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Demographics of *Eucalyptus grandis* and implications for invasion

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Alien invasive species can have negative impacts on the functioning of ecosystems. Plantation species such as pines have become serious invaders in many parts of the world, but eucalypts have not been nearly as successful invaders. This is surprising considering that in their native habitat they dominate almost all vegetation types. Available theory on the qualities that characterise invasive species was used to assess the invasive potential of *Eucalyptus grandis* – a common plantation species globally. To determine rates of establishment of *E. grandis* outside plantations, we compared population demographics and reproductive traits at two locations in Mpumalanga, South Africa: one at higher elevation with more frost. *Eucalyptus grandis* has a short generation time. We found no evidence that establishment of *E. grandis* was limiting its spread into native grassland vegetation, but it does appear that recruitment is limited by frost and fire over much of its range in Mpumalanga. Populations at both study locations displayed characteristics of good recruitment. Size class distributions showed definite bottlenecks to recruitment which were more severe when exposed to frost at higher elevations. Generally, the rate of spread is low suggesting that the populations are on the establishing populations' invasion stage. This research gives no indication that there are any factors that would prevent eucalyptus from becoming invasive in the future, and the projected increase in winter temperatures should be a cause for concern as frost is currently probably slowing recruitment of *E. grandis* across much of its planted range.

Conservation implications: Eucalyptus plantations occur within indigenous grasslands that are of high conservation value. Frost and fire can slow recruitment where they occur, but there are no obvious factors that would prevent *E. grandis* from becoming invasive in the future, and monitoring of its rates of spread is recommended.

Introduction

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 often 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 last few hundred years, geographical barriers 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. Fixed transport infrastructures can also provide platforms for biotic interchange, for example, the Panama and Suez canals (Wilson et al. 2009).

When looking at aspects of invasions, it is useful to conceptualise processes that limit or facilitate invasions as an invader negotiating a series of barriers (Blackburn et al. 2011; Kruger, Richardson & Van Wilgen 1986; Richardson et al. 2000). There are many factors that affect the chances of a species moving from one stage of invasion to another. The invasion process has a series of stages, and in each stage, a species or population needs to overcome a barrier to proceed to the next stage (Blackburn et al. 2011). Failure by a species to overcome the barriers to proceed to the next stage reduces the chances of the species becoming invasive.

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 & Pysek 2008). Potential determinants of invasiveness that are frequently studied include introduction history and pattern, species traits, and ecological and evolutionary processes. The invasion

probability of a species is usually high if it was introduced a long time ago (long residence time) as it may take time for introduced species to build up to the point that they start spreading (Richardson et al. 2000). Additionally, if a species is introduced in multiple locations, it can also dramatically affect the rate at which it spreads (Richardson & Pysek 2008). The number of individuals introduced is the most prevalent correlate of establishment success in non-native populations. Studies have shown that the number of individuals introduced can lead to establishment success (Blackburn et al. 2013; Lockwood, Cassey & Blackburn 2009).

Species traits normally associated with invasiveness are short generation times, production of copious amounts of viable seeds and dispersal ability of the seeds (Rejmánek 2000). The first two traits affect the rate at which new individuals can be produced, and the third trait affects the ease with which individuals spread into new environments. For example, eucalypts produce seeds that just fall from the tree and is only carried to very short distances by the wind. The very small seed sizes mean that fire is often required to clear competing vegetation and allow eucalypt seedlings to establish. Both biotic (competition or predation) and abiotic factors can control the ease with which a species spreads into new environments. Invasives are often released from natural predators or pests when introduced to new environments (Kruger et al. 1986; Richardson et al. 2000), but the extent to which the abiotic environment limits alien spread appears to depend on particular circumstances; therefore many invasive species have a larger climatic niche than in their natural habitat. This enemy release hypothesis is also a good example for arguable results of empirical tests, for example, Maron and Vilà (as cited in Jeschke & Heger 2014) found that exotic plants can attract native herbivores which negatively affected the survival of the alien plants. Invasive species are a good ecological test of our understanding of vegetation distribution, and the relative roles of ecological versus evolutionary processes in determining a species range.

Size (or age) 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 from invading. An inverse J-shaped curve – with more juveniles than adults and a smoothly declining function – is expected in a recruiting population (Lehmann, Prior & Bowman 2009; Moritz 2003), because it allows for mortality and competitive effects on the probability of progressing to the next size class. 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 size class distributions among plant populations (Lehmann et al. 2009) when the bottleneck is 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. A unimodal curve shows the absence of juveniles indicating that there is no recruitment at all. This could be as a result of something preventing seedling establishment.

The natural occurrence of *Eucalyptus grandis* W. Hill ex Maiden is in Australia from Newcastle, New South Wales northwards to Bundaberg, Queensland on lower slopes of fertile valleys and is usually found in open woodlands or grasslands fringing rainforests (Crisp, Cook & Steane 2012). The altitude is mainly from sea level to 600 m, but up to 1100 m in the tropical north (NSW Department of Primary Industry 2010). The mean maximum temperature of the hottest month across its distribution ranges from 24 °C to 30 °C, and the mean minimum temperature of the coldest month ranges around 7.3 °C – 19.4 °C. Rose gum is well adapted to fire – it resprouts vigorously and maintains a seed bank in its canopy for recruiting after fire (Booth 2012; Williams & Woinarski 1997). In Queensland (Northern Australia) where *E. grandis* is native, fire is a recurring element where most of the landscape is burnt every year (Booth 2012).

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). South Africa's eucalyptus plantations cover a broad range of environments, particularly in the subtropical and the humid warmer temperate regions (Otim 2008). *Eucalyptus grandis* plantations cover a much wider range of climates in South Africa than it does in Australia. The plantation areas in South Africa fall into high rainfall zones. The fast growth rate of *E. 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 Australia.

