Seed ecology and growth comparisons of native (*Virgilia divaricata*) and invasive alien (*Acacia mearnsii* and *A. melanoxylon*) plants: implications for conservation

By

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DECLARATION

I, Stefan Albert Goets (210033134), hereby declare that the thesis for the degree *Magister Scientae* is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

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ABSTRACT

The abundance of invasive alien plants, with their numerous associated negative effects, has resulted in challenging and costly management requirements in South Africa. Management of invasives is further complicated when species have rapid inherent growth rates, atmospheric nitrogen fixing capabilities and large, persistent seed banks. Management strategies other than the usual mechanical, chemical, and biological (and combinations thereof) methods may be more effective. An alternative strategy is ’habitat management’, whereby management may be aimed at favouring native species. If the native species could compete favourably with, and possibly exclude, the invasive species, which is more likely when the species are ecologically similar, management may be more effective. This study investigated the competitive performance of two invasive species, *Acacia mearnsii* De Wild. and *Acacia melanoxylon* R.Br., and an indigenous ecological analogue, *Virgilia divaricata* Adamson, on the southern Cape Coast of South Africa. Both acacias are included among the five worst invasive species in the native forest and fynbos shrubland ecosystems. Performance was compared among the three species in terms of germination success (responses to five stimuli, namely chipping, hot water exposure, dry heat pulse, smoke, and control, incubated at 12 or 20°C), soil-stored seed bank densities and viability at different soil depths, and individual growth performance in seedling and sapling stages (and the effect of inter-specific competition on the latter). *Virgilia divaricata* performed comparably to the acacias in most aspects. Responses to germination stimuli at both temperature regimes were comparable among species, with chipping and hot water exposure resulting in the highest germination success. *Acacia melanoxylon* displayed poorer germination response under the cool temperature regime than the warm regime. Of the three species, *A. mearnsii* (7 596 seeds m^{-2}) had the highest seed bank density, followed by *V. divaricata* (938 seeds m^{-2}) and *A. melanoxylon* (274 seeds m^{-2}). Seed viability was high (87-91%) in all three species. Neither seed density nor seed viability differed significantly between soil depths, and there were no clear differences in this aspect between species. In terms of growth during the seedling stage, *V. divaricata* outperformed *A. mearnsii*. In the sapling stage, growth was comparable between the three species and was not affected by the extent of competition from neighbouring saplings. Overall, the findings of this study suggest that the success of *A. mearnsii* as an invader is primarily attributable to its large seed banks.

However, the good performance of *V. divaricata* seedlings and no apparent negative effect of competition on sapling growth from *A. mearnsii* and *A. melanoxylon* suggest that it may be used in the management of the acacias along with other management strategies. Due to the similarity observed between the three species, any management operation (such as fire) that would benefit *V. divaricata* recruitment would benefit the acacias equally (except for potentially reduced germination of *A. melanoxylon* in cooler seasons). Management should thus attempt to prevent the germination of *Acacia* seeds. Alternatively, dense localised *Acacia* seed banks may be reduced by repeat burning. On a small scale, areas where *V. divaricata* would occur naturally (or which are completely compromised ecologically) can be seeded with pre-treated (chipped or hot water exposure) *V. divaricata* seeds. If *V. divaricata* is given enough time to establish dense stands, subsequent germination and growth of the acacias should be suppressed and simultaneously promote forest re-establishment. To further decrease *Acacia* success, biocontrol (seed-boring weevils, flower-galling midges, and rust fungus) should be widely disseminated.

Keywords: habitat management, germination requirements, invasive alien plants, performance comparison, rehabilitation, sapling growth, seedling growth, soil-stored seed bank density and viability, southern Cape Coast, South Africa, weed management.

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GENERAL INTRODUCTION

RATIONALE

The introduction of alien plant species coincides with human movements around the world, often being related to the functional, aesthetic, or resource value of the species (Henderson, 2001; Mack et al., 2000; Singh, 2010). After having overcome several barriers, an alien plant species may colonise a new environment and spread to new areas, thus becoming invasive (Vermeij, 1996). Most areas around the world with permanent human populations have at least some invasive alien plants (IAPs). IAPs often have many negative impacts on the invaded environment, which may impact humans as well. Some of these impacts include a reduction in biodiversity, alteration of fire regimes or nutrient cycles, and a reduction in water yield from mountain catchments (de Wit et al., 2001; Dye and Jarmain, 2004; Giraud et al., 2007; van Wilgen and Richardson, 1985). Since 2013, approximately 751 species of shrubs and trees have globally been considered as serious invaders (Rejmánek and Richardson, 2013). In South Africa, 379 plants are listed as invaders by NEMBA (National Environmental Management: Biodiversity Act No. 10 of 2004, 2014; OECD, 2013), whilst the southern Cape is a region that has large numbers of alien plants, many of which are invasive (Baard and Kraaij, 2014). Two invasive species, *Acacia mearnsii* De Wild and *Acacia melanoxylon* R.Br., have become well established in South Africa and the southern Cape after being introduced in the mid-1800s for their resource value (Baard and Kraaij, 2014; Bromilow, 1995; Hierro et al., 2005; Louppe et al., 2008). Both species originate from south to south-eastern Australia and Tasmania (Louppe et al., 2008; Searle, 1997) and are fast growing, medium to tall trees from the Fabaceae family (Miller et al., 2011; Searle, 1997).

Management of IAPs, depending on the species, generally involves combinations of manual, chemical, biological, or habitat management techniques (Wittenberg and Cock, 2001). IAPs that have dense, long-lived, soil-stored seed banks tend to require extensive and repeated management input (DiTomaso and Barney, 2012). Such seeds often require a specific stimulus before they can germinate (Baskin and Baskin, 2001), which means an area previously cleared of IAPs can be recolonised if the correct stimulus is present. If not managed correctly, species with long-lived seed banks may require major operational investment, as numerous follow-up treatments may be required (Holmes et al., 2008). Management therefore needs to consider the number and longevity of seeds remaining in the soil after an individual (or stand) has been removed, and what factors may cause them to germinate. Both of the studied acacias, *A. mearnsii* and *A. melanoxylon*, have seeds which may remain dormant in the soil for at least 50 years and germinate rapidly following disturbances such as fire (Richardson and Kluge, 2008). Management of these species thus require both the management of the trees and the biophysical environment. A management strategy often used in integrated pest management, referred to as habitat management (Horne and Page, 2008), may be an effective alternative. Habitat management involves the management of the environment to favour a preferred species and be detrimental to unwanted species (i.e. IAPs). This may, for instance, involve altering fire regimes to favour germination of indigenous species, or using indigenous species as competitors.

Virgilia divaricata Adamson is a tree native to the southern Cape coast of South Africa, occurring primarily in forest-fynbos ecotones where it provides microclimates in which forest species can establish (Coetsee and Wigley, 2013; Geldenhuys, 1994). It also belongs to the Fabaceae family and is considered ecologically analogous to *Acacia mearnsii* and *Acacia melanoxylon* in terms of growth rate and production of long-lived seed (Geldenhuys, 1994; Phillips, 1926; Praciak et al., 2013; Richardson and Kluge, 2008; Searle. 1997). Due to its ecological similarity to the acacias, it is expected that *V. divaricata* may be able to compete with or even suppress the two invasive species. In another study (McDowell and Moll, 1981), a congeneric species, *Virgilia oroboides* (P.J.Bergius) Salter, was able to suppress germination and seedling development of two other invasive species, *Acacia longifolia* (Andr.) Willd. and *Paraserianthes lophantha* (Willd.) I.C. Nielson (formerly *Albizia lophantha*). This ‘limiting similarity theory’ has been well documented (see Cleland et al., 2011), but does contradict the theory of adaptive evolution, whereby an invasive species possesses traits which allows it to adapt genetically to novel environments (Molinier et al., 2006). Understanding how native and invasive species interact may inform management in terms of potential integrated approaches to manage the invasive species.

This study is aimed at providing an understanding of the competitive performance, in terms of germination success, seed bank density, viability and persistence (using depth within the soil as a proxy for age), and growth rates between *V. divaricata* and the two invasive acacias. The data chapters (2, 3, and 4) are written in paper format, resulting in some replication of text and separate reference lists. The thesis is structured as follows:

Chapter 1 provides the rationale for the study by reviewing the literature on the ecological process of invasion and methods of IAP management, with emphasis on the use of native species in management approaches.

Chapter 2 compares the germination responses (both in terms of total response and response over time) of the three study species to different stimuli at two temperatures (representing the cool and warm seasons), with the use of germination chambers. This chapter was submitted as a research paper to S.A. Journal of Botany: 11/2016.

Chapter 3 quantifies the seed bank densities and seed viability of each species, and its vertical distribution in the soil profile, under the canopies of mature trees in the field.

Chapter 4 compares the growth rates of the three study species during the seedling (nursery study) and sapling stages (field study) and explores the effect that competition has on sapling growth.

Chapter 5 synthesises the findings of the various chapters. Recommendations are also made to improve the management of the acacias.

STUDY AREA

The study area is located on the southern Cape coast of South Africa, between the towns of George (33°58’S, 22°27’E) and Nature’s Valley (33°58’S, 23°33’E), with the Outeniqua and Tsitsikamma Mountains to the north. The area has a temperate climate with year-round rainfall (peaking in April and October) averaging 800 mm annum^{-1} in the west to 1078 mm annum^{-1} in the east. The area experiences mild temperatures, with minimum and maximum daily temperatures ranging from 7°C and 19°C (respectively) in June (winter) to 15°C and 26°C (respectively) in January (summer) (Bond, 1981; Southwood, 1984). The underlying geology of the area consists of sandstone, quartzite, and shales from the Table Mountain Group. The study sites were distributed on the coastal plateau and lower slopes of the mountains with colluvial and alluvial soils with yellow-brown to grey-brown colour and sandy loam to silty loam textures (Schafer, 1992). The quartzitic and sandstone origin of the soils results in a generally low pH (3.5-5) (Schafer, 1992). The major soil groups in the area are duplex (Estcourt and Klapmuts), hydromorphic (Longlands and Katspruit), and podzols (Lamotte and Witfontein) (Soil Classification Working Group, 1991).

The native vegetation of the area comprises fynbos shrublands, which are fire-dependent and fire-prone (average fire return intervals being 8-26 years; Kraaij et al., 2013), and Southern Afrotemperate forests, which do not burn except under extreme hot and dry conditions (Geldenhuys, 1994; Mucina and Geldenhuys, 2008; Rebelo et al., 2008). Extensive commercial pine plantations and agricultural land in the region have created a fragmented and disturbed environment, resulting in high densities of IAPs (Kraaij et al., 2011; Baard and Kraaij, 2014). *A. mearnsii* has been ranked as the most prominent invasive species in fynbos ecosystems, and third-most prominent in forest ecosystems, while *A. melanoxylon* has been ranked fifth in fynbos and fourth in forests (Henderson, 2007).

STUDY SPECIES

Virgilia divaricata

Virgilia divaricata, originally thought to be a form of *Virgilia oroboides*, is a tree in the Fabaceae (legume) family indigenous to a narrow strip along the southern Cape coast of South Africa (Coates Palgrave et al., 2002). As with many species in the Fabaceae family, it has the ability to fix atmospheric nitrogen (Ramirez-bahena et al., 2013; Vardien et al., 2014). Virgilias are some of the most rapidly growing tree species in South Africa (van Wyk, 1982), attaining heights of 5-8m within four years following germination (Philips, 1926). The lifespan of *V. divaricata* is on average 20 years, although it may live to 40 years (Phillips, 1926). One of its most important ecological functions is as a pioneer species particularly for Southern Afrotemperate forest establishment after fire damaging forest margins (Coetsee and Wigley, 2013). The persistent, soil-stored seed bank, which may remain dormant for at least 230 years, enables dense populations of *V. divaricata* to rapidly establish after fire (Geldenhuys, 1994). The fast growth rate, long-lived seed banks, and nitrogen fixing capabilities of *V. divaricata* make it ecologically analogous to the two acacias, which may allow it to compete favourably with the invasives in habitats suitable for its own persistence (Daehler, 2003; Strauss et al., 2006; Turnbull et al., 2005). Studying the competitive ability of *V. divaricata* in relation to that of the alien acacias may provide insight into its potential for incorporation in the various IAP management strategies implemented in parts of South Africa.

Acacia mearnsii

Acacia mearnsii (black wattle) is a fast growing, woody species in the Fabaceae family originating from south-east Australia and Tasmania within eucalypt forests and woodlands (Searle, 1997). This species has been introduced to many parts of the world and is considered to be one of the 100 most invasive species in the world (Lowe et al., 2000). It was initially introduced into the Natal Province of South Africa in the mid-1800s for use in windbreaks, however, extensive planting of *A. mearnsii* in plantations occurred after its use for the tannin industry was realised in 1889 (Browmilow, 1995; Searle, 1997). *Acacia mearnsii* timber is also used for pulp and firewood, as well as for poles in the mining industry (Bromilow, 1995). There are currently 110 000 ha of managed (commercial, corporate, and small-scale growers) *A. mearnsii* plantations in South Africa (Chan et al., 2015). Since its introduction, the species has spread and has become well established in areas outside of commercial plantations, especially where disturbance has occurred (Hierro et al., 2005). The extent of *A. mearnsii* invasions in South Africa has been estimated at *c.* 459 000 condensed ha (total area covered by species condensed to indicate the area covered at 100% density; Forsyth et al., 2011). This is an area four to five times larger than the area managed as plantations, with fynbos, grasslands, savannas, native forests, and Albany thickets most affected by invasions (Henderson, 2007). It is also the most problematic alien plant in riparian zones in South Africa and the species with the greatest impact on water resources (Holmes et al., 2005; Le Maitre et al., 2016). As an invasive, it has been given the status of transformer, which indicates the species' ability to "change the character, condition, form, or nature of ecosystems over a substantial area"

(Richardson et al., 2000). *Acacia mearnsii* has an average lifespan (in natural conditions) similar to that of *V. divaricata*, i.e. an average of 20 years (Praciak et al., 2013). Invasions of *A. mearnsii* are associated with various negative ecological impacts. Along water courses, reduced surface flow occurs due to the increased plant biomass resulting in increased rainfall interception and transpiration (Le Maitre et al., 2011). Increases in plant biomass may also result in increases in the intensity of fires that remove more vegetation thus increasing surface runoff, while the dense nature of stands can restrict access for fire-fighting operations (de Wit et al., 2001; Le Maitre et al., 2011). There can also be an increase in erosion following a fire, due to the exposed soil surface (de Wit et al., 2001), which is further exacerbated by the shallow rooting depth of *A. mearnsii* (Searle, 1997). Other losses include that in biodiversity due to the formation of monospecific stands of *A. mearnsii*, loss of grazing potential in grassland areas, a decrease in recreational and aesthetic values and an overall loss of ecosystem services (Le Maitre et al., 2011). An additional effect of *A. mearnsii* occurring within fynbos, is the addition of nitrogen (through fixation of atmospheric nitrogen) in a system that is adapted to nutrient-poor soils (Witkowski, 1989). This provides the opportunity for other competitive, nutrient-requiring IAPs (e.g. grasses) or other non-fynbos species to colonise the area (Hobbs and Huenneke, 1992; Yelenik et al., 2004).

Management of *A. mearnsii* is particularly challenging and mostly requires multiple follow-up treatments, which often prove ineffective in decreasing the density of invasion (Kraaij et al., in press; van Wilgen et al., 2016). This is due to its ability to resprout from the base of the stem if damaged (Mandle et al., 2011) and the formation of dense (5 314 - 38 340 seeds m^{-2}; Pieterse, 1997; Milton and Hall, 1981) long-lived, soil-stored seed banks (Richardson and Kluge, 2008). Current active management procedures include labour-intensive felling and subsequent treatment of the cut surface with herbicide (Holmes et al., 2000), and foliar application of herbicide to seedlings (Viljoen and Stoltsz, 2008). Passive management, through biological control, is also in effect in the form of a seed-boring weevil (*Melanterius maculatus* Lea) and flower-galling midge (*Dasineura rubiformis* Kolesik) (Impson et al., 2008, 2009).

Acacia melanoxylon

Acacia melanoxylon (black wood) is a fast growing, long-lived tree in the Fabaceae family, originating from eastern Australia where it grows in swamp forest, riverine rainforest, and wet eucalypt forests (Louppe et al., 2008; Praciak et al., 2013). It was introduced into Cape Town, South Africa, in 1848 and into the southern Cape in 1856 (Geldenhuys, 1996) for its valuable timber used especially in the production of high quality furniture (Louppe et al., 2008). *Acacia melanoxylon* was planted in forest gaps resulting from indigenous timber harvesting and burnt patches occurring within indigenous forests since 1876, with the first large-scale introduction into native forests occurring in 1909 (Seydack, 2002). Large-scale planting was ceased in 1927, presumably due to the study conducted by Phillips (1928) indicating the invasive nature of *A. melanoxylon*, and thereafter undertaken only sporadically until the 1960s (Seydack, 2002). Since the early 1980s, the approach to management of *A. melanoxylon* in State Forests of the southern Cape has gone through various stages ranging from aiming for sustainable management of a timber resource to regarding it as an undesirable invasive species that requires management (Geldenhuys, 1986, 1992, 1996; Grewar, 1982; Seydack et al., 1982). In 1981, the planting of *A. melanoxylon* in forest gaps ceased, with trees greater than 10cm diameter at 1.3m left standing to be harvested for timber utilisation (Geldenhuys, 2004; Vermeulen and Seydack, 2000). As of 2014, South African National Parks, a parastatal organisation now managing extensive State forests in the southern Cape, has implemented the policy of managing *A. melanoxylon* as an invasive species, as opposed to a sustainable resource (Moolman and Rikhotso, 2014). Since its introduction, and through its propagation and exploitation as a timber species, it has become well established within natural forests, in the interior of which they do not dominate, whilst in areas subject to disturbance, such as forest gaps, forest-fynbos margins and riparian areas, it can proliferate and form monospecific stands (Louppe et al., 2008). The species has seed that are dispersed by water and birds (Praciak et al., 2013), thus becoming increasingly problematic in some fynbos areas, riparian areas intersecting forest and fynbos (Baard and Kraaij, 2014), forest-fynbos ecotones, as well as fynbos areas that have been subject to prolonged disturbance or degradation such as in former pine plantations (the latter comprising extensive areas in the southern Cape; Kraaij et al., 2011). This species is problematic due to its ability to resprout from root suckers (Praciak et al., 2013) and the production of large quantities of seed (2 860-94 420 seeds m^{-2}; Donald 1959 cited in Milton and Hall, 1981) that can remain dormant in the soil for at least 50 years (Richardson and Kluge, 2008). To prevent vigorous coppicing, herbicides are used on cut stumps or ring-barked trees (Holmes et al., 2000; van Wilgen et al., 2011). In addition to active management, a seed-boring weevil (*Melanterius acaciae* Lea) has been introduced in the area with extensive success (Dennill et al., 1999; Impson et al., 2009, 2011).

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CHAPTER 1 - Literature review: The dynamics and effects of plant invasions, and the management thereof, also considering seed ecology and plant growth competition

INTRODUCTION

Few areas of the world are free of alien species, including invasive alien plants (IAPs), and the negative effects these have on the environment (Mack et al., 2000; Randall et al., 1996). Alien invasions have increased rapidly over the past few centuries (Richardson and Rejmánek, 2011), as a result of expanding human migrations and commerce (Mack et al., 2000). In 2013, 751 species of trees and shrubs were globally considered as serious invaders (Rejmánek and Richardson, 2013). There are several reasons why alien species are introduced into an area and may have the potential of becoming invasive. Certain species have a high economic value when grown and harvested for various end-uses (Singh, 2010). Some of the primary uses obtained from plants include timber, poles, and pulpwood (e.g. *Pinus radiata* D.Don; Mead, 2013) as well as chemicals such as rubber (e.g. *Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg.; Singh, 2010). Other reasons for introducing aliens include the provision of services such as dune stabilisation (e.g. *Acacia cyclops* G.Don and *A. saligna* (Labill.) Wendl.; Kutiel et al., 2004; Turnbull, 1987), wind breaks and hedgerows (*Hakea* species), and aesthetic/ornamental purposes (e.g. *Lantana camara* L.) (Henderson, 2001). When alien species that are of economic value are managed in a precautionary manner, negative impacts can often be localised to small areas. There are, however, factors that enable alien plant species to become invasive in an area. Such factors include the absence of that species' natural competitors or predators, severe degradation of the habitat associated with the exclusion of potential native competitors, increased global trade, and presence of dispersal agents such as vehicles as well as local species of fauna such as birds, mammals and ants (Nentwig, 2007; Schiffman, 1997).

In pre-colonial Southern Africa (pre-1652), the country would have been relatively free from exotic plant species, excepting for those species used by the native agro-pastoralists (Ross, 2008). In 1652, van Riebeeck and a group of Dutchmen (representing the Dutch-East-Indian Company) established a trading post in the vicinity of modern day Cape Town, which later became a permanent Dutch colony (Ross, 2008). Intentional and unintentional introduction of alien plant species subsequently occurred and have continued to occur, with some of these species becoming invasive. In 1997, it was estimated that *c.* 10 million hectares (ha) have been invaded in South Africa by 180 IAP species (van Wilgen et al., 2001) with a more recent study estimating *c*. 20 million ha affected by 379 species (OECD, 2013; National Environmental Management: Biodiversity Act No. 10 of 2004, 2014). In addition to the recognised IAPs, at least 9 000 additional casual or naturalised alien plant species are present in South Africa (Irlich et al., 2014), some of which may also have the potential to become invasive (van Wilgen et al., 2001).

The negative impacts associated with IAPs can range from minor, localised effects to major, landscape effects that can under particular conditions lead to regional catastrophes (Hillebrand et al., 2008). The type and scale of effects depend predominantly on the ecology of the invading species in relation to the ecology of the receiving area, and its density within that area (Vilà and Weiner, 2004). South Africa has a rich diversity of species, many of which are endemic and require specific ecological drivers, such as fire, to occur in order to flourish (Linder et al., 2010).

IAPs alter habitats and ecological processes which may have negative impacts on the native fauna and flora within those areas, occasionally resulting in extinction (Gurevitch and Padilla, 2004). This is of concern in the Cape Floristic Region (CFR), where approximately 9 000 plant species (of which 69% are endemic) exist within a relatively small area of 9 000 000 ha (Goldblatt and Manning, 2000). In the CFR, it is estimated that approximately 1 021 plant taxa are threatened due to invasive species, which is second only to the 1 307 taxa threatened by habitat loss (Rouget et al., 2014). Management of IAPs based on an understanding of the pathways and processes of invasion and their effects could ameliorate the impacts the IAPs have on native species and ecosystems.

THE DYNAMICS OF PLANT INVASION

Before a species can be considered as invasive, it must first complete four successive stages of invasion, and failing to survive past the initial stages would inevitably prevent the species from becoming invasive (Vermeij, 1996). Understanding the dynamics of invasion can greatly influence the way in which IAPs are managed and whether or not an invasion will succeed or fail (Lockwood et al., 2007).

Stages of invasion

All IAPs follow the same sequence of stages when invading a new region, although certain species may advance through the stages more rapidly than others. This section will discuss the process of invasion according to the different stages described by Theoharides and Dukes (2007).

Transport

The transport stage involves moving the propagule/s of a species from one biogeographic region to another, either by accident or intentionally (Theoharides and Dukes, 2007). Propagules may include the plant itself, the seeds, or any part of a plant (leaves, hardwood or softwood stem, roots, corms, and tubers) that would be able to reproduce vegetatively (Bird, 2014). The overall probability of invasion partly depends on the quantity of propagules transported, as well as the probability of the propagules to survive being transported over long distances (Simberloff, 2009; Theoharides and Dukes, 2007). Transporting of propagules may occur through international trade, tourism, travel, or transport industries, with most alien species having been introduced into new areas through trade (Burgiel et al., 2006; Perrings et al., 2000; Westphal et al., 2008).

The trading of exotic plants and animals is a large industry internationally, and has increased significantly following the industrial revolution of the 1800s (Hulme, 2009). Numerous studies have related the establishment of IAPs to various anthropogenic factors. Measures indicating economic activity, such as GDP per capita, real estate gross state product, the Human Development Index, as well as human population density, may serve as surrogates for ecological disturbance and alien plant propagule pressure, thus facilitating IAP establishment (Vilà and Pujadas, 2001; Westphal et al., 2008).

Propagules can easily be transported along with materials such as gravel, timber and thatching (Burgiel et al., 2006; Hulme, 2009). Another method of introduction is by being attached to vehicles (Hulme, 2009), for example along with cargo ships' ballasts.

International shipping lanes therefore provide transport for many aquatic and terrestrial species through the movement of large volumes of water within ship ballasts (Keller et al., 2011). For instance, in the Great Lakes region of North America, 60% of introduced IAPs are attributed to the commercial shipping sector (Horan and Lupi, 2005). Land based vehicles can also be vectors, i.e. seeds lodged in mud stuck to the underside of a vehicle (Clifford, 1959) or sucked into air intakes (Lonsdale and Lane, 1990). Road and railway networks therefore act as corridors for introduction of alien species (Hansen and Clevenger, 2005; Kalwij et al., 2008). The use of imported fodder for livestock has also resulted in the establishment of invasive species, especially grasses (de Villiers and Cooper, 2008). The dispersal strategy of certain plants involves the propagules having special structures (e.g. spines or barbs) or covered in sticky substances that allow them to become attached to vectors (Howe and Smallwood, 1982). Naturally, animals would act as vectors when the propagules stick to their fur or in their skin (Manzano and Malo, 2006). Humans therefore act as vectors for plants when propagules become attached to clothing, transporting species over large distances unintentionally (Pickering and Mount, 2010).

Colonisation

Propagules of alien species that have survived the transport stage do not necessarily create a new population (Mack, 2000). They must be able to survive in the new edaphic and climatic conditions, as well as adapting to the biotic processes of the new habitat (Sakai et al., 2001; Theoharides and Dukes, 2007). The newly introduced population must achieve positive growth rates whilst still at a low density (Chesson, 2000; Sakai et al., 2001). Due to the small population sizes and low densities of founder population/s, factors such as stochastic events, low genetic variability, and the Allee effect can hamper or completely halt colonisation (Sakai et al., 2001). The Allee effect refers to the inverse density dependence occurring at low population densities, and occurs as a result of the loss of population fitness due to genetic inbreeding, demographic stochasticity, and a reduction in cooperative interactions within the species population (Courchamp et al., 1999).

Limitations to colonisation can be divided into two major categories, namely propagule pressure and an interaction between abiotic filters and species traits (Theoharides and Dukes, 2007). Propagule pressure relates to the number of propagules arriving in the new area during a single introduction event, and the number of individual introduction events (Lockwood et al., 2005; Pauchard and Shea, 2006). Multiple introduction events occurring across a wide region of the new area will increase the likelihood of the propagules being introduced in an area conducive to colonisation (Lockwood et al., 2005). Repeated introductions to the same area will increase the probability of the founder population's persistence, as well as improving its genetic variability (Lavergne and Molofsky, 2007; Lockwood et al., 2005; Sakai et al., 2001).

The interaction between the abiotic filters and traits of the colonising species can improve or reduce the probability of successful colonisation (Theoharides and Dukes, 2007). This interaction refers to the requirements of the species in relation to abiotic factors such as local climate and resource availability, as well as edaphic and physiographic conditions (Mitchell et al., 2006). Climatic differences between the colonising species' native range and the new region can affect the species' survival (Rejmánek, 1999). However, climate alone does not always determine the success of the colonisation, as there are records of species successfully colonising a new area under different climatic conditions and others failing to colonise under conditions similar to its native distribution (Mack, 1995). A species that has a wide native range with varying climates, will be more likely to colonise under variable climatic conditions and have improved resistance to stochastic events (Goodwin et al., 1999).

The availability of resources, such as space, nutrients, light, and water can impede or promote colonisation, depending on the traits of the colonising species (Davis et al., 2000). These traits include the effectiveness of resource use, the ability to grow under various light conditions, or the ability to fix nitrogen from the air (Funk and Vitousek, 2007). The variability in resource availability affects different colonising species differently. Species that are able to utilize available resources effectively will have an advantage in an area that has undergone a disturbance but has abundant resources (Sher and Hyatt, 1999). Conversely, a disturbed area with low nutrient availability will have little competition from native, unspecialised species and will benefit colonising species that are nitrogen fixers. The propagule pressure required for successful colonisation therefore depends on the state in which the new region exists. A region which has undergone a disturbance, which removes native competition, may require less propagule pressure than an area with intense competition from the native plant communities (Lockwood et al., 2005). Due to these limiting factors, only *c.* 10% of species that have survived the transport phase are able to colonise the new area (Williamson and Fitter, 1996).

Establishment

For establishment to take place, the colonising individuals must form a self-sustaining population, which are able to spread beyond the area of the initial introduction (Theoharides and Dukes, 2007). The establishment stage may have a longer duration than colonisation, and can occur over a larger spatial scale (Theoharides and Dukes, 2007). During this stage, the establishing populations are more exposed to biotic filters, which are limiting factors to an invasion that originates from the presence or actions of other living organisms affecting vitally important aspects of the establishing species such as growth, survival, and reproduction (Theoharides and Dukes, 2007). Additionally, the establishing populations are sensitive to stochastic catastrophic events, such as droughts or fire (Mack, 1995). To increase the probability of successful establishment, the establishing species must have traits that would increase its competitive performance and reduce overlap of niches or resource acquisition strategies between the alien and native plant species (Dietz and Edwards, 2006; Lloret et al., 2005). Another trait that improves competitive performance and survival is the production of secondary metabolites to which the native flora and fauna are not accustomed, and includes compounds that would deter herbivory or suppress the growth of nearby plants (Callaway and Ridenour, 2004; Dietz and Edwards, 2006).

Competition is an important biotic filter, but unlikely to fully account for the exclusion of IAPs (Levine et al., 2004). Competition rather forms part of a complex set of interactions which takes place at the community scale, and also includes interactions such as predation or disease (Levine et al., 2004; Theoharides and Dukes, 2007). During the establishment stage the seed banks within populations of the invading species will have become more abundant, safeguarding the population against factors such as competition and stochastic events in the long term (for more detailed descriptions see ‘competition’ and ‘seed ecology’). Abiotic filters also have an interaction at the community level. For example, the amount of nutrients available for use by an IAP can depend on the structure and intactness of the native community (Theoharides and Dukes, 2007). The diversity of the community, the interaction among the species within the community, the interaction among trophic levels, and the interaction between the community and the abiotic filters are factors contributing to the area’s resistance to invasions by plant species (Dukes, 2001; Knops et al., 1999; Ruijven et al., 2003). An intact community would therefore have a greater resistance against even a highly aggressive invader as a collective, even if the individual native species are not highly competitive (Hooper et al., 2005).

Landscape spread

A successfully established population of an introduced plant will often undergo a lag phase before landscape spread (the final stage of invasion) can occur. This often depends on the IAP’s rate of adaptation to the new environment and native community, as well as the availability of adequate genetic variability of the introduced species (Barney, 2006; Sakai et al., 2001). The lack of suitable habitat for new introductions, climate variability, or low densities of the introduced species may prolong the lag phase (Pyšek and Hulme, 2005). The lag phase may be shortened by repeated introduction events and a high degree of migration and gene flow among established populations (Sakai et al., 2001).

Landscape spread occurs at the scale of the regional metacommunity (Theoharides and Dukes, 2007), with a metacommunity consisting of a group of populations in a region, interconnected through long-distance dispersal (Melbourne et al., 2007). Spread is similar to long-distance transport, although the transport stage occurs at an inter-regional scale, whereas spread occurs within a region (Theoharides and Dukes, 2007). At the metacommunity scale, there are communities existing in various stages of colonisation or establishment, and landscape spread therefore incorporates all three preceding stages (Theoharides and Dukes, 2007). Exponential growth in numbers occurs until an area is fully occupied, whereafter the population becomes a source for optimal spread during further invasion of the region (Arim et al., 2006). A source population is a population in which the growth rate, genetic variability, and production of offspring are high and the amount of emigration through dispersal is higher than immigration (Ronald Pulliam, 1988). From the source populations, the IAP can then spread to new regions via natural and anthropogenic transport pathways (Davis and Thompson, 2000). The rate of spread is determined primarily by factors such as variability in landscape patterns and the occurrence of dispersal barriers (Theoharides and Dukes, 2007).

Seed ecology

The non-mobile nature of plants limits them in terms of dispersal and necessitates their reliance on mobile propagules (seeds, spores, and vegetative parts) for dispersal (Bell and Hemsley, 2000). Plant species have evolved to utilise a variety of propagules and accompanying dispersal and protection mechanisms (Croteau, 2010). Dormancy is one such mechanism whereby germination is prevented until specific conditions favourable for growth, referred to as stimuli, occur (Baskin and Baskin, 2001; Lambers et al., 2013). Dormancy promoting characteristics include a water-impermeable testa, and sensitivity to light or specific chemicals (Tran and Cavanagh, 1984). Physical dormancy is maintained by a layer of cells which is impermeable to water (Baskin and Baskin, 2001; Finch-Savage and Leubner-Metzger, 2006). Breaking of physical dormancy may be accomplished by disrupting the impermeable layer (thereby allowing imbibement) by means of physical scarification, such as mechanical or heat interactions, or by abrasive chemicals (Kelly et al., 1992). Based on what is known of the germination requirements of the study species, they all appear to have physical seed dormancy, as their dormancy may be broken simply through disturbance (Louppe et al., 2008; Richardson and Kluge, 2008; Searle, 1997). Other types of dormancy include physiological (presence or absence of certain chemicals or long-term temperature stratification), morphological (underdeveloped embryos requiring time for ripening), and combinations of morphological and physiological, and physical and physiological (Finch-Savage and Leubner-Metzger, 2006).

Dormancy indirectly facilitates dispersal of seeds in space and time, and the formation of a seed bank within the soil (Levin, 1976; Simpson, 1989; Venable and Lawlor, 1980). Soil-stored seed banks allow a species' population to have a reserve of seeds available in an area from which the population can recover easily after stochastic catastrophic events

(Briggs, 2009). This allows populations of IAPs to persist long after mature plants have been removed, making effective management of the species difficult (Richardson and Kluge, 2008). Many factors affect the formation of the seed bank including geological and topographical features (affecting seed movement within the soil profile), seed production, and number of events resulting in germination (Parker, 1989). The seeds of the two IAPs in this study remain dormant for at least 50 years (Richardson and Kluge, 2008), whereas seeds of *V. divaricata* may remain dormant for at least 230 years (Geldenhuys, 1994).

An important factor which affects plant invasiveness and the management thereof is soil seed bank density (Richardson and Kluge, 2008). The soil seed bank density is primarily dependent on the rate of seed production and seed longevity (Parker et al., 2012). The rate of accumulation is not only affected by seed production, but also the extent of predation on seeds, lateral seed drift (i.e. on a slope or from water flow) as well as the presence of seed dispersal agents (Milton and Hall, 1981; Richardson and Kluge, 2008). A soil-stored seed bank decreases over time through predation, pathogens, germination events, and general decay (Richardson and Kluge, 2008). An understanding of the seed ecology and seed bank dynamics of an IAP may inform suitable management approaches by incorporating the management of the seed banks as well (e.g. management aimed at the reduction of seed production through the introduction of pathogens and/or seed predators or depletion of the soil seed bank through the facilitation of germination events).

Competition

All species of flora are subjected to competition during some stage of their lifetime due to the non-mobile nature of established plants (Meiners and Cadenasso, 2005). One form of competition is for resources such as soil nutrients, water, space and sunlight, which becomes more limited as plant density increases (Grime, 1979). Wherever the propagule of a plant establishes, there is a high likelihood for it to have to compete for the limited resources with plants from other species, or the same species. Competition among individuals can be one-way, where one individual negatively affects the other, or two-way, where both of the competing individuals are affected equally (Gurevitch, 2011).

Competition among individuals also has a factor of symmetry, wherein two similar-sized individuals use equal amounts of resources (symmetric competition) or one uses proportionally more resources (asymmetric) (Freckleton and Watkinson, 2001; Schwinning and Weiner, 1998). The negative effects can be observed in the increased susceptibility to abiotic and biotic factors, and an increase in stress that manifests as the reduction of growth rates, foliage production, inflorescences, and seed (Huston and Smith, 1987). Certain species have traits such as fast inherent growth rates, efficient resource uptake mechanisms, or the capability to fix atmospheric nitrogen, which provides them with a competitive advantage over other species (Gurevitch, 2011; Rejmánek and Richardson, 1996). In such a case, the negative effects of competition are less pronounced on the individuals with these traits. The inability of weaker individuals to compete with stronger rivals for available resources may impact their growth and reproduction so severely that it results in the exclusion and ultimately the death of the weaker individuals (Firbank and Watkinson, 1990). As the density of neighbouring individuals increase, the effects of competition becomes more pronounced (i.e. all individuals have less resources available and weaker competitors are impacted more negatively). Seed ecology, as discussed in the previous section, may also be considered as a form of competition. The density of a seed bank, the rate of seed bank accumulation, the persistence of the seeds, and the methods by which the seed germinates may also contribute to the competitive performance of a species.

Competition from native species is an important factor that may reduce the colonisation effectiveness of an IAP. The majority of IAPs have the most success when establishing in a disturbed area with little or no competition from native species (Kennedy et al., 2002). These IAPs then exclude the native species, either by reducing resource availability due to their high density (MacDougall and Turkington, 2005), or by rendering the area unfavourable for the native species through the release of chemicals or alteration of disturbance regimes (Hierro and Callaway, 2003). Actively managing for the successful germination and growth of native species that possess similar traits as the IAP, may reduce the effectiveness of an IAP to establish or re-establish in an area (Kennedy et al., 2002). This task may become more difficult as the size of the area increases, and also depends on the species concerned and methods of introducing the native species, but may for example be used strategically to disrupt landscape continuity of an IAP population.

EFFECTS OF INVASIVE ALIEN PLANTS

Due to the increasing prevalence of IAPs globally, it is important to understand the effects that IAPs have on the environment in order to make informed decisions on the prioritisation and management of IAPs. IAPs can have negative as well as positive effects on both the ecological and socio-economic aspects of the environment, which will be discussed in more detail in this section. The effects on ecological aspects are often direct and immediate, whereas the effects on social-economic aspects are usually more indirect and occur due to ecological aspects being affected.

Negative ecological effects

IAPs can have numerous negative impacts on the ecology of invaded areas, and any particular IAP may have multiple impacts, potentially altering or completely disrupting the functioning of native species, communities, or ecosystems (Vilà et al., 2011). IAPs often change the environment around them to make it less suitable for native species (Hierro and Callaway, 2003) and this includes changes to soil chemical composition and nutrient content, soil pH, soil moisture, micro-organism activity, and litter decomposition rate (Vilà et al., 2011). Changes in the local environment can place endemic species, with narrow ranges and specific habitat requirements, at a disadvantage and can cause local population or species declines or extinctions (Işik, 2011). Species may furthermore have long-lasting alteration effects on the habitat which they occupy, even after removal, requiring greater investment to restore the habitat to its original state (Gordon, 1998). The two invasive study species have multiple negative effects on ecosystems in South Africa including on fire regimes, nutrient cycling, hydrology, and forest dynamics (de Wit et al., 2001; Richardson and van Wilgen, 2004; van Wilgen et al., 2008).

Many biome types are dependent on fire for a functioning ecology and to prevent any single species or growth form from dominating the system (Bond and Keeley, 2005; DeBano et al., 1998). Numerous plant species are dependent on fire for processes such as germination and seed dispersal (serotinous species), and removal of competition (see

Mucina et al., 2006; Rebelo et al., 2006; Rutherford et al., 2006). Variables of a fire, however, need to be within a certain range to be beneficial to species and ecosystems (Buhk et al., 2006). Changing the variables of fire such as intensity, interval, and seasonality may result in changes in the species composition, ecosystem and landscape functioning (Bond et al., 2003). Of the two invasive study species, only *A. mearnsii* can be considered to have an effect on fire due to its higher prominence in fire-prone habitats. Low density *Acacia* infestations (scattered trees or small clusters) in fynbos typically produces areas of higher fuel load (although with high moisture content) within the native vegetation, which may increase the intensity of fires in localised areas (van Wilgen and Richardson, 1985). Individuals of *A. mearnsii* will resprout shortly after a fire unless treated with herbicide (see 'Chemical') (Mandle et al., 2011). Resprouting, along with fire-stimulated recruitment from seed, will result in a denser stand of trees, potentially increasing the fuel load to greater volumes (van Wilgen, 2009). The large quantity of moist fuel of an infestation above a certain density, however, may reduce fire return intervals and fire intensities.

Another negative impact that the two invasive species have is changing the nutrient cycling in their immediate environment, due to their nitrogen fixing capabilities (Giraud et al., 2007). *Virgilia divaricata* and other native species also fix nitrogen, but due to the relatively short period that it is present in an area (as pioneer to forest) or low density at which other species may occur, these effects would not be as persistent as those of dense stands of the invasive species (Yelenik et al., 2004). Most plants in the fynbos biome are adapted to the low nutrient substrates on which they occur, and an increase in nitrogen and phosphorous could potentially enable seedlings of pioneer/competitive native and exotic species to have a competitive advantage over other native seedlings and may dominate the landscape (Cowell, 2007; Yelenik et al., 2004).

Water is a limited resource in South Africa due to low annual precipitation and runoff (Alexander, 1985). Studies have compared the water use of invasive species and plantations with native species in order to determine whether invasive stands use more water than native species (Le Maitre et al., 2002). When comparing the two invasive trees to native riparian vegetation the water use is relatively similar; however when compared to fynbos and grassland, it is higher (Dye and Jarmain, 2004). High density infestations of *A. mearnsii* may reduce the overall water yield and quality of a catchment and decrease the minimum volume of stream flow during droughts (Dye and Jarmain, 2004). Streams can also be directly impacted when the invasives grow on the river banks or within the stream bed. The extent of shading by dense stands may reduce the temperature of the water (Giller and Malmqvist, 1998). Trees growing within the flow of the river act as an impediment, slowing down the flow rate of the river and therefore increasing the rate of sediment deposition (Tal et al., 2004). There is also increased bank erosion and decreased flood amelioration from vegetation, as the invasive species' root characteristics are not conducive to withstanding the force of flooding and are easily uprooted (Lockwood et al., 2007).

The ecology of Southern Afrotemperate forest is less dependent on the formation of large gaps than with most other forest types, as the seeds of the former are able to germinate and grow under closed canopy conditions (Midgley et al., 1990). *Acacia melanoxylon* is more prevalent in forests than *A. mearnsii*, and its effect is therefore also more notable in the Afrotemperate forests (Kotzé et al., 2010). Its shallow root system increases the likelihood of the tree being uprooted by strong wind (de Zwaan, 1982), resulting in larger and more frequent gap-forming events than would be the case in uninvaded indigenous forests; this would change the disturbance dynamics of these forests with *A. melanoxylon* thus acting as a transformer. The frequent formation of large gaps in turn benefits *A. melanoxylon* as it is dependent on light for germination and growth (Phillips, 1928).

Positive ecological effects

There are some positive ecological effects associated with IAPs, which are often far outweighed by more prevalent negative effects. The most notable positive effect is IAPs' facilitation of native plant species. A recent study by Matthee (2014) carried out in the Little Karoo, South Africa, found that the invasive *Salsola kali* L. (Russian tumbleweed) facilitated the growth of native species such as *Osteospermum sinuatum* (DC.) Norl. by providing shade and a microclimate, as well as deterring predators. *Acacia melanoxylon* is also known to act as a nurse species for native tree species in Southern Afrotemperate forests (Geldenhuys, 1986). Given their competitive nature and colonising abilities, IAPs, and grasses in particular, are often useful for restoration where native vegetation cover is slow to establish and where soil erosion is a problem (Yoshida, 2007).

Negative socio-economic effects

The negative ecological impacts of IAPs often include negative impacts on socio-economic aspects such as human health and economic progress (Pejchar and Mooney, 2009; Pimentel et al., 2005; Pyšek and Richardson, 2010). As the ecology of an area is degraded by an infestation of IAPs, so too does the ecosystem services in the area change or become completely disrupted (Pejchar and Mooney, 2009). Ecosystem services are functions of an ecosystem beneficial to man and include water and air purification, carbon sequestration, resource production, flood amelioration, and the provision of opportunities for recreational activities (Daily, 1997). Synthetically mimicking these functions, if at all possible, would require capital spent on a service that would have been provided naturally (Rees et al., 2007). A decrease in local biodiversity and loss of overall natural aesthetic value affect the availability of local resources (e.g. horticultural genetic material, medicines and direct resource harvesting) as well as affecting tourism numbers and therefore impact the affected country's economy (Steiner et al., 2003).

Positive socio-economic effects

There are some positive socio-economic effects associated with IAPs. They can provide many resources such as building material, firewood or charcoal, ground cover, compost, fodder, food, and medicinal chemicals (de Neergaard et al., 2005; Liengme, 1981; Palm and Sanchez, 1991). Such resources can greatly improve the livelihoods of people, especially within rural and impoverished communities, and can also generate income through trade. The presence of IAPs within countries with high unemployment rates can increase job opportunities associated with labour-intensive invasive plant management actions; for example the Working for Water programme in South Africa (see 'Invasive alien plant management in South Africa' and van Wilgen et al., 1998). People employed in invasive plant management schemes not only receive remuneration, but also acquire training and valuable work experience.

MANAGEMENT OF INVASIVE ALIEN PLANTS

The negative effects associated with IAPs have resulted in the implementation of various management and control strategies. The methods range from preventing establishment of IAPs to the control or, if possible, the eradication of established IAPs (Wittenberg and Cock, 2001). The use of an integrated pest management strategy can often provide the highest degree of success in the most cost-effective manner (Hatcher and Melander, 2003; Wittenberg and Cock, 2001). Integrated pest management involves the use of multiple management methods in conjunction with one another (Wittenberg and Cock, 2001) and should be implemented into an adaptive management scheme that would use constant monitoring and assessment to determine the optimum integrated management approach (Foxcroft, 2004). The different management methods will be discussed in more detail in this section.

Prevention

Prevention is the first option in the management of IAPs, and also the most cost-effective (Wittenberg and Cock, 2001). It is the first 'line of defence' and most often rely on national legislation and vigilant monitoring of possible pathways through which an invasive species may enter a country (Burgiel et al., 2006). The propagation of alien species for their resource value has been practised for millennia and has increased in scale across the world over the past few centuries (Sauer, 1993). There are, however, measures put in place in many countries in an attempt to prevent such species from entering the country and becoming invasive.

Vegetative cloning, whereby a vegetative part of a plant is used to propagate a new individual that is genetically identical to the original plant (Priestley and Swingle, 1929), is a method that is used with certain species with high resource value. If the species is self-incompatible this method of cloning will prevent the propagated individuals from sexual reproduction and therefore from becoming invasive (Shi and Brewbaker, 2006). Another system that may assist in the prevention of invasion is certification schemes. Certification is a process whereby an independent third party gives written assurance that a product, process, or service meets specific requirements (Auld et al., 2008). Although certification is voluntary, the certified company may receive benefits such as reduced taxes and selling products to a growing market demanding eco-friendly certified products (Fuerst and McAllister, 2011; Rivera, 2002). This creates incentives for sectors to manage IAPs originating from their practice (e.g. forestry) (Gullison, 2003).

The international trade and transport sectors are difficult to monitor, as are the implementation of any preventative measures (Burgiel et al., 2006). Preventing the introduction of species through international trade and tourism relies largely on local and regional authorities and international agreements, most of which are voluntary (Burgiel et al., 2006; Segerson and Miceli, 1998). The most stringent national or regional legislative efforts may be subverted if local authorities at entry points (border control posts) are not enforcing the legislation. Conversely, local authorities are unable to act if the national legislation does not include preventative measures for the import of alien species (Burgiel et al., 2006).

Early detection and containment

If an alien species is introduced and becomes established, the next action would be to determine in which stage of invasion it is and attempt to contain it in as small an area as is possible (Junak et al., 1993; Soria et al., 2002; Wotherspoon and Wotherspoon, 2002). The stages of invasion during which detection and containment would have the highest probability of success, would therefore be transport (if prevention has failed) and colonisation. Determining the extent of colonisation and impact posed by the IAP at the earliest stage possible will help restrict its range extension and environmental impact (Simpson et al., 2009). Early containment of an IAP will also greatly reduce the total amount of capital and labour units needed for species removal (Rejmánek and Pitcairn, 2002). Early detection relies on accurate identification of a possible IAP, which can be a problem in many instances where people lack the technical and botanical expertise, or where knowledge of the species' invasive capabilities is inadequate (Simpson et al., 2009). Even on a local scale, the manpower available to environmental organisations and authorities may be insufficient to detect all the establishing IAP timeously. The use of volunteer and amateur botanists, as well as citizen scientist programmes can increase the efficiency of the detection and containment efforts and allow for improved management of localised introductions (Crall et al., 2010). In Cape Town, South Africa, the Early

Detection and Rapid Response programme of the Invasive Species Unit relies on a web-based spotter network which makes use of volunteers (Gaertner et al., 2015).

Eradication

After successfully containing the IAP, or if the containment of the IAP has failed, the next step is to attempt to eradicate all the established populations of the IAP timeously (van der Weijden et al., 2007). Eradication, when attempted at an advanced stage of invasion (establishment and landscape spread), is usually not possible. Costs and the likelihood of success should be determined before implementing eradication programmes (Wittenberg and Cock, 2001). The methods discussed in the following section are typically used to manage an invasion, but can be used for eradication where viable.

Management for risk mitigation

When prevention, containment and eradication have failed to neutralise the impacts, the remaining management option is to prevent further spread and mitigating negative impacts of the IAP (Wittenberg and Cock, 2001). This can be achieved by using the control methods mentioned below to reduce and maintain the density and/or spread of the IAP below a predetermined threshold (Wittenberg and Cock, 2005). Mitigating impacts at an advanced stage of invasion focuses more on the native species affected and not the IAPs themselves. This includes strategies such as relocating sensitive and endangered species to more intact habitats (Wittenberg and Cock, 2001). Following adaptive management is the only effective method to maintain the IAP within reasonable densities, reducing its impacts, and mitigating its impacts on native species whilst minimising effort and capital spent (Foxcroft, 2004).

Manual

Manual control makes use of inexpensive and easily operated equipment (axes, saws, and other cutting tools) (Kaufman and Kaufman, 2013), therefore making it the method of choice where minimal training is required (DiTomaso et al., 2007). As the size of the invaded area, the duration of invasion, or the density of the IAPs increases, the requirements for tools and labour also increase, decreasing the cost-effectiveness of manual control (Pickart, 2011). The simplest and most effective method of manual control involves uprooting the plant completely by hand pulling or using specialised tools such as a weed wrench or root talon (Kaufman and Kaufman, 2013; Wittenberg and Cock, 2001). Uprooting is only successful on species with relatively shallow root systems, but does have the drawback of creating soil disturbance that could lead to erosion (Kaufman and Kaufman, 2013). Non-resprouting, small plants and bushes can be cut down manually with the use of a brush cutter (Venner, 2006). Larger plants or trees, which do not resprout, can be cut down completely or killed by removing the cambium layer in a ring around the stem (ringbarking or girdling) (Czarapata, 2005). Plants that do resprout require a combination of techniques which in most instances includes chemicals (Pickart, 2011). In some cases, resprouters can be killed through repeated cutting or defoliation that may eventually deplete the plant of its stored resources (Wittenberg and Cock, 2001); or alternatively treated with herbicide in conjunction with cutting or ringbarking.

Chemical

Chemical control makes use of different herbicides that kill the plant directly or indirectly. Herbicides vary considerably in terms of cost, selectivity, efficacy and safety (Kaufman and Kaufman, 2013). Careful planning is necessary and must take into account aspects such as the ecological health of the invaded area, whether multiple IAPs occur in the area, the age of the plants, and the climate (Wittenberg and Cock, 2001).

Herbicides can be divided into two categories, namely contact and systemic (Kaufman and Kaufman, 2013). Contact herbicides kill plant tissue on contact and must be applied directly onto the plant surface. The mode of action of systemic herbicides depends on the active ingredient and are either non-selective or selective (Kaufman and Kaufman, 2013; Rao, 2000). Non-selective or broad-spectrum herbicides are designed to control almost any plant species (Kaufman and Kaufman, 2013). Once absorbed, systemic herbicides are translocated through the plant’s vascular system and, depending on their mode of action, may disrupt metabolic reactions, cell membrane functionality, or through inhibiting lipid synthesis (Kaufman and Kaufman, 2013). Systemic herbicides can also be applied to the soil (soil active herbicides tend to be residual as they need to remain in the soil to allow uptake), or the plant, and can likewise be selective or non-selective (Rao, 2000). Selective herbicides are designed to target a specific species or growth form, and therefore have limited risk of collateral damage to plants, whereas non-selective herbicides have a higher risk of collateral damage and should be used in more mono-specific invaded areas (Manahan, 2006).

Certain types of herbicide, especially those in the selective systemic category, often have to be used in conjunction with manual/mechanical methods. Such methods include cutting the plant down completely and applying herbicide to the exposed surface, or cutting into the cambium layer and applying the herbicide (Kaufman and Kaufman, 2013). The safe use of herbicide requires training with regards to its correct application methodology and species identification to prevent off-site and off-target impacts (Dikshith, 2008).

Biological

Biological control relies on the use of other life forms (or by-products) to kill or suppress a specific species (Wittenberg and Cock, 2001). This includes the use of predators (herbivores), natural competitors, parasites, and naturally synthesised substances (Pilgeram and Sands, 2010; Wittenberg and Cock, 2001). Two categories of biological control exist, those that are self-sustaining, and those that are not. Self-sustaining methods involve an initial introduction of specimens into an area that are then able to reproduce and spread freely within and among invaded areas (Wittenberg and Cock, 2005). This method requires testing to be conducted before application due to the risk of the control species having non-target species impacts (Messing and Wright, 2006). Methods that are not self-sustaining include the use of sterile individuals, biochemically produced compounds, or specimens that will not reproduce and survive for long periods in the ecosystem (Wittenberg and Cock, 2001). Non self-sustaining methods would require repeated introductions or applications, or should be applied to infestations small enough that they require only a single introduction or application.

Biological control agents generally target a specific part of the plant (i.e. flowers, seeds, roots, or growth tips), reducing overall fitness and reproductive capabilities of the specific plant (Hajek, 2004). Typical control agents used for weeds include insects (beetles, weevils, midges, and wasps), mites, and fungi (rust) (Bellows and Headrick, 1999;

Rosskopf et al., 1999). Since 1913, 106 control agents have been tested and released in South Africa; 75 have established successfully and are used to control 48 species of IAPs (Klein, 2011). Of the 48 species that have been targeted by biological control agents, ten have been completely controlled and 18 substantially controlled (Klein, 2011). Control agents used against invasive acacias generally include gall-forming insects, seed-feeding insects, and pathogens (Dennill et al., 1999, Morris, 1991, 1999). Agents released to control *A. mearnsii* include a gall-forming midge (*Dasineura rubiformis* Kolesik), which is highly effective (but still localised), and a seed weevil (*Melanterius maculatus* Lea) that is moderately effective (Adair, 2004; Impson et al., 2008, 2009). Another seed weevil (*Melanterius acaciae* Lea) was released for the control of *A. melanoxylon*, with extensive effectiveness (Dennill et al., 1999; Impson et al., 2009, 2011).

Habitat management

Habitat management, also termed 'cultural control', involves using strategies to change the habitat or habitat functioning to obtain the desired effects such as decreased growth rates, densities and germination rates of IAPs (National Academy of Science, 1968). The principles associated with habitat management are used in other fields such as agriculture (Leihner, 2002). The main objective of habitat management is to reduce the success of the IAP with one of many, often contextually specific, management techniques (Cronk and Fuller, 2014). This includes techniques such as introducing or changing fire regimes, making use of mowing or herbivory, timing of control measures, and bolstering native plant populations to decrease the IAP's competitive ability (Wittenberg and Cock, 2005). Active management of habitat to increase the density of a native species, especially those that may compete favourably with an IAP (as is explored in this study), may require high effort initially, but should reduce follow-up effort and rehabilitation requirements.

Rehabilitation and restoration

When a habitat has been degraded or altered by IAPs, rehabilitation is often required to reinstate ecosystem functioning or prevent further degradation (Campbell, 2000). Rehabilitation of a degraded area is achieved through the systematic introduction of native vegetation through manual reseeding or the replanting of desired (often pioneer) species (Palmerlee and Young, 2010). Rehabilitation aims to return the disturbed area to a functional, albeit dissimilar, state in comparison to its original state, whereas restoration attempts to convert disturbed areas to their pre-disturbed state (Callicott et al., 1999). Complete restoration is often unachievable or impractical, as it requires significant management intervention and capital investment (Hobbs, 2007). Rehabilitation requires the system to be altered in such a way that it is able to maintain its functions without intervention, whereafter autogenic recovery is more likely (Hobbs, 2007). There are numerous methods, which can be used independently or in conjunction with others, to promote rehabilitation or restoration. A successful method is, however, often contextual to a specific area and the correct method can only be discovered through trial and error, and collaboration (Funk et al., 2008).

Invasive alien plant management in South Africa

South Africa has a long history with regards to IAPs, and thus has a long history of research and management of invasions (Richardson and van Wilgen, 2004). A government-subsidised programme, Working for Water (WfW), was established in 1995 to conduct and coordinate IAP management in South Africa (Richardson and van Wilgen, 2004; van Wilgen et al., 1998). WfW initially only operated in watersheds and riparian zones, but has since expanded to lead IAP management initiatives in South Africa and is one of the world's biggest (Richardson and van Wilgen, 2004) and most ambitious IAP management programmes (McConnachie et al., 2012). Since its inception, WfW has spent over 3.2 billion ZAR on clearing operations and in the period from 2002 to 2008, an area of approximately 144 310 condensed hectares of the most prominent species (throughout all the biomes) was cleared (van Wilgen et al., 2012a). However, van Wilgen et al. (2012a) also noted that between 1996 and 2008, the estimated occupancy of IAPs increased from 1.7 to 1.8 million condensed hectares in South Africa, indicating that clearing efforts may not be as successful as believed. Challenges and shortcomings experienced within the programme include success being highly localised, increasing invasions in inaccessible regions such as mountains, the majority of invaded areas occurring on privately owned land, and that too much focus is placed on the clearing itself and not the management of the habitat (van Wilgen et al., 2012b).

CONCLUSION

Despite the fact that the dynamics of alien plant invasions have been intensively studied, there are few performance comparisons of co-occurring native and alien species (Daehler, 2003) in the South African context. Despite *A. mearnsii* and *A. melanoxylon* ranking amongst the worst invaders in South Africa (Henderson, 2007), there is inadequate understanding of species-specific germination responses, including that of *V. divaricata*. Information on soil-stored seed banks and their viability for the three species is either outdated (e.g. Philips, 1926) or not assessed under similar conditions that would allow for interspecific comparisons. Furthermore, competitive performance in terms of growth at various life stages has not been quantified for the study species. Incorporating these three aspects into performance comparisons of the co-occurring native and alien species, can provide an indication of the potential for using *V. divaricata* in the management of the acacias.

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CHAPTER 2 - Can the application of germination stimuli aid the management of invasive alien plants?

ABSTRACT

Invasive alien plants that have seeds with innate dormancy, and thus large, persistent soil-stored seed banks, are particularly difficult to manage. Dormant seeds typically require specific stimuli as cues for germination, resulting in mass recruitment. Sound understanding of germination stimuli may provide options to aid the management of invasives. We investigated the response of two invasive trees, *Acacia mearnsii* and *A. melanoxylon*, and an indigenous ecological analogue, *Virgilia divaricata*, to different germination stimuli to explore how their germination requirements may be used to favour *V. divaricata* in areas cleared of the invasives. We assessed these species' germination responses to five stimuli (manual chipping, hot water exposure, dry heat pulse, smoke, and no treatment), at two temperature regimes (winter ~12°C and summer ~20°C) in a controlled germination experiment. Chipping and hot water exposure resulted in the highest germination in all three species. *Virgilia divaricata* responded marginally better than the invasives to the dry heat pulse, particularly at 20°C. However, the three species mostly responded comparably to the treatment combinations, suggesting that manipulation of stimuli is not a feasible option for management of the invasives at a large scale. In the absence of any stimulus (~akin to conditions associated with aboveground clearing of alien vegetation cover), germination was poorer in *V. divaricata* than in the invasive species, especially at 20°C, providing motivation for focusing *Acacia* management operations in cooler seasons in areas where *V. divaricata* seed banks occur. Another option is to sow *V. divaricata* seeds to which chipping or hot water exposure stimulus has been applied in areas cleared of the invasives of which the seeds would not have received stimuli.

INTRODUCTION

Plant species use various strategies to increase the likelihood of survival of both the adult plant and its propagules (Craine, 2009). One such strategy is seed dormancy and the requirement for a specific stimulus to break dormancy (Bewley et al., 2006; Finch-Savage and Leubner-Metzger, 2006). Stimuli often involve the presence of particular environmental conditions that ensure optimal germination success and seedling survival in space and time (Parker, 1989). Presence of the required stimuli for germination is thus instrumental to the success (or failure) of plant establishment, including that of invasive alien plants (IAPs).

IAPs have numerous negative impacts on the ecology of invaded ecosystems, including the exclusion of indigenous species, and alteration of fire, flooding, and nutrient cycling regimes (de Wit et al., 2001; Richardson and van Wilgen, 2004). The changes in ecology as a result of IAPs often require intensive management to restore the ecological functioning of the area (van Wilgen and Richardson, 1985). In the absence of natural predators, IAPs with high degrees of seed dormancy form large, persistent seed banks (D’Antonio and Meyerson, 2002; Suding et al., 2004), which complicate management efforts due to the extended period over which seeds germinate if a stimulus occurs.

Germination response is one aspect of performance in competition among plant species, including between native and invasive species. The outcome of such competition is often dependent on condition and situation, but it is possible for native species to outperform IAPs where they co-occur in space and time (Daehler, 2003). Understanding how different stimuli affect both native and invasive plant species may offer potential for more effective management of IAPs through the manipulation of environmental conditions (one example of habitat management) to favour the germination of native species over the IAPs. Habitat management also includes managing for desirable species and increasing their cover to suppress undesirable species (Masters and Sheley, 2001).

Numerous different types of germination stimuli exist, many of which have differing effects on different species (Baskin and Baskin, 2001). Fire and its associated effects is one of the most pronounced, and most studied, germination stimuli (see Bell et al., 1993; Keeley, 1991; Went et al., 1952) and significantly affects the distribution and composition of some of the world’s major biomes (Archibold, 1995). Fire provides both direct and indirect stimuli to seeds (Brown and Botha, 2004). Direct stimuli involve damage to the seed testa by heat, and breaking of seed dormancy with a chemical such as butenolide found in smoke (Brown and Botha, 2004; de Lange and Boucher, 1990). Indirect stimuli provided by fire involve increased light intensity and resource availability resulting from removal of aboveground plant biomass, as well as a reduction of soil pathogens and allelopathic compounds (Ahlgren, 1974; Botha and Le Maitre, 1992; Melkiana, 1992; Rosenzweig, 1995). Physical or chemical scarification also breaks seed dormancy (Baskin and Baskin, 2001). Physical scarification, resulting from trampling and other disturbances (Bradbeer, 2013), involves damage to or removal of the seed testa/endocarp to allow water into the seed (imbibition). Chemical or acid scarification involves the breakdown of the testa by a corrosive chemical such as stomach acid and is often seen in plant species dispersed by mammals or birds (Barnea et al., 1990).

We undertook a case study to investigate whether the application of different germination stimuli could aid the management of IAPs and restoration of indigenous vegetation. We selected three study species from the Fabaceae (legume) family, two of which (*Acacia mearnsii* De Wild and *Acacia melanoxylon* R.Br) are aggressive alien invaders in South Africa that are particularly difficult to manage (van Wilgen et al., 2012). The third is an ecologically analogous, but indigenous, species (*Virgilia divaricata* Adamson), which is a pioneer tree with seed ecology similar to that of the IAPs. In its native range, it plays an important role after fire (~disturbance) in the ecotone of forest and fire-prone fynbos shrublands (Geldenhuys, 1994). The responses of these three species to five germination stimuli at two temperature regimes were explored to determine how their germination requirements may be used to favour *V. divaricata* in areas cleared of the two IAPs.

METHODS

Study area

The study area is situated along the southern Cape coast of South Africa, between the towns of Mossel Bay in the west and Stormsriver in the east, with the Outeniqua and Tsitsikamma Mountains in the north. The area forms part of the Cape Floristic Region known for its high levels of biodiversity and endemism, which are threatened by IAPs amongst other disturbances (Goldblatt and Manning, 2000). The vegetation of the area consists of fire-prone fynbos shrublands and fire-sensitive Southern Afrotemperate forest

(Mucina and Geldenhuys, 2006; Rebelo et al., 2006). The region has a temperate climate with year-round rainfall (peaking in April and October) averaging approximately 800 mm per annum and summer and winter temperatures averaging 20°C and 12°C, respectively (Tyson and Preston-Whyte, 2000). Disturbances occur frequently in the study area in the form of floods (Russell and Kraaij, 2008), fires (at 10-26 year intervals; Kraaij et al., 2013), and disturbances associated with commercial forestry and agriculture operations. IAPs are considered to be the most important ecological threat to biodiversity conservation in the area (Baard and Kraaij, 2014).

Study species

Acacia mearnsii is a fast growing tree species in the Fabaceae family, originating from south-east Australia where it occurs as a pioneer understorey species in eucalypt forest (Praciak et al., 2013; Searle, 1997). The fast growth rate and early flowering age (two years under favourable conditions) allows for early commencement of seed production, which may remain viable in the soil for at least 50 years and form large seed banks (Praciak et al., 2013). The soil-stored seed banks respond rapidly to disturbance, such as fire (heat) and physical scarification, resulting in prolific germination (Jeffrey et al., 1988; Kulkarni et al., 2007; Searle, 1997). These characteristics contribute to the invasion success of *A. mearnsii* and it is being considered one of the 100 most invasive species globally (Lowe et al., 2000). *Acacia mearnsii* was introduced into South Africa in the early 1880s for its bark used by the tanning industry and has become well established (planted and invasive) over large areas of South Africa, including forest and fynbos in which it is ranked the third and first most prominent IAP, respectively (Browmilow, 1995; Forsyth et al., 2011; Henderson, 2007). *Acacia mearnsii* has the status of transformer, indicating an ability to 'change the character, condition, form, or nature of ecosystems over a substantial area' (Richardson et al., 2000). *Acacia mearnsii* has many negative effects on the ecosystems it invades, including an increase in fire intensity and frequency, decreased biodiversity and ecological functioning, reduction in water yield from mountain catchment areas, and changing sedimentation and flooding dynamics in rivers (de Wit et al., 2001).

Acacia melanoxylon is a large, fast-growing tree up to 40m in height and living up to 100 years (Forestry Tasmania, 2005; Louppe et al., 2008; Praciak et al., 2013). Its native distribution is similar to that of *A. mearnsii* (Miller et al., 2011), but within this range it occurs in swamp forest, wet eucalypt forest, and serves as a pioneer for riverine rainforest (Louppe et al., 2008). Mature trees can produce large amounts of seeds, dispersed by birds and water, which may remain dormant in the soil for at least 50 years (Milton and Hall, 1981; Praciak et al., 2013; Richardson and Kluge, 2008). Seed germination occurs in response to disturbance such as fire, physical scarification, and chemical scarification (stomach acids from ingestion) (Burrows et al., 2009; de Zwaan, 1978, 1982; Louppe et al., 2008; Richardson and Kluge, 2008). This species also has the ability to resprout from the base of the stem or from the root system after felling or injury, which promotes its invasiveness (Praciak et al., 2013). *Acacia melanoxylon* was introduced into South Africa in 1848 for its high-quality timber and has subsequently become well established in indigenous forests and fynbos (where it is the fourth and fifth most prominent IAP, respectively; Henderson, 2007), especially in areas that frequently undergo disturbance (Geldenhuys, 1996; Louppe et al., 2008). Due to its shallow root system, *A. melanoxylon* is prone to windfall, and may alter the disturbance (gap-) dynamics in the fine-grained forests of the study area, favouring mass recruitment of its own shade-intolerant seedlings (de Zwaan, 1982; Louppe et al., 2008).

Virgilia divaricata is a medium-sized, fast-growing tree (Coates Palgrave et al., 2002; van Wyk, 1982) with a narrow native range along the south-eastern coast of South Africa (Coates Palgrave and Drummond, 2002). *Virgilia divaricata* produces less seed than the two acacias in terms of numbers of pods per inflorescence and seeds per pod (compare Phillips, 1926 and Milton and Hall, 1981), but the seeds have greater longevity and may persist in the soil for at least 230 years (Geldenhuys, 1994). The hard seed coat is impermeable to water and requires short exposure to intense heat, 'heat shock', from fire to break dormancy (Jeffrey et al., 1988). Similar to the acacias, *V. divaricata* occurs in ecotonal, disturbance-prone areas, possibly allowing it to be used as a dual-purpose management tool to compete with the acacias and provide suitable habitat for forest establishment (Geldenhuys, 1994).

Seed collection and trial design

Seed pods were collected (November 2015) from the canopies of approximately ten trees per species interspersed in the study area. Seeds were extracted from the pods, and all undamaged seeds of a species combined in a composite sample. Seeds were stored in paper bags at room temperature until trial commencement in April 2016. Subsamples of 100 seeds per species were selected randomly and tested for viability by cutting each seed longitudinally and submerging one half of each seed in a tetrazolium chloride solution overnight and enumerating stained (i.e. viable) embryos (Porter et al., 1947).

The germination trial comprised of a factorial design (3x5x2) of the three species, five stimulation methods (smoke water, dry heat pulse, hot water exposure, mechanical scarification, and control), and two temperature regimes (constant 12°C and 20°C). These 30 treatment combinations were each replicated three times. For each replicate, 33 seeds (99 seeds per treatment combination) were placed inside a 5cm petri dish on top of a sheet of filter paper. The filter paper was moistened with 2ml of 0.2% Dithane M45 (fungicide) solution, and kept moist with the same solution for the duration of the trial (Buts et al., 2014). The smoke water stimulus involved soaking SmokePlus seed primer discs (obtained from http://www.seedsforafrica.co.za/) in water for an hour and then soaking the seeds in the smoke solution for 24 hours, as per product instruction. Dry heat pulse stimulus was applied by soaking the seeds in a 70% isopropyl alcohol solution for one minute, removing all the seed from the alcohol and igniting the mass. After three seconds, the flame was extinguished by placing a petri dish over it (Sugii, 2003). The hot water exposure stimulus was applied by placing the seeds in a container and pouring rapidly boiling water over them and leaving the seeds in the water for 12 hours (Pérez-Garcia and González-Benito, 2006). Dry heat pulse (high heat) and hot water exposure (moderate heat) are representative of the temperature range experienced during an average fire in the top two centimetres (80°C to 120°C) and deeper two centimetres (20°C to 70°C) of the soil profile respectively (Behenna et al., 2008). A forward-looking infrared (FLIR) camera was used to determine post-stimulus temperatures of seeds subjected to hot water exposure (measured after three seconds, 10 seconds, one minute and three minutes of submersion) and alcohol flame (measured directly after extinguishing the flames, and every ten seconds for one minute). Seed temperature measured directly after alcohol flame exposure ranged between 65°C and 90°C (with flame temperatures ranging from 120°C to 200°C), cooling down to ~30°C in less than a minute. Seed temperature measured immediately after being extracted from hot water ranged between 60°C and 65°C (irrespective of the time submerged and an initial water temperature greater than 90°C) but retained heat for longer, decreasing by only 10°C within the first minute. The scarification stimulus involved chipping a small piece of the testa of each seed with a scalpel. The control group was not subjected to any stimulus. Two growth chambers were used to maintain two constant temperature regimes, 12°C and 20°C, representative of winter and summer conditions (calculated as the average temperature over 24 hours during the three coldest and three warmest months of the year) in the study area, respectively. Since all three species regenerate from soil-stored seed banks, the trial was conducted in the dark. Seeds were considered to have germinated when a radicle could be discerned, or when the radicle has started to push the seed out of the testa. Germinated seeds were recorded and removed daily for 30 days after trial commencement.

Data analysis

Germination count

Germination count was determined as the total number of seeds per replicate that had germinated by the end of the trial (30 days). In isolated instances, parasitism of seeds was noticed after trial commencement. These seeds (maximum incidence in any one replicate was three seeds) were subsequently excluded and germination counts adjusted *pro rata*. Data did not conform to assumptions of normality and homogeneity of variance and were subjected to a rank transformation (Montgomery, 2013). The ranked values were then analysed for the effects of species, stimulus and temperature and their interactions in a three-way factorial analysis of variance (ANOVA) and Tukey post-hoc tests using STATISTICA v.13 (Dell Inc., 2015).

Germination rate

Germination rate was determined from the total number of seeds per replicate that had germinated by the end of each day. The effects of species, stimulus and temperature on germination rate were analysed using Cox proportional hazard (Cox PH) regression models (Allison, 1995, 2010). Cox PH models determine the likelihood, or risk, of an individual to transition from one state to another at any given time. These models are used to analyse survival rates, but can also be used to analyse germination rates if the seed is considered as living, and the onset of germination as mortality (McNair et al., 2012). When used on germination data, Cox PH models can be interpreted as the likelihood of a seed to have germinated at a specific time. The model was fitted as a factorial, testing for the effects of the factors (species, stimulus and temperature) and their interactions on germination rate using R 3.2.4 (R Core Team, 2016) and the 'RCommander' package (Fox, 2005) with the 'survival' plugin (Therneau and Grambsch, 2000). To assist interpretation, interactions were only modelled to the second degree. The coefficient outputs of the model were analysed using ANOVA with Type-3 tests, and significant main effects further investigated through simultaneous tests for general linear hypotheses using the 'glht' function in the 'MultComp' package (Bretz, et al., 2011).

RESULTS

Germination count

Differences in germination counts between the study species were marginally non-significant ($F_{(2,60)} = 3.04$; $p = 0.055$). A total of 38% of seeds germinated across all species (*V. divaricata* 37%; *A. mearnsii* 40%; *A. melanoxylon* 36%), stimuli (including the control), and temperatures. Germination count was significantly affected by stimulus ($F_{(4,60)} = 237.17$; $p < 0.001$), temperature regime ($F_{(1,60)} = 21.96$; $p < 0.001$), and the interactions between species and stimulus ($F_{(8,60)} = 2.45$; $p = 0.023$) and species and temperature ($F_{(2,60)} = 12.29$; $p < 0.001$). Stimulation accounted for most variation in the data (84% of total mean squares (MS)), followed by temperature (8% of total MS) and species (1% of total MS). Between the different stimuli, control and smoke were comparable, but differed significantly from the other stimuli, while the other stimuli also differed significantly between one another (Figure 1). Chipping resulted in the highest mean germination (96.6%) across all three species (*V. divaricata* 95%; *A. mearnsii* 100%; *A. melanoxylon* 95%), comparable to the viability test results of 93% across species (*V. divaricata* 94%; *A. mearnsii* 99%; *A. melanoxylon* 88%). Hot water exposure resulted in the second highest mean germination success (70%), followed by dry heat pulse (15%), control (5%), and smoke (4%). The interaction between species and stimulus indicated that *A. melanoxylon* responded better than the other species to the smoke stimulus (6%) and *V. divaricata* to the dry heat pulse stimulus (21%) (Figure 1a). The interaction between species and temperature indicated that *A. melanoxylon* responded more positively to warmer temperature than the other two species (Figure 1b).

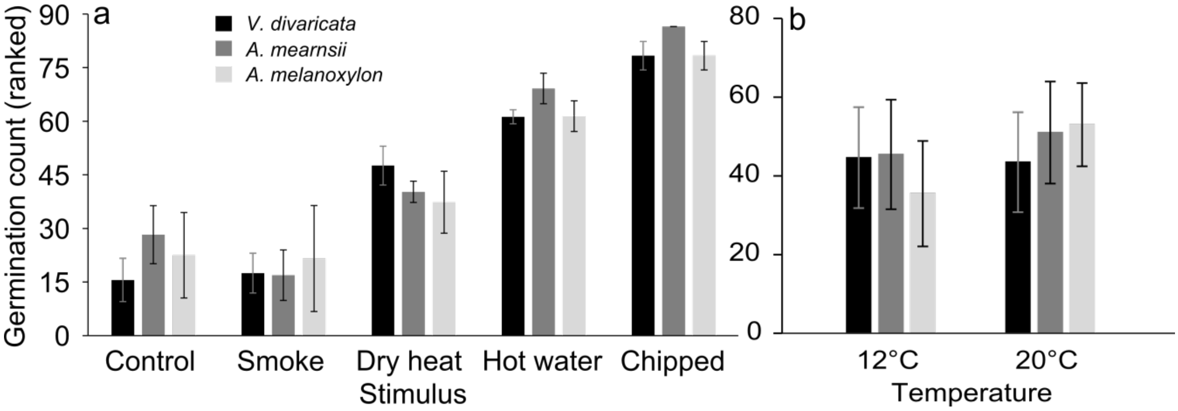

Figure 1: Germination responses (ranked values) of *Virgilia divaricata*, *Acacia mearnsii*, and *A. melanoxylon* to (a) stimuli, (b) and temperature regime (error bars denote 95% confidence limits).

Germination rate

Germination rate was significantly affected by stimulus (Likelihood ratio (LR) χ^2 = 993; *d.f.* = 4; $p < 0.001$), temperature (LR χ^2 = 15.4; *d.f.* = 1; $p < 0.001$), and the interactions between species and stimulus (LR χ^2 = 17.93; *d.f.* = 8; $p = 0.022$) and stimulus and temperature (LR χ^2 = 10.42; *d.f.* = 4; $p = 0.034$). Chipping and hot water exposure resulted in significantly higher germination rates than the other stimuli, and dry heat pulse resulted in a significantly higher germination rate than smoke (Table 1).

Table 1: Pairwise comparisons of the effect of stimuli on germination rate.

Linear Hypotheses	Estimate	Std. Error	Z value
Hot water - Dry heat == 0	1.9371	0.2721	7.119 ***
Chipped - Dry heat == 0	2.2682	0.2673	8.485 ***
Control - Dry heat == 0	-0.8629	0.4986	-1.731
Smoke - Dry heat == 0	-1.6467	0.6007	-2.741 *
Chipped - Hot water == 0	0.3311	0.1273	2.601
Control - Hot water == 0	-2.8000	0.4396	-6.370 ***
Smoke - Hot water == 0	-3.5838	0.5532	-6.478 ***
Control - Chipped == 0	-3.1311	0.4365	-7.173 ***
Smoke - Chipped == 0	-3.9149	0.5509	-7.106 ***
Smoke - Control == 0	-0.7838	0.6929	-1.131

Significantly different at *p<0.05; **p<0.01; ***p<0.001.

Under both temperature regimes, chipping resulted in the most rapid onset of germination (by days four and three for *A. mearnsii* at 12°C and 20°C respectively) and the most rapid attainment of 100% germination (by days six and five for *A. mearnsii* at 12°C and 20°C respectively) (Figure 2). Hot water exposure also resulted in high germination responses, but this was protracted over the trial period and with greater variability among species in timing of germination. Dry heat pulse resulted in both low (10-20%) and slow (delayed) germination rates for all three species under both temperature regimes, except *V. divaricata* showing an improved response at 20°C.

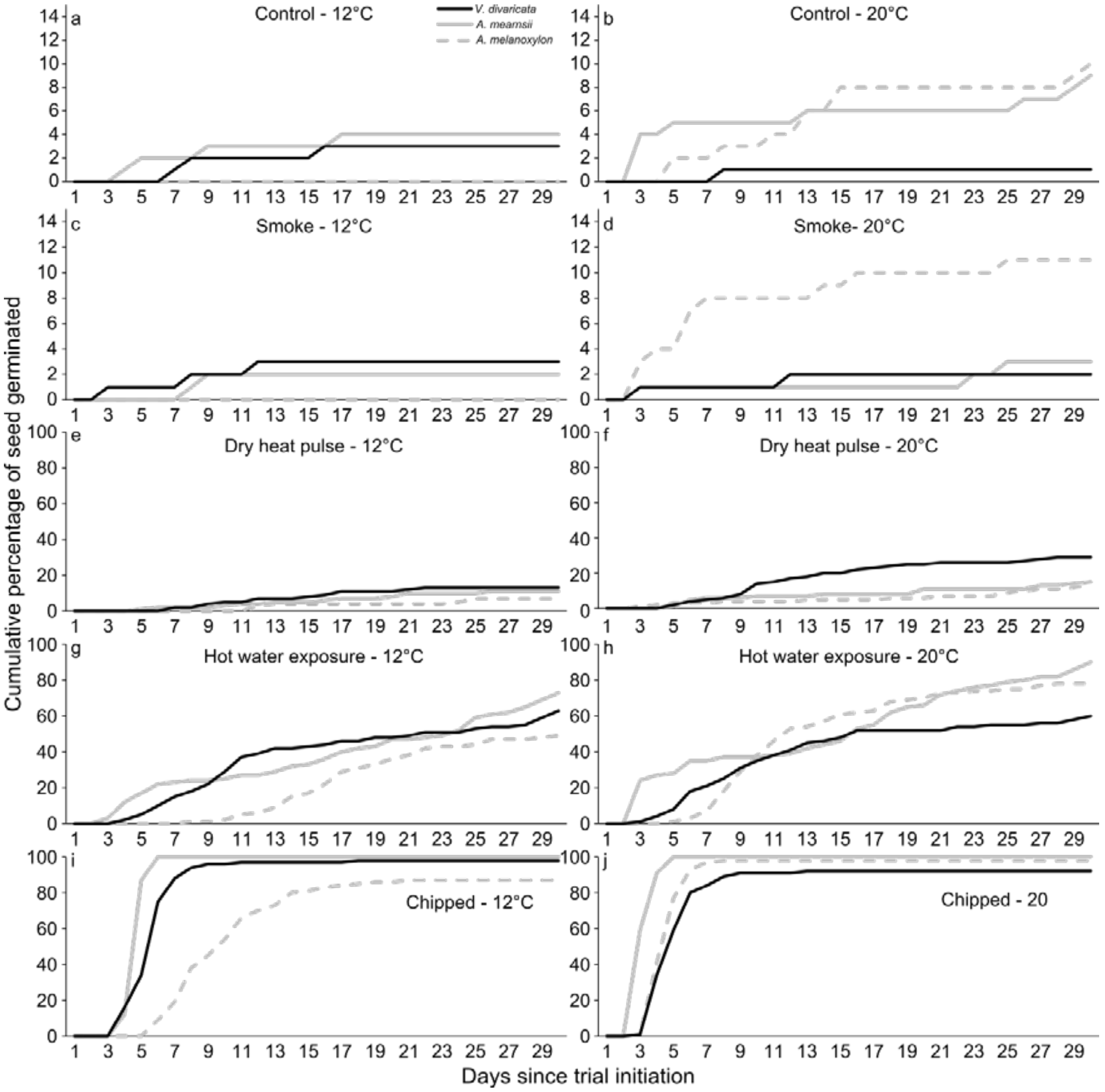

Figure 2: Germination rates of *Virgilia divaricata*, *Acacia mearnsii*, and *A. melanoxylon* in response to five germination stimuli (chipped, hot water exposure, dry heat pulse, smoke, and control) applied to the seeds and thereafter incubated under two temperature regimes (winter ~12°C and summer ~20°C).

Smoke and the control resulted in the lowest (2-11%) and slowest germination rates for all three species at both temperature regimes. Although *A. melanoxylon* showed zero germination in response to smoke and the control at 12°C, it outperformed the other two species at 20°C.

DISCUSSION

Germination responses of the three study species to stimuli and temperature regimes were generally comparable, which may be explained by their water-impermeable seed coat dormancy. Seeds displaying a high degree of dormancy often have a testa impermeable to water, thus requiring scarification before germination will occur (Baskin and Baskin, 2001). This likely explains why chipping resulted in rapid onset of germination and attainment of high final germination counts (comparable to seed viability results) for the three study species. Doran and Gunn (1986) found that chipping produced the best and most reliable germination responses across a range of acacias, approximating the species' seed viability. Compared to chipping, hot water exposure also resulted in a high germination response in the three study species, albeit at slower rates, with more variation in the timing of germination events between the species. Strong but variable germination responses of *Acacia* seeds to hot water at varying temperatures and exposure periods were also observed by Doran and Gunn (1986). Dry heat pulse stimulus resulted in poorer germination responses than hot water exposure and chipping, but slightly better than smoke and the control. It is unlikely that temperatures experienced by seeds (i.e. 65-90°C) due to the alcohol flame treatment could have resulted in seed mortality, as the lethal temperature for *A. saligna* and *V. oroboides* seeds was found to be ~215°C when experienced for longer than a minute whereas optimum heat treatments were 80°C for 30-60 minutes (*V. oroboides*), and 100-150°C for 2-30 minutes (*A. saligna*) (Jeffery et al., 1988). In a more recent study, Hall et al. (2016) observed seed mortality in *A. saligna* at a temperature of 150°C, whereas the optimum temperature was 100°C. The poor germination response to dry heat pulse stimulus suggests an inadequate period of heat exposure of the seeds. The lack of a response to smoke (relative to the control) further indicates the study species' dependence on physical scarification (through fire or other means), rather than on the chemicals produced by combustion.

A comparison of the two acacias shows that *A. mearnsii* germinates more rapidly and has a higher germination response than *A. melanoxylon* in almost all treatments (except smoke at 20°C; Figure 2). It is noteworthy that some seeds, especially of *A. melanoxylon,* showed signs of impending germination (imbibement) and remained in that state for two to three weeks. Bewley (1997) also observed, but could not explain, imbibed dormant seed which had completed all metabolic processes required for germination but failing to undergo radicle extension.

Virgilia divaricata did not respond significantly better to any of the stimuli at either temperature regime than the two invasive acacias. This precludes the use of potential large-scale management strategies such as precisely timed (in relation to climate) fires or other disturbances to promote the germination of *V. divaricata* while inhibiting germination of the acacias. The reduced germination response of *A. melanoxylon* at 12°C (relative to *V. divaricata* and *A. mearnsii*) potentially presents an opportunity to suppress this species' germination by focussing management strategies in cooler seasons. In the absence of any germination stimulus (~control treatment), which may be akin to conditions associated with aboveground clearing of IAPs, *V. divaricata* appeared to have been severely outperformed by the acacias under the warmer temperature regime (~summer), providing further motivation for focussing *Acacia* management operations in the cooler seasons in areas where seed banks of *V. divaricata* also occur. An alternative strategy that could be considered at a small scale (albeit effort intensive), would be to sow locally obtained *V. divaricata* seeds that have been subjected to chipping or hot water treatment stimuli in areas cleared of the acacias. The sowed seeds should germinate better than the *Acacia* soil-stored seed banks (not receiving such stimulus) and potentially afford the indigenous species a competitive edge (Daehler, 2003). Such a strategy would be most appropriate in areas where *V. divaricata* and subsequent forest would naturally occur, or otherwise in areas that have been degraded ecologically. Such a strategy may augment an integrated pest management approach (Dent, 1995) in conjunction with other techniques such as selective thinning and herbicide application.

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CHAPTER 3 - Comparing soil-stored seed banks between two invasive alien species (*Acacia mearnsii* and *A. melanoxylon*) and an indigenous analogue (*Virgilia divaricata*)

ABSTRACT

The success of invasive alien plants in a new environment is largely determined by propagule pressure, amongst other aspects. For example, invasive species that produce large, persistent seed banks may respond rapidly to their respective germination stimuli, resulting in mass recruitment and complicating their management. An understanding of the seed bank densities, and their degree of persistence, may aid the management of invasive species and reduce the need for unnecessary follow-up treatments of the area. We compared the soil-stored seed bank densities and viability (at different depths in the soil profile) of two invasive alien trees, *Acacia mearnsii* and *A. melanoxylon*, and an indigenous analogue, *Virgilia divaricata*, on the southern Cape coast of South Africa to explore whether *V. divaricata* may compete with the acacias in terms of the propagule pressure exerted by mature trees. *Acacia mearnsii* had the largest seed banks (7 596 seeds m^{-2}), followed by *V. divaricata* (938 seeds m^{-2}) and *A. melanoxylon* (274 seeds m^{-2}). The low seed densities of *A. melanoxylon* can be attributed to the species being bird-dispersed, as well as the presence of a seed-boring biological control agent. Seed bank densities were largely comparable between soil depth classes in each of the study species. Seed viability within the seed bank did not differ between species (88% for *V. divaricata*; 91% for *A. mearnsii*; 87% for *A. melanoxylon*) but differed marginally between depth classes within species (trends in this aspect differed between species). The presence of biological control agents may reduce the amount of seed produced and thus reduce the future accumulation of seed banks, but do not reduce the existing soil-stored seed banks. Management of the acacias should focus on reducing the remaining seed banks after trees have been killed, while also supplementing the seed banks of *V. divaricata* with locally obtained seeds. *V. divaricata* seeds may even be treated with appropriate stimuli and then sowed in the area in order to provide *V. divaricata* with an advantage over the acacias, possibly allowing it to outcompete them.

INTRODUCTION

The ability of a plant to succeed in an environment is determined by a number of factors, including its interaction with other plants (Dukes, 2001; Knops et al., 1999; Ruijven et al., 2003). Another such factor involves the reproductive dynamics of the species in terms of seed production and longevity (Lockwood et al., 2009). For alien (non-native) plants introduced into a new environment, propagule pressure in the form of seed abundance and viability is a particularly important determinant of the success of invasion (D'Antonio et al., 2001). In addition to seed production, the longevity of seeds would also affect propagule pressure through time, where under particular conditions the seed of some species can remain dormant for hundreds to thousands of years (Porsild et al., 1967). As a survival strategy, dormancy allows a period over which seeds can be dispersed across landscapes and vertically within the soil profile (Simpson, 1989). Remaining dormant within the soil profile enables the seed to escape unfavourable conditions through time, and germinate when conditions become more favourable for growth (Crocker and Barton, 1953).

Propagule pressure is an important component of plant vigour when considering the competitive performance of co-occurring native and invasive alien plants (IAPs) (Daehler, 2003; Lockwood et al., 2009). We compared seed bank densities and seed viability between two serious alien invaders (*Acacia mearnsii* De Wild and *Acacia melanoxylon* R.Br.) and an indigenous, ecologically analogous species (*Virgilia divaricata* Adamson) in the southern Cape of South Africa. The two acacias originate from south-east Australia and were introduced into South Africa in the 1800s for their useful resources (Browmilow, 1997; Henderson, 2007). *Virgilia divaricata* is native to a narrow region along the south-eastern coast of South Africa (Coates Palgrave et al., 2002), where it plays an important role in the expansion of indigenous forests (Coetsee and Wigley, 2013). All three species (*A. melanoxylon* to a lesser extent) have fast growth rates and early flowering ages, as are often observed with pioneer species (Coates Palgrave et al., 2002; Louppe et al., 2008; Praciak et al., 2013; Searle, 1997). These species form long-lived soil-stored seed banks (at least 50 years; Clarke, 2002; Geldenhuys, 1994; Harrington, 1972; Seydack, 2002), which can respond rapidly to germination cues (chapter 2), making the management of the two acacias particularly difficult (van Wilgen et al., 2012). The longevity of their seeds allows for large seed banks to accumulate, and with increasing residence time in the invaded environment, propagule pressure increases, thereby impeding control efforts (see review by Richardson and Kluge, 2008). The maximum recorded seed bank densities for both the invasive species (Donald, 1959 cited in Milton and Hall, 1981; Pieterse, 1997) appear to be higher than that recorded for *V. divaricata* (Phillips, 1926), but the latter has not been the subject of recent studies. These studies furthermore employed disparate sampling techniques, were conducted under different circumstances and on seed banks with varying accumulation periods, rendering comparisons between species less meaningful.

Estimates of seed bank density and distribution within the soil profile under comparable conditions of, for example, cover density are not available for the study species. Variation in seed viability with depth within the soil profile is not known for all three species. We aimed to address this lack of information, in order to (i) improve understanding of the persistence of invasions and risk of recolonisation where these invasive species have been cleared, and (ii) screening the potential for using an indigenous analogous species to outcompete the invasives.

METHODS

Study area

Thirty study sites (ten per species) were located along the southern Cape coast of South Africa, between the towns of George (33°58’S, 22°27’E) and Nature’s Valley (33°58’S, 23°33’E). The climate of the study area is temperate with an average of 800 mm (west) to 1 078 mm (east) of year-round rainfall (peaking in April and October) and daily summer and winter temperatures averaging 20°C and 12°C, respectively (Tyson and Preston-Whyte, 2000). The underlying geology of the area consists mostly of rocks from sandstone, quartzite, and shale forms of the Table Mountain Group. All the study sites occurred on the coastal plateau, with mostly colluvial and alluvial soils with yellow-brown to grey-brown colours and sandy loam to silty loam textures (Schafer, 1992). The major soil groups of the area are duplex (Estcourt and Klapmuts), hydromorphic (Longlands and Katspruit), and podzols (Lamotte and Witfontein) (Soil Classification Working Group, 1991). The soils have generally low pH (3.5-5) due to the sandstone and quartzitic origin (Schafer, 1992). The vegetation in the area comprises fire-sensitive Southern

Afrotemperate forest (Mucina and Geldenhuys, 2006) and fire-prone fynbos shrubland (Rebelo et al., 2006). Invasion of fynbos by alien plants is of particular concern as fynbos contains many endemic, often endangered taxa, which may be negatively impacted by the IAPs and their impacts (Goldblatt and Manning, 2000). Disturbances, facilitating invasion by alien plants (Hierro et al., 2005), occur frequently in the area in the form of agriculture and forestry operations, regular floods (Russell and Kraaij, 2008) and recurrent fires (at 10-26 year intervals in fynbos; Kraaij et al., 2013).

Data collection

Seed banks were sampled from underneath the canopies of ten trees for each of the three study species. Trees were selected based on criteria regarding stem diameter at 50 cm above ground level (20-50 cm), slope (<30°), extent of canopy overlap (<30%) with conspecifics, and habitat type. Samples were not taken where the two acacias occurred together in the same location due to difficulties associated with the differentiation of similar-looking seed. Habitat types in which sampled trees were located included Southern Afrotemperate forest (six trees), fynbos (ten trees), forest-fynbos ecotone (four trees), each with varying degrees of disturbance, and lastly, severely disturbed or transformed agricultural or roadside habitat (ten trees) (Figure 1). We aimed for comparable representation of habitat types in the sampling of each of the study species.

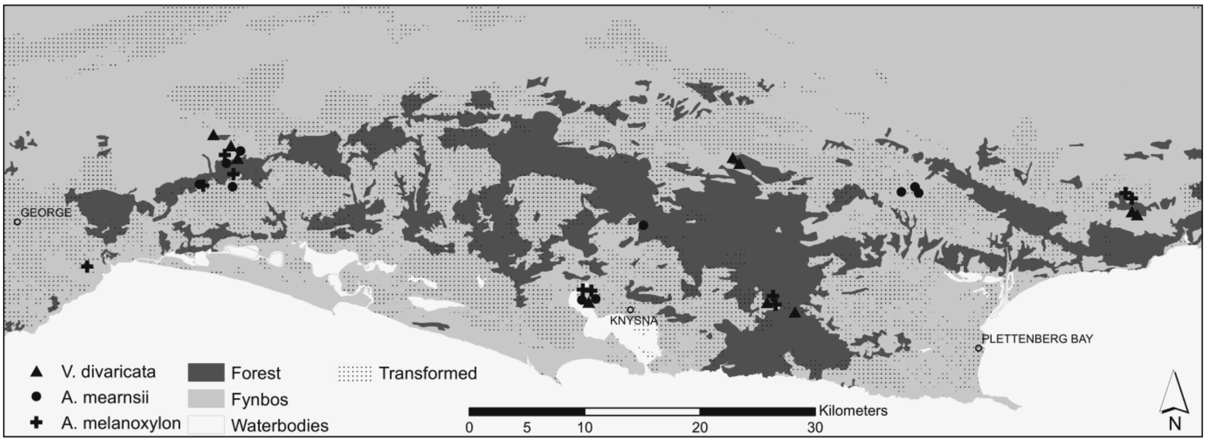

Figure 1: Map of sampling locations of soil-stored seed banks of *Virgilia divaricata*, *Acacia mearnsii*, and *A. melanoxylon* across various habitat types.

For each site, the sampling of soil cores was carried out at predetermined positions along four transect lines radiating outward from the stem of the sampled tree, at angles of 45°, 135°, 225° and 315° relative to a 0° line directed upslope. Each transect had two sample positions at distances of 45 cm and 90 cm from the stem from where samples were collected (i.e. a total of eight sample plots per tree). This sampling strategy was designed to account for potential seed drift down slopes (although seed densities did not differ significantly between sampling locations occurring up-slope *vs.* down-slope of tree stems; paired t-test $t_{(29)} = 1.79$, $p = 0.084$). At each sample location, six litter samples were collected from a 15.9 cm^2 area. A 4.5 x 20 cm cylindrical core sampler with slide hammer was used to collect soil cores from the same location where the litter was sampled. Six cores were taken from the surface soil at a depth of 0-5 cm ('shallow') and from two of these areas cores were taken at a depth of 5-15 cm ('deep'). Seed bank density data comprised of seed counts for each soil depth class, and were combined for all eight sample plots per tree. This resulted in ten replicates (trees) per species x depth class combination. Characteristics of each sampled tree (stem diameter at 50 cm above ground level, crown diameter, and height) and site characteristics (habitat type, landform, slope, soil type, percentage rock, soil moisture status, and density of study species) were recorded. The samples were stored in open plastic bags at room temperature until processed for seed extraction.

Seeds were extracted from the litter samples, first though the removal of coarse litter with sieves, with the remaining material sorted by hand. Seeds were extracted from the soil core samples in one of two ways, depending on the characteristics of the soil. Seeds from friable or unconsolidated loam soil were extracted by dry sieving, whereas non-friable or consolidated soil samples (containing more clay) were placed in a sieve (1 mm mesh size) and rