, trees at Graskop were shifted towards the smaller size classes (Table 3.5) – the location had smaller median and maximum diameters, and this was statistically significant ($P<0.01$ – Kolmogorov Smirnov test). Graskop had fewer mature trees than White River; Graskop had no trees at all in the 30-60 cm classes. Using height instead of diameter to define the size-class distributions gave similar patterns (Figure 4.4). The step drop in individuals from the smallest size classes at Graskop is even more apparent when considering height – with most of the individuals being less than 5 m.

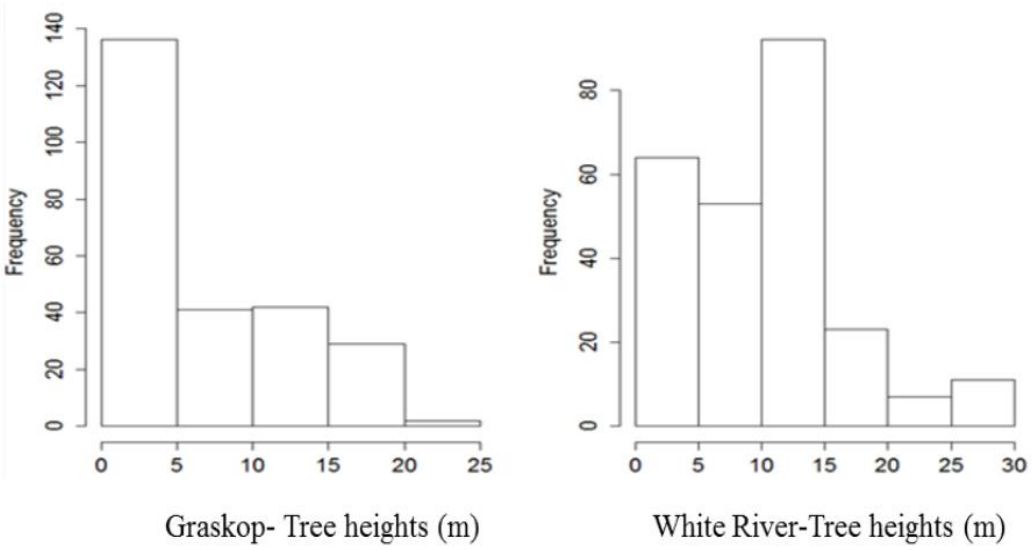


Figure 4.4 *Height size class distributions of all the populations in Graskop and White River.*

Table 3.5 *Some descriptive statistics of the diameters in Graskop and White River.*

Diameter (m)	White River	Graskop
Minimum	0.3	0.1
1st quartile	2.4	1.4
Median	5.5	3.0
Mean	7.2	5.0
3rd quartile	9.1	7.5
Maximum	57	24.2

There was a strong relationship between height and diameter, as would be expected (Figure 4.5). However, at Graskop there were some very small trees that still had significant diameters. These trees could be the result of several resprouting events after disturbance – where the tips and shoots of the sapling were damaged but the stem survived and continued to increase in size.

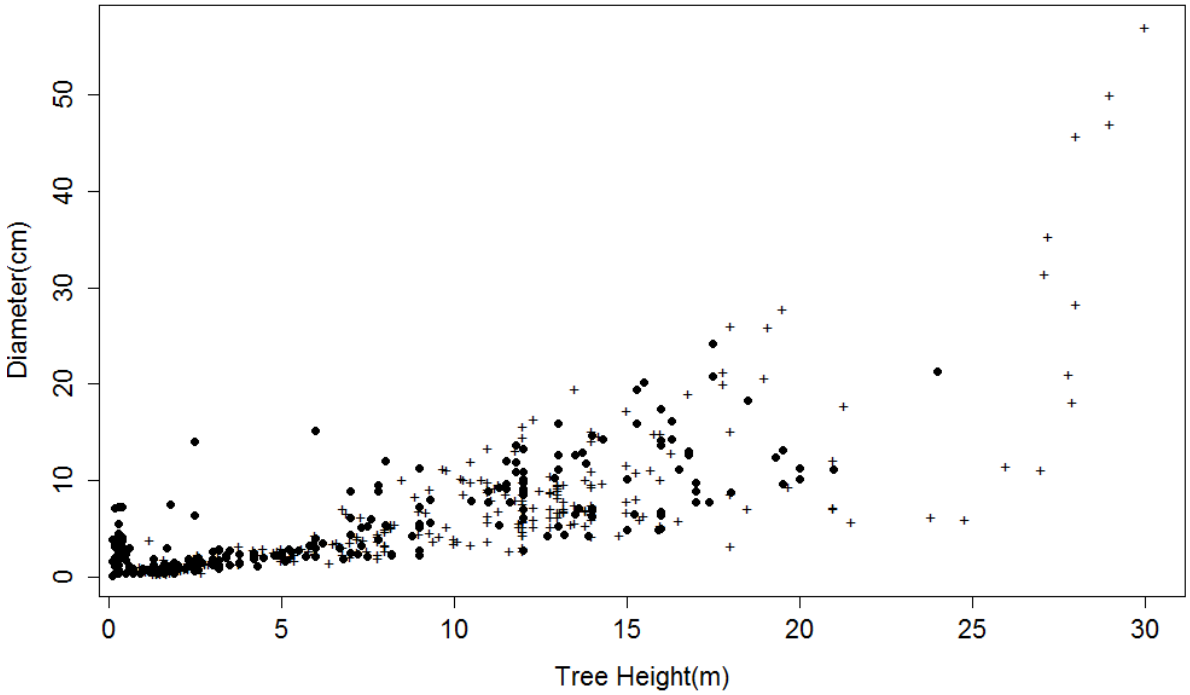


Figure 4.5 *Relationship between height and diameter in Graskop (solid circles) and White River (crosses).*

Although there is obviously strong recruitment at both locations showed a reverse-J shaped distribution indicating strong recruitment (i.e. *E. grandis* is spreading from the plantations into the natural vegetation), there was considerable variability in size-class distributions between sites within a location and this was larger than the variability between locations (Figure 4.6) with both locations having some sites with strong reverse-J distributions, and others with uni- or bi-modal distributions. This indicates that various site-specific factors might also control the spread rates.

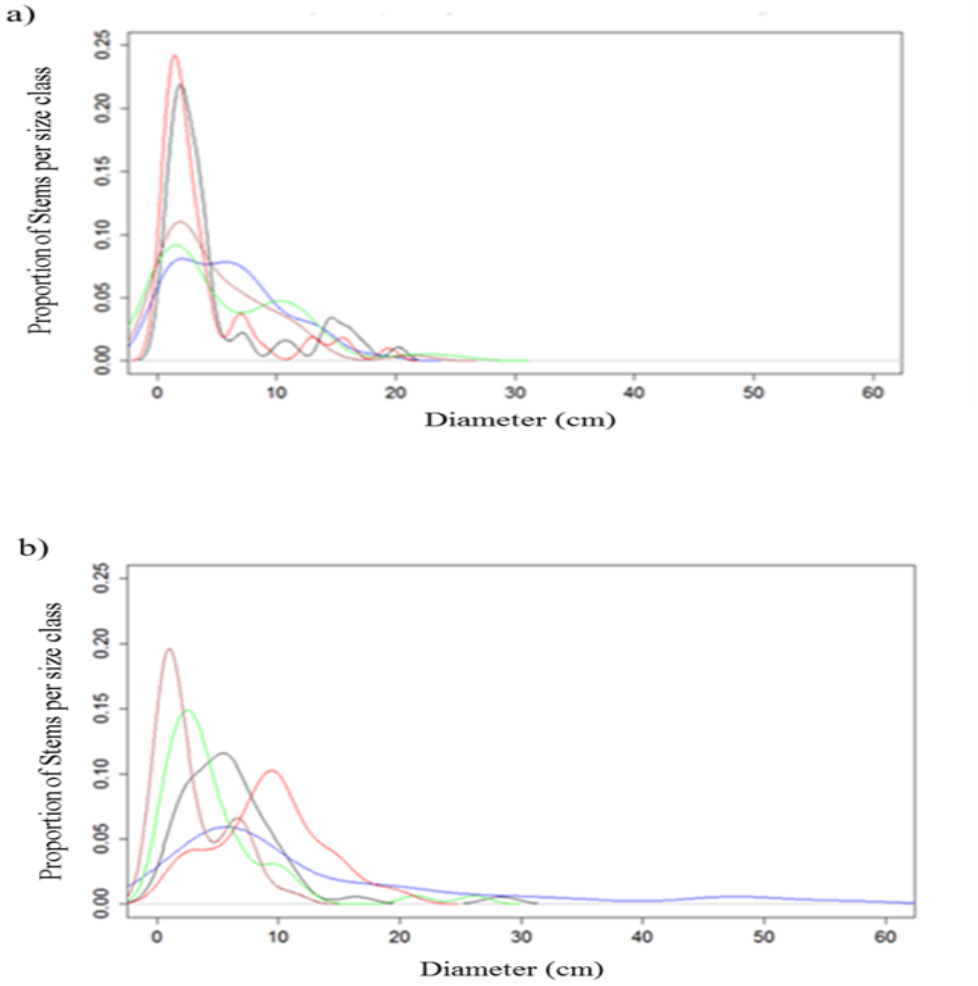


Figure 4.6 *Density plot showing the variability in diameter size-class distributions between sites: a) Graskop sites; b) White River sites (For each location: site 1= black, site 2= blue, site 3= green, site 4= red, site 5= brown).*

To investigate this more closely we fitted Weibull distributions to diameter size-class distributions at each site and compared values of the c-parameter. The diameter distribution at location level (all sites at each location) had a negative exponential (reverse-J) distribution (Table 3.6). Four of the sites in Graskop exhibited a negative exponential distribution (shape parameter not significantly different from 1) indicating healthy populations with good recruitment at those sites whilst at site 2 the function was unimodal (c =1.2) showing little recruitment as evidenced by few juveniles.

Two of the sites in White River had a negative exponential distribution (healthy and stable populations) whilst all the other sites had unimodal functions: site 1(1.5- absence of juveniles), site 3 (1.1-little recruitment), site 4 (2.1- no recruitment at all). There were no monotonic functions exhibited in White River. The b values confirm what was found previously which is that trees in White River are larger on average than in Graskop.

Table 3.6 *Weibull shape (c) and scale (d) parameters for the sites in Graskop and White River. A c value close to 1 represents a negative exponential function (or a reverse-J shaped distribution). Values much higher than 1 indicate a unimodal distribution–with a lack of juveniles relative to larger size classes. Values below one indicate a generally increasing function.*

Location	Site	c (standard deviation)	b (standard deviation)	Loglik
Graskop	All Sites	1.05 (0.05)	5.10 (0.32)	-651.82
Graskop	1	1.06 (0.11)	4.95 (0.69)	-128.46
Graskop	2	1.27 (0.14)	6.37 (0.74)	-136.92
Graskop	3	0.94 (0.10)	5.48 (0.86)	-136.33
Graskop	4	1.01(0.10)	3.81(0.56)	-116.63
Graskop	5	1.09 (0.12)	4.99 (0.68)	-128.35
White River	All Sites	1.05 (0.04)	7.37 (0.46)	-743.71
White River	1	1.53(0.15)	6.85 (0.67)	-133.71
White River	2	1.05 (0.11)	13.31(1.89)	-178.12
White River	3	1.14 (0.11)	5.04 (0.66)	-127.33
White River	4	2.17 (0.24)	10.41(0.71)	-144.91
White River	5	1.02 (0.11)	2.94(0.43)	-103.44

Shape parameter (c) values of the Weibull distribution decreased with increasing altitude (Figure 4.7), indicating that the proportion of juveniles: adults were generally higher at the high-altitude sites.

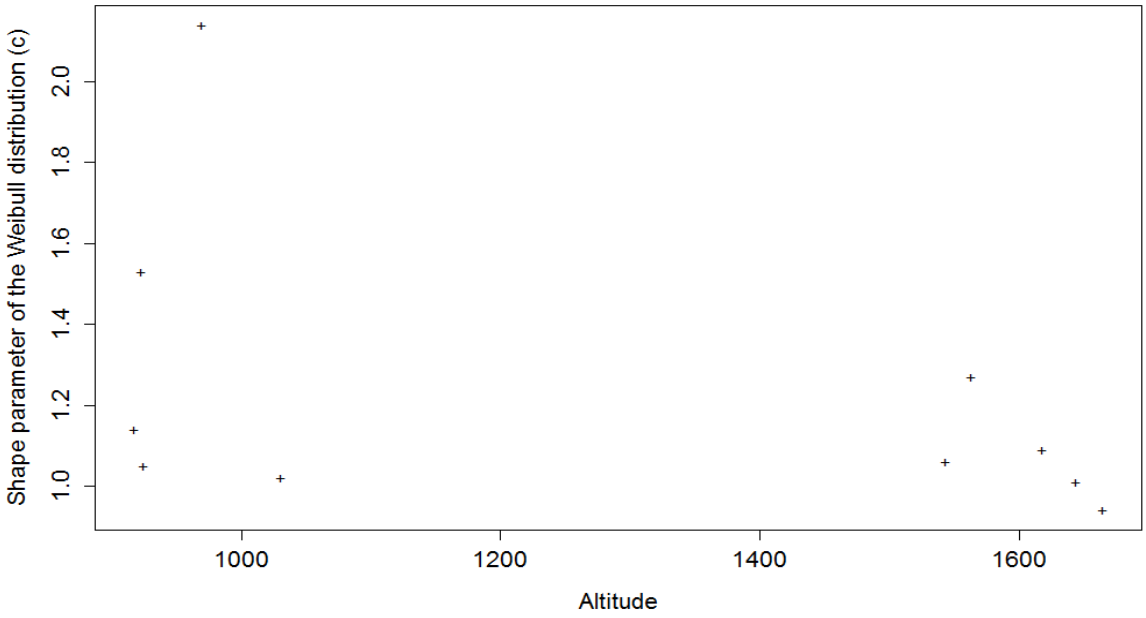


Figure 4.7 *Effect of altitude on the Weibull shape parameters.*

Higher densities were mostly associated with shape parameters equivalent or approximately equal to 1 (Figure 4.8).

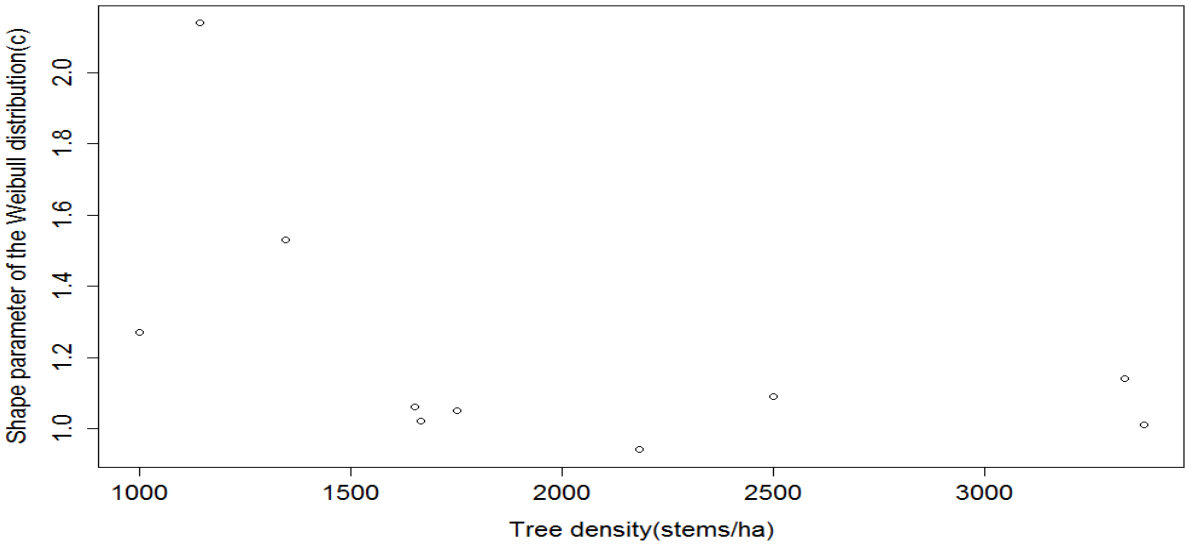


Figure 4.8 *Relationship between tree denisty and Weibull shape parameters.*

3.4 Discussion

Our results suggest that *Eucalyptus grandis* has the following characteristics that are associated with invasive species: high regeneration levels, thrives in new environments that do not have biotic constraints and thrive in environments with similar abiotic conditions to native range. The high regeneration and recruitment levels of *E. grandis* are evidenced by the reverse-J curves exhibited in both Graskop and White River populations. This shows that on average the populations are expanding, and that nothing is preventing seedling establishment in either location. Recruitment dynamics is a key influencing factor of plant population growth and persistence (Franco and Silvertown, 1996). Establishment of new young trees is a necessity for the spread of these populations into new environments. Therefore *Eucalyptus grandis* has a great potential to spread. The fact that at both locations there were some sites with unimodal/different size class distributions does indicate that one should consider other factors that might affect seedling establishment – and might result in cohorts of trees. Outbreaks of pests could be an explanation, or very severe frosts that kill, rather than top-kill the seedlings.

We found a significant difference in the diameters between the two locations, with Graskop having smaller diameters compared to diameters in White River. This could just be that trees in White River grow faster because it is warmer, or it could be as a result of frost in Graskop as the plants would be channelling most of their resources to their biological mechanisms which serve to avoid freezing. The sudden drop in numbers in Graskop from height class 0-4.9 metres to height class 5-9.9 metres is an indication that there is a demographic bottleneck at this stage – most likely related to frost/fire-induced top-kill. This is confirmed by the large numbers of trees resprouting in Graskop which can be an outcome of frost or other disturbance events.

The interaction with fire might also exacerbate this: all the study sites experienced fires with return times of 3-4 years (Figure 3.4) and if the *E. grandis* individuals in Graskop have not attained a height that enables them to survive fires then they would be facing two major recruitment bottlenecks: fire and frost. Plantation trees are made vulnerable to attack by pests and diseases as a consequence of frost damage (Swain and Gardner, 2003), but the number of trees infected with pests was low at both sites, and slightly higher in White River compared to Graskop where there is frequent frost.

Therefore we think the contribution of pests to the recruitment of the populations is minimal, although heavy pest outbreaks in past years might explain the odd size-class distributions in some of the White River sites. Population size structure is a result of both the outcome of past demographic events and an indicator of the population's demographic future (Bullock *et al*., 1996). Old (post-bottleneck) trees at the sites with very few juveniles show that appropriate regeneration conditions were present in the past. The few old trees in Graskop are evidence that there is something knocking down most of the "adult" tees thus preventing them to fully develop into old trees or that they are growing more slowly and have not yet become adult trees.

Although there are some bottlenecks in both populations, especially in Graskop, the probability that a "sapling" individual will survive the few years (generation time) required to become sexually mature is higher in White River compared to Graskop. As reproductive output increases exponentially with height the few old trees in Graskop reduce their chances of contributing to future generations thus limiting the spread of *Eucalyptus grandis.* Considering these results in relation to Chapter 2 I would expect rates of population growth to be higher at White River than Graskop. This is because 44% of the trees at Graskop are less than 3m tall and there is very little (<20%) reproduction in these size classes. On the other hand, at White River 19 % of the trees are less than 3m, indicating that more of the population is reproductively active. On the other hand, it is clear that if the demographic bottleneck (presumably a combination of fire/frost) at Graskop were released due to warmer winters or fire protection, then the rates of population growth might also increase quickly, as all the juvenile trees grow to become reproductively mature adults.

3.5 Conclusion

Chapter 3 analysed the role of the environment in the population dynamics of *E. grandis.* The main aim of this chapter was to assess whether the rate of spread of *E. grandis* has anything to do with the environment in which it is found in South Africa. The results showed that there is recruitment at both locations, Graskop and White River. On average the populations had a reverse J-curve with a lot of juveniles. Frost is one environmental factor that is probably negatively affecting the recruitment of populations in Graskop but possibly episodic events such as pest-outbreaks are also slowing the rate of spread of *E. grandis* at both sites as there were several populations with uni-or bi-modal distributions.

The proportion of small individuals was much higher at Graskop than White-river however, and as in Chapter 2 we show that these small individuals are not reproductively active yet, and are probably still in the frost/fire trap, we can conclude that the rate of spread of individuals at Graskop is probably slower than at White River.

CHAPTER 4

CONCLUSION

4.1 Conclusion

This study was set out to investigate the ability of *Eucalyptus grandis* to become invasive in South Africa. The ability to spread was explored by studying its population dynamics in different environments as well as assessing its reproductive potential. The main results were chapter specific and were summarised within the respective chapters: Assessing invasive species traits and Environmental suitability. According to the results of the species traits, *Eucalyptus grandis* has a potential to be a serious invader as evidenced by their viability of 97% and short time required for them to be reproductively mature. The seeds of *Eucalyptus grandis* were found to be of high vigour suggesting that maybe establishment of the seedlings and survival of saplings rather than germination is the limiting stage for regeneration in areas that have frost. Saplings are more vulnerable to frost and this can stop their development into mature individuals.

The environmental suitability results show that frost and other unknown demographic factors are slowing the rates at which *E. grandis* individuals mature but there are a lots of *E. grandis* individuals spreading at a high rate from the plantation edge. In Chapter 3 I showed that even though the overall size class distribution in Graskop had a clear reverse-J-shaped curve, there is a sharp drop in frequency from the 2-6 cm diameter size classes (the 2-5 m height size classes) in Graskop: evidence of a frost/fire trap which is supported by the substantial number (>30%) of resprouting individuals in these populations. So frost might be hindering the rate of spread. Interestingly, in Chapter 2 I show that most of these resprouting individuals in Graskop seem to delay reproduction for longer than individuals at White River – so not only is the rate of transition to adult size classes slower in Graskop, but the generation time is longer and the total amount of seed produced probably lower than in the White River populations.

Whether these factors might act to prevent invasion in the long term in high-altitude sites in South Africa is not clear. These results on the rate of spread may suggest that the *Eucalyptus grandis* populations are still at the establishing population stage of invasiveness (Williamson *et al*., 2006). This thesis demonstrates that looking at the demographics of alien populations can give clues about a) the rates at which they might be spreading and b) the factors preventing them from spreading. A similar approach might well be used for other species of concern such as *Eucalyptus camaldulensis Dehnh.*

There has been much emphasis on the need to understand the population dynamics of key stone or endangered species to preserve them but I think invasive alien species should also get some attention. About 7% of South Africa's water resources are being used by invasive alien trees and Eucalypts are well known for using a lot of water (Le Maitre *et al*., 2000). Also, there is a shift in recent years from growing Eucalyptus as part of large commercial industries to having emerging farmers and subsistence farmers growing individual stands of Eucalyptus on their properties as a means to earn extra income. This means that *E. grandis* will now be able to spread more widely throughout the country, and that its rates of spread into native vegetation will probably be less strictly controlled.

In this study we found evidence that frost and some other factors limit the rate of spread of *E. grandis* into native vegetation. Other factors like the limited seed dispersal of Eucalypts might limit their spread. The seeds are dispersed by wind over quite short distances and they have no adaptations for dispersal (wings or fleshy tissues). The lack of compatible ectomycorrhizal fungi can also be a factor limiting the spread. There have been suggestions that lack of ectomycorrhizal fungi may be important for the spontaneous establishment of seedlings away from plantations (Rejmánek *et al*., 2011). However, in this study we found absolutely no indication that there was a fundamental constraint on its ability to spread into native vegetation. For this reason the new dispersed forestry industry that is developing around *E. grandis* should be a cause for concern. Similarly, if the incidence of frost decreases with the projected increase in winter temperatures (Engelbrecht *et al*., 2009) then more parts of the country will become suitable for rapid expansion of Eucalyptus.

So the further study and understanding of population dynamics of alien species can boost the confidence in tackling the problems caused by alien invasive species. Population dynamics of alien species must be further studied in relation to other environmental factors such as soils and geology and disturbance processes like illegal cutting down of the trees by locals to use for fencing. A soil seed bank study would also have would have boosted this study on population dynamics of *E. grandis*. Analysis of the population structure is the first procedure to gather information about the factors that might be affecting them. However, there is need of long-term demographic studies that will give more detailed information. The chances of natural regeneration and spread of *Eucalyptus grandis* have proven to be very high if the demographic bottlenecks are suppressed.

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