We studied the invasion potential of *E. grandis* in South Africa. *Eucalyptus grandis* has not been nearly as successful in invading alien environments as other widely planted trees such as pines (Forsyth et al. 2004; Higgins & Richardson 1998) and legumes. The reasons why eucalypts are not more invasive are not well understood but it is agreed that the limited dispersal of the seeds, high mortality of the seeds and lack of compatible mycorrhizal fungi make the eucalypts less invasive (Lake & Fisherman 2004). Although most *eucalypts* are not currently highly problematic invaders in South Africa, they are still listed as potential invaders in many national and international lists (Dept. of Agriculture, Regulation No. 15, 2001; Richardson, Williams & Hobbs 1994). *Eucalyptus grandis* is a successful invader in the Tzaneen area and in KwaZulu-Natal along rivers (Versfeld, Le Maitre & Chapman 1998).

Four major frost 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). Cold-damaged

plantations are more vulnerable to fires and are prone to consequential damage through pest or disease attacks (Swain & Gardner 2003). If the frost is severe, the affected leaves wither and the shoots may die back. Due to its sensitivity to cold, mean annual temperatures (MATs) that are below 18 °C and altitudes above 1050 m are not suited for planting *E. grandis*, according to Swain and Gardner (2003).

Cold-tolerant species such as *Eucalyptus nitens* or hybrids of *Eucalyptus dunnii* and *E. grandis* are sometimes used at sites above 1200 m which are prone to frost and frequent snowfalls. The frequent frosts in the Highveld of South Africa might therefore 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).

In some ways, a frost event can be similar to a fire in its impacts on woody plants (Whitecross et al. 2012). Both fire and frost can damage above-ground biomass of small trees ('top-kill') and therefore act to prevent trees from growing to adults. Although frost is rare in the Australian range of *E. grandis*, fire is common, and the species resprouts vigorously and is able to survive top-kill. It is therefore not clear what effect frost (and fire) would have on the recruitment and spread of this alien species. This study used the theory on the qualities that characterise invasive species to assess the invasion potential of *E. grandis* with the help of a field study. The study had the following objectives: (1) to test whether *E. grandis* is expected to be a serious invader based on its reproductive traits and (2) to assess the impact of frost on the rate of spread of *E. grandis* into neighbouring vegetation from plantations.

Methods

Study area

A field study was used to determine whether there is any indication that *E. grandis* is in fact invading from plantations in Mpumalanga (Figure 1). To test specifically for the role of frost in preventing *E. grandis* invasion, we chose sites that were similar in terms of their fire regimes, but were exposed to very different frost frequencies. Five sites were selected near Graskop at high elevation (1600 m a.s.l.) where they are exposed to frost (24° 55″ S, 30° 46″ E) with mean minimum temperature of 4.8 °C and the other five at a low elevation area (953 m a.s.l.) with infrequent frost near White River (25° 09″ S, 31° 02″ E) with mean minimum temperature of 7 °C. Sites at Graskop experience 'heavy' frost in more than 80% of the years, whereas in White River severe frost occurs less than 20% of the time (Schulze & Maharaj 2007). 'Heavy' frost is when the temperature of ≤ 0 °C is recorded on a Stevenson Screen assuming that the temperature on the ground would be even lower.

The plantations have trees that can be as tall as 60 m and are being managed for timber. Fire return periods at these sites



Source: Department of Geography, Wits University, 2013

FIGURE 1: Site map showing sampling locations.

were similar – on average once every 3–4 years (Archibald et al. 2010). Plantations are usually protected from wild fires by annual firebreaks to protect the plantations from grassland fires, and during this process, saplings are usually cleared. However, many plantations are no longer actively managed in this way, which will probably increase invasion probability. This neglected management provided an opportunity to assess natural rates of spread of eucalypts into surrounding natural grassland vegetation. We studied populations that were close to the plantation plots where no firebreaks had been made before.

We identified sites that had not been actively managed for at least 8 years. We sampled five different populations at each location to account for variability related to topographic position and plantation age. The veld surrounding the plantation plots consisted of grass with a mixture of old and young pine trees – *Pinus patula*. We did not measure the diameters and heights of the pine trees. The sampling was done over a period of 17 days, the first field work was carried out from 07 to 14 June 2013, and the second one was carried out from 19 to 29 November 2013.

Transect layout

Belt transects (5 m by 50 m) were laid out from the edge of the plantation into the natural veld in each of the naturalised populations that are next to the plantations. We ensured that we sampled pure *E. grandis* stands – not hybrid stands – as hybrids of *E. grandis* and *E. dunnii* are often used in colder parts of the country (K. Padayachee [University of the Witwatersrand], pers. comm., 2013). On each transect, the height, distance along the transect (Figure 2) and stem diameter at 30 cm above the ground of all the *E. grandis* individuals encountered within 2.5 m either side of the transect, were measured and recorded. Tree callipers were used to measure the stem diameters, and a 2.5-m pole was used to visually help estimate the tree heights. 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).

Demographic study

We assessed a minimum of 50 trees on each site. The locations' starting and ending points of all transects, as well as the location of all *E. grandis* individuals, were recorded in the field on a handheld GPS. The distances of the *E. grandis* individuals along the transects were also noted, which allowed us to calculate the population density at the site [number of trees/(transect length × transect width)]. If plants had resprouted, this was noted, as well as any signs of pests or pathogens. The presence of flowers or fruits on each tree was also recorded, so as to have an idea of the size when *E. grandis* starts to become reproductively mature (i.e. generation time).

Size structure studies in tree communities usually measure DBH (diameter at breast height), basal diameter (Baker et al. 2005; Coomes & Allen 2007; Wang, Hao & Zhang 2009) and tree height (Helm & Witkowski 2012; Lehmann 2009). 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. We assessed size structure both in terms of basal diameter (diameter at 30 cm) and tree height. The number of saplings and adult individuals was determined. Saplings were defined as those individuals less than 3 m in height – which is generally considered the cut-off height for when saplings have escaped the fire trap (Bond & Midgley 1995).

Germination rates study

A germination study was undertaken to assess the vigour of *E. grandis* seeds. The aim was to test how quickly eucalyptus seeds germinate and what proportion of their seeds is viable. Seeds were harvested from mature fruits of a random selection of five trees in Graskop and White River to be germinated in the lab. The seeds from different trees at each site were mixed together, and 20 seeds were placed on a Petri dish (5 replicates for each location). Two 90-mm sheets of filter papers were placed in the lid of the 90-mm Petri dishes; the seeds were placed in the lid and moistened with distilled water. The base of the Petri dish was used to seal, and the seeds were incubated at 25 °C.

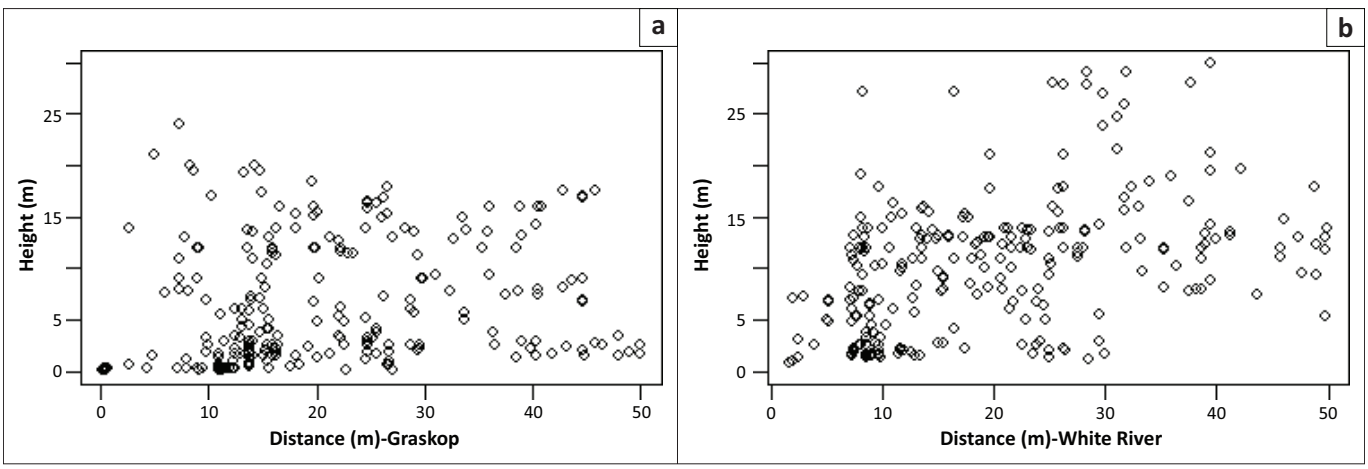


FIGURE 2: Heights of the invasive eucalypts along the 50-m transects. (a) Graskop and (b) White River.

The number of seedlings germinating was counted at 24-h intervals and continued until there was no change in germination percentage for 10 days. A seed was considered germinated if it had radicle longer than 1 mm. The proportion of viable seeds (pV), germination index (GI, Zanjan & Asli 2012) and the time taken for 50% of the seeds to have germinated (T50) germination were computed by using the following formulas:

$$pV = N/S \quad [Eqn\ 1]$$

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

$$GI = \Sigma\ (Ti \times Ni) / S \quad [Eqn\ 2]$$

where Ti is the number of days after planting, Ni is the number of seeds that germinated on day 1, and S is the total number of seeds placed in each dish (Zanjan & Asli 2012).

$$T50 = ti + (0.5\ N - ni)\ (ti - tj) / ni - nj \quad [Eqn\ 3]$$

where N is the final number of germinated seeds, ni and nj are the cumulative number of seeds germinated by adjacent counts at times ti and tj when ni < 0.5 N 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 a short time to germinate are considered to be more vigorous.

Statistical analysis

A multiple logistic regression analysis was performed where flowering state (yes or no) was predicted by the two explanatory variables (height and location). We also looked for interactions between height and location, to see whether size of first flowering was influenced by the environmental conditions of the site. The Bayesian Information Criterion (BIC) was used to compare the models. For each site, we determined the height when 80% of the trees were reproductively mature, and using literature on growth rates of *E. grandis* at the two locations (DAFF 2000), we converted this height to an estimated generation time.

Statistical modelling was carried out 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. To give a quantitative basis for the 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 characterise 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 parameterisation, which was used for the probability density of the Weibull distribution, is as follows:

$$f(d) = cd\ c{-}1/bc\ \exp\ (-(d/b)\ c) \quad [Eqn\ 4]$$

where diameter $d > 0$, $b > 0$ and $c \geq 0$.

The scale parameter (b) gives an indication of the characteristic diameter or height size of the population (it represents the 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 representing a healthy recruiting population with more juveniles than adults (Everard 1995; Moritz 2003). 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). The germination 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.

Results

Generation time

There was high variability in flowering height in the populations – some very small individuals (< 2 m) did have flowers or fruit, but other individuals greater than 20 m showed no signs of being reproductively active. For every one metre increase in height, the odds of having flowered increased by 1.18 [exp (0.16934)] overall. 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 had a BIC of 515 (Table 1) which was an 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 3).

It appears that reproductive maturity occurs more quickly at White River than Graskop (Figure 3) with individuals ± 6 m tall having a 60% probability of being reproductively mature, whereas at Graskop it took until ± 15 m for 70% of the individuals to be reproductively mature. On the contrary, at Graskop a significant proportion (± 20%) of the very small trees (< 3 m) were already flowering.

TABLE 1: Comparison three logistic models.

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

F, flowering; H, height; LOC, location.
^{ns}, not significant.
***, $p < 0.001$

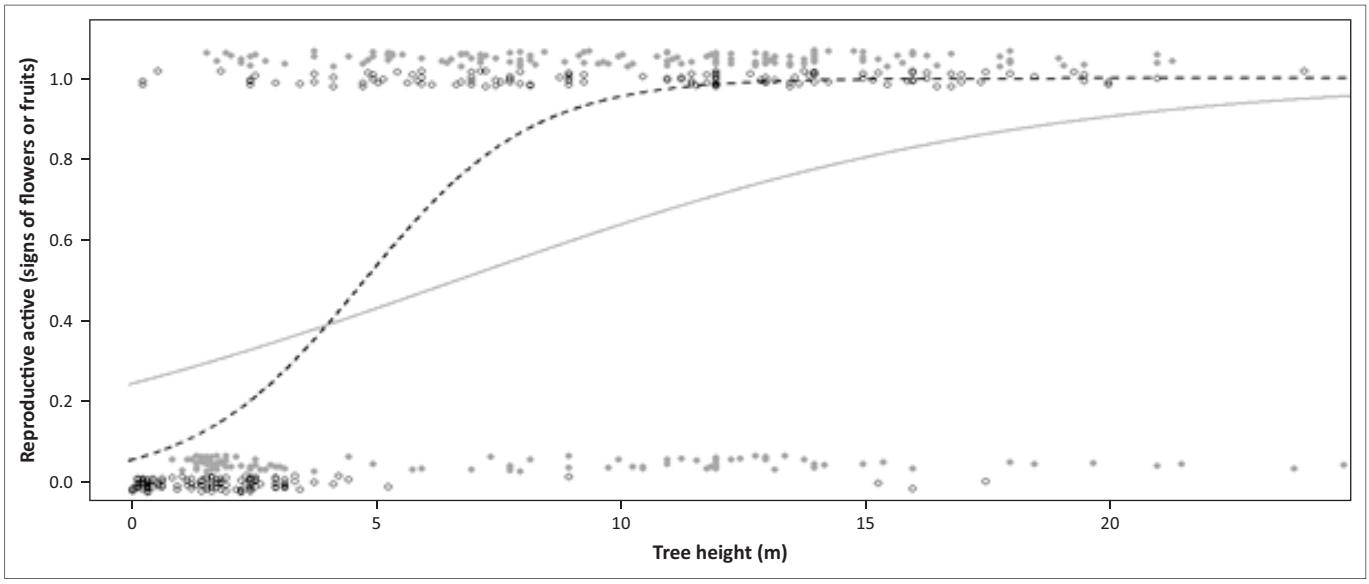


FIGURE 3: Height at first flowering of Graskop sites (black circles–dotted black line) and White River sites (dark grey solid circles–solid dark grey line). The Graskop data have been shifted up slightly (using the R function 'jitter') to make the comparison clear.

Demographics

Trees in White River were taller than those found in Graskop. The tall trees were found closer to the edge of the plantations at both locations, distance less than 10 m along the transects. These tall trees produced seeds thus spreading the eucalypts along the transects. The population densities in the sampling sites (from the edge of the plantation into the natural veld) ranged from 1000 stems/ha to 3378 stems/ha. There was no significant difference between the population densities in Graskop and White River (Mann–Whitney U test: $p = 0.64$). Resprouting was significantly different between sites (Mann–Whitney U test: $p = 0.02$) – with resprouts representing 46% of the population in Graskop and only 11.6% in White River. For all locations, resprouting increased with altitude ($R^2 = 0.70$, $p = 0.02447$; Figure 4).

Graskop and White River populations both had large numbers of individuals in the smallest stem diameter classes which follow the reverse-J curve, characteristic of good regeneration (Figure 5). However, in Graskop, there was a sharp step between the smallest and next smallest size class (67% of all individuals were < 5 cm) suggesting some sort of bottleneck. In White River, the distribution was smoother. Graskop also had fewer old trees (diameter > 20 cm) in the 'adults' class compared to White River.

Using height instead of diameter to define the size class distributions gave similar patterns (Figure 6). 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 3 m tall.

There was a strong relationship between height and diameter, as would be expected (Figure 7). 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.

Although there is obviously strong recruitment at both locations, there was considerable variability in size class distributions between sites (Figure 8) 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. 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, whereas 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), whereas all the other sites had unimodal functions: site 1 (1.5, absence of juveniles), site 3 (1.1, little recruitment) and 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, that is, trees in White River are larger on average than in Graskop. Shape parameter (c) values of the Weibull distribution decreased with increasing altitude, indicating that the proportion of juveniles: adults were generally higher at the high-altitude sites.

Germination rates

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 (Figures 8b and 9a) in Graskop and White River population (Mann–Whitney U test: $p = 0.29$).

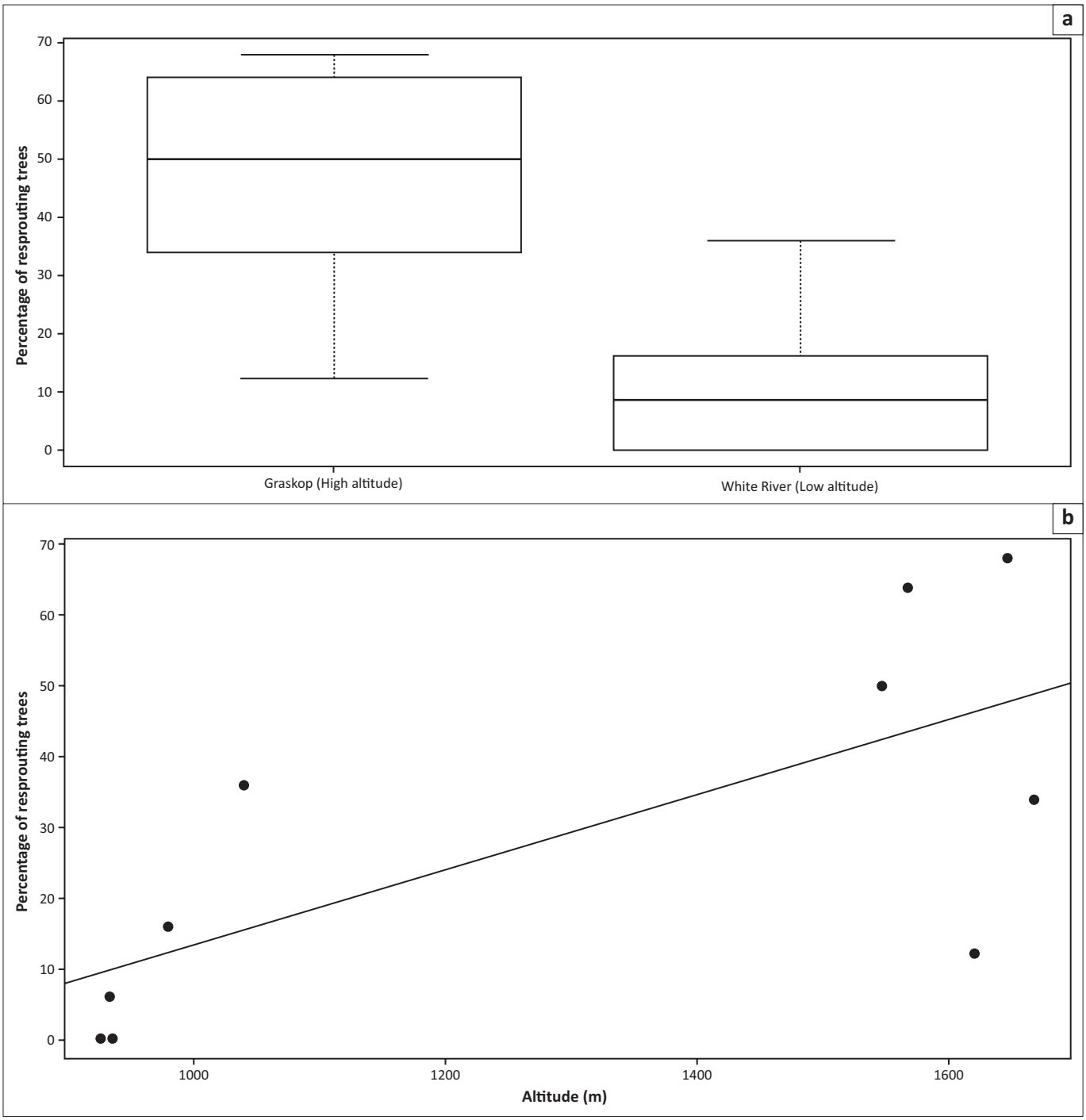


FIGURE 4: (a) Boxplots showing the percentage of resprouts across the sites in Graskop and White River. (b) Relationship between altitude and percentage of resprouts.

The time taken for 50% of the seeds to germinate ranged from 1.83 to 4 days (Figure 10), but again there was no significant difference between the germination rates between the two sites (Mann–Whitney U test: $p = 0.141$; Table 2).

Discussion

In terms of reproductive traits assessed, *E. grandis* has a potential to be a serious invader. Its seeds are viable, with short germination times, and no dormancy. The germination parameters of *E. grandis* are similar to those of other known invasive species such *Mikania micrantha* which has a mean germination index of 2.5 (Yang et al. 2005). At both sites, a significant proportion of the population was reproductively active by the time it was 5 m, and given that *E. grandis* can grow several meters a year (Oballa et al. 2010), this is in line with the 2- to 3-year generation times reported in the literature (NSW Department of Primary Industry 2010).

Importantly, these generation times are in the same range of other known invasive species which are causing a lot of problems, for example, *Pinus patula* can be reproductively mature in 2 years (Barrett & Mullin 1968), *Eucalyptus camaldulensis* in 3 years (CAB International 2000) and *Acacia*

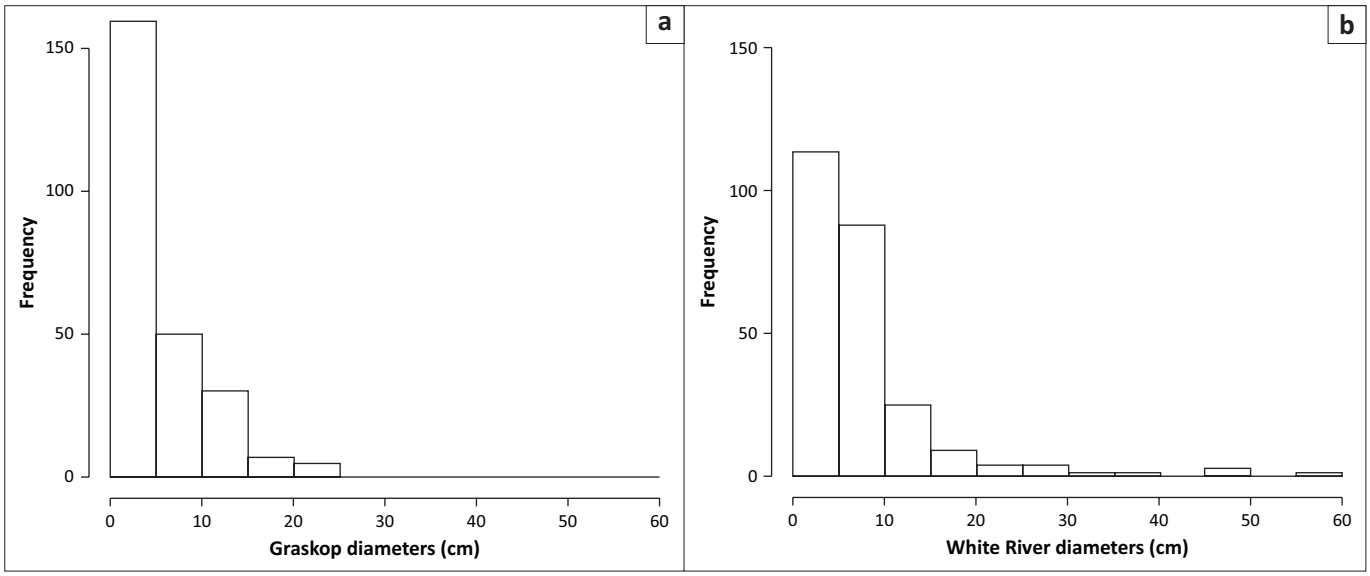


FIGURE 5: Diameter size class distributions of all the populations in (a) Graskop and (b) White River.

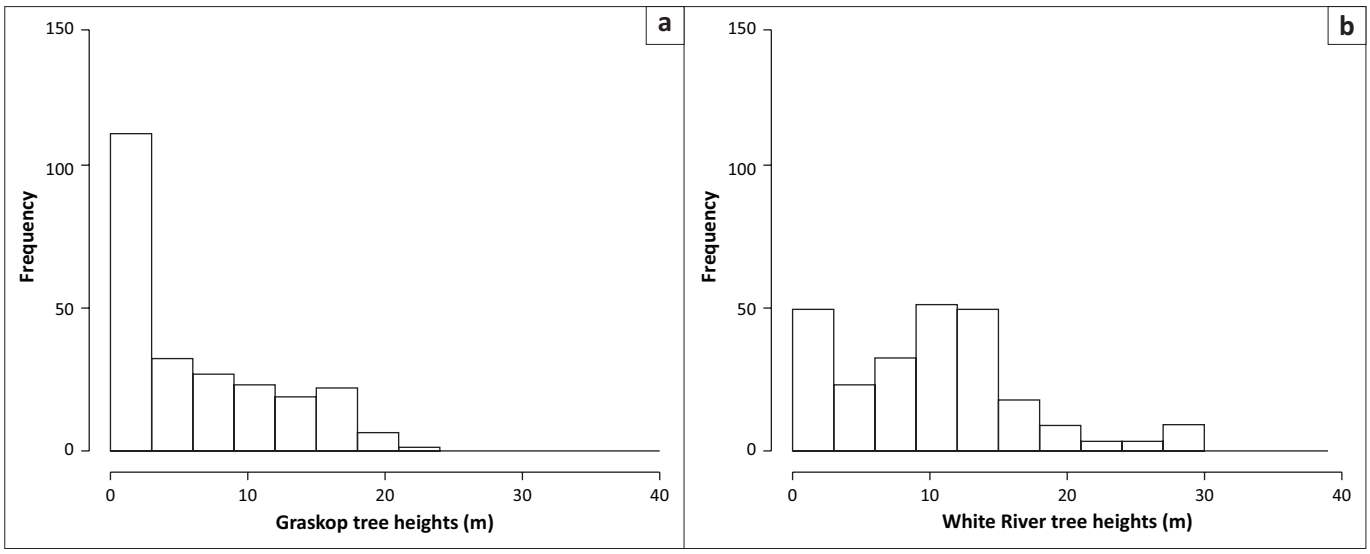


FIGURE 6: Height size class distributions of all the populations in (a) Graskop and (b) White River.

mearnsii in 20 months (FAO 2014). The demographics show that frost and other unknown demographic factors are slowing the rates at which *E. grandis* individuals mature. The high-altitude Graskop site had a clear reverse-J-shaped curve, with a sharp drop in frequency from the 2 cm to 6 cm diameter size classes (the 2 m – 5 m height size classes) (see Figures 4 and 5): evidence of a frost or fire trap which is supported by the substantial number (> 30%) of resprouting individuals in these populations.

These results suggest that frost might be hindering the rate of spread. Interestingly, we also showed 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 is 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.

Considering the high number of juvenile individuals in both populations and lack of evidence of mortality in the resprouting individuals at Graskop, these results suggest that the *E. grandis* populations are still at the establishing population stage of invasiveness (Williamson 2006). However, unlike other invasive species, which often have a dense seedling layer of newly recruiting individuals (Richardson et al. 1994), we recorded very few seedlings at our sites. Thus, there could be a demographic bottleneck at the seedling establishment phase that was not considered in this study.

Conclusion

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, Versfeld & Chapman 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 (SAPPI 2006). 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. Given that one of the strongest predictors of invasion is the number of introduction events and the spatial distribution of these introduction events, this is likely to increase the probability that *E. grandis* could become invasive. In this study, we found evidence that frost and some other factors (Table 3) 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 limit the spontaneous establishment of seedlings away from plantations (Rejmánek & Richardson 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

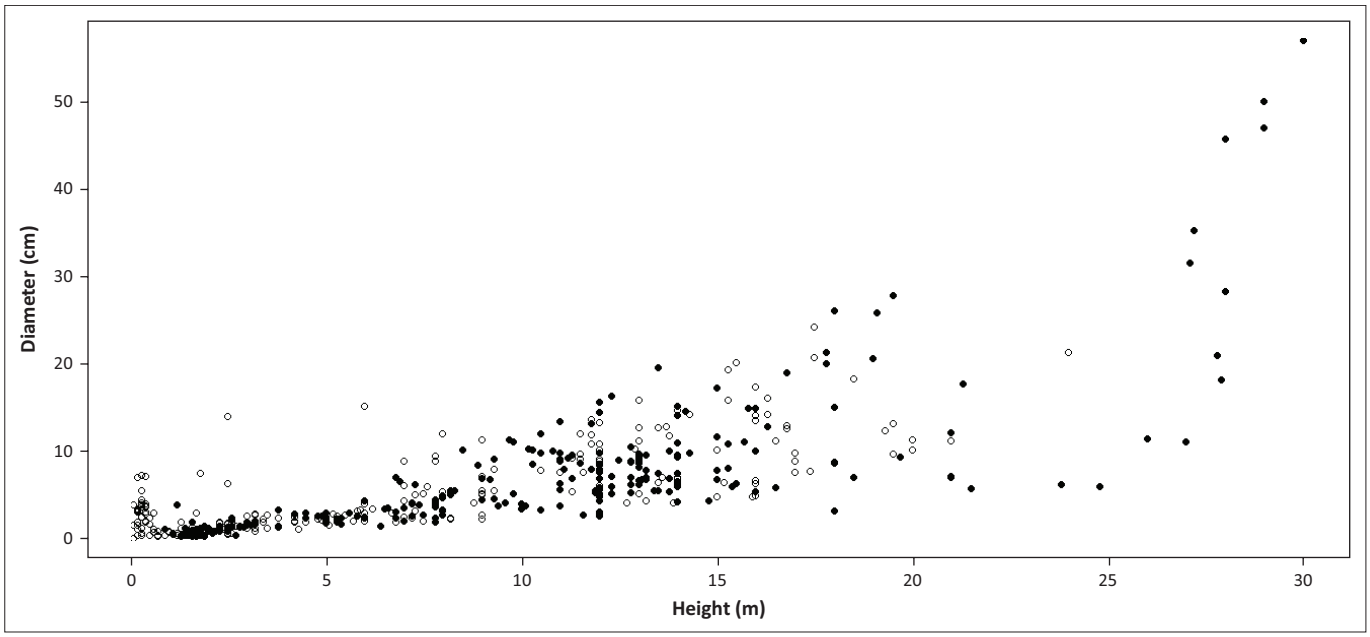


FIGURE 7: Relationship between height and diameter in Graskop (grey circles) and White River (solid black circles).

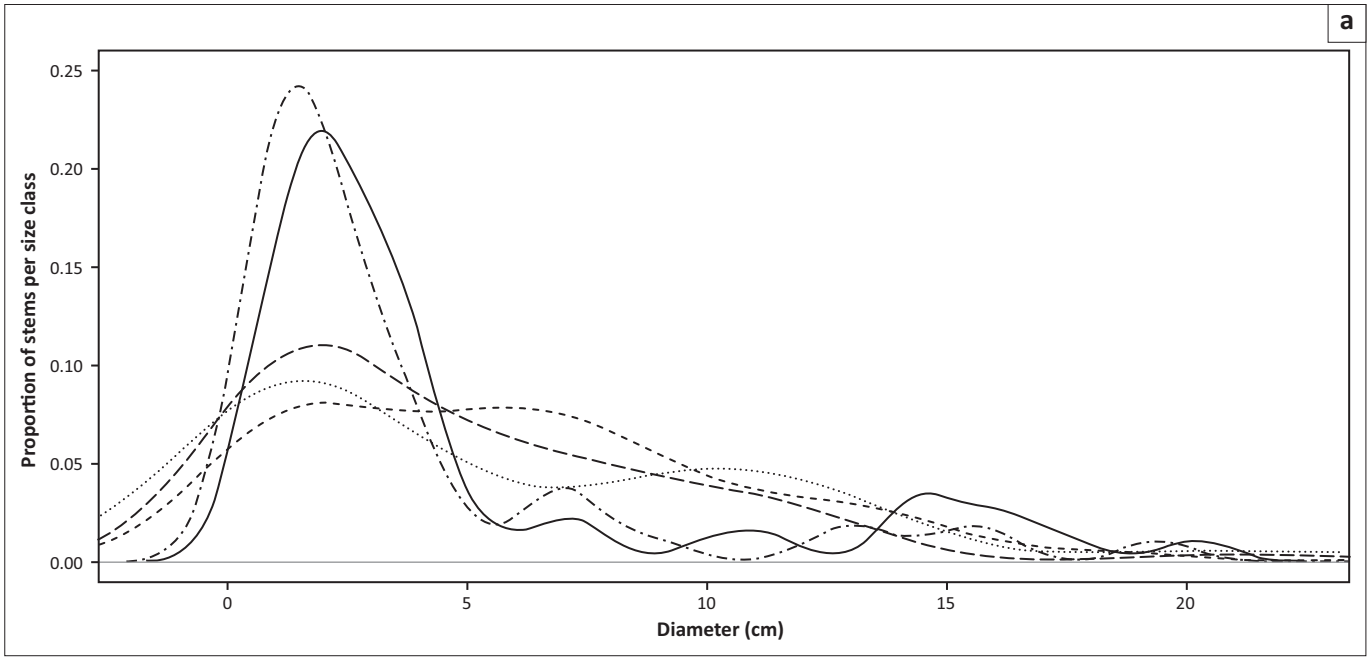


FIGURE 8: Density plot showing the variability in diameter size class distributions between sites: (a) Graskop sites and (b) White River sites (five sites for each location).

Figure 8 continues on the next page →

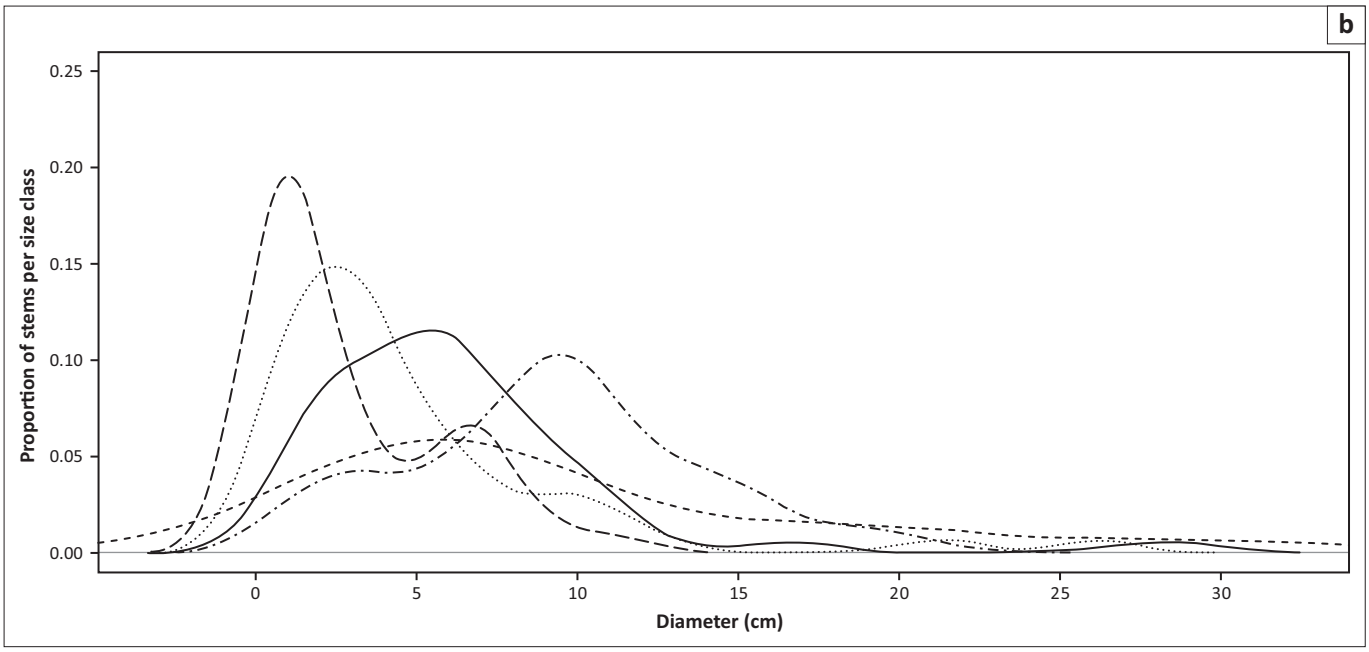


FIGURE 8 (Continues...): Density plot showing the variability in diameter size class distributions between sites: (a) Graskop sites and (b) White River sites (five sites for each location).

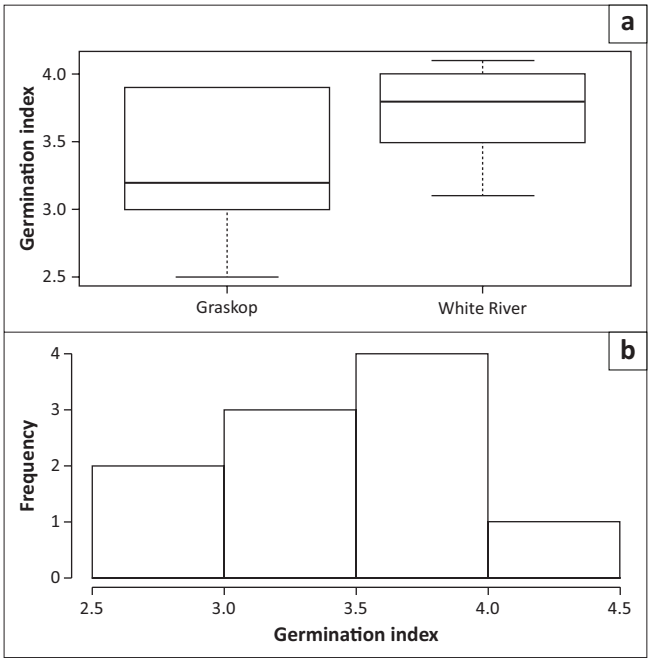


FIGURE 9: (a) Boxplots showing germination indices of Graskop and White River seeds. (b) Histogram showing the range of germination indices recorded in the 10 replicate samples (both White River and Graskop are included here as there was no difference between sites).

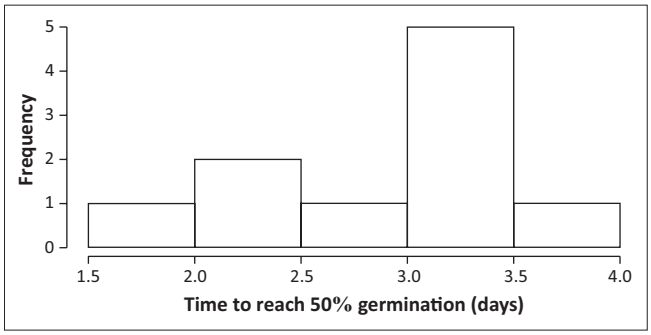


FIGURE 10: Histogram of the time taken to reach 50% germination.

TABLE 2: Summary of the descriptive statistics of eucalyptus seeds germination.

Location	Germination index		Time to 50% germination	
	Mean	Lower & upper quartile	Mean	Lower & upper quartile
Graskop sites	3.20	3.0–3.9	2.40	2.40–3.30
White River sites	3.80	3.5–4.0	3.44	3.43–3.47
All sites	3.70	3.1–3.9	3.40	2.40–3.50

TABLE 3: Summary of results in relation to demographic stage – and which factors might be important but were not considered in this study.

Demographic stage	Important factors	Factors considered	Impact on invasion
Seed germination	Germination rates, environmental controls on germination, seed predation	Germination rates	Unlikely to prevent invasion
Seedling establishment	Resources to grow and develop	None	Unknown, but data on seedling density indicate that it is much lower than other invasive species
Sapling release	Fire, frost, growth rates	Top-kill, environmental conditions, resprouting	Frost in combination with fire could slow invasion in cold areas
Adult reproductive output	Age at first flowering, growth rates	Flowering age	Unlikely to prevent invasion

incidence of frost decreases with the projected increase in winter temperatures (Engelbrecht, McGregor & Engelbrecht 2009), then more parts of the country will become suitable for rapid expansion of eucalyptus.

This article demonstrates that looking at the demographics of alien populations can give clues about (1) the rates at which they might be spreading and (2) the factors preventing them from spreading. Analysis of the population structure is the first step to gather information about the factors that

might be affecting populations of alien species. A similar approach might well be used for other species of concern such as *Eucalyptus camaldulensis Dehnh*. However, this study also, demonstrates that the factors controlling transition between all demographic stages need to be considered to conclusively assess invasive potential. Nonetheless, we show here that the chances of natural regeneration and spread of *E. grandis* have proven to be very high if the demographic bottlenecks are suppressed. Protected areas such as the Wolkberg centre of biodiversity which has red-listed plant species are already under threat and this can be worsened by the spreading of *E. grandis* once the demographic bottlenecks are suppressed.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

S.A. was the project leader and did the experimental and project design. K.M. was also responsible for the project design and collected the data in the field.

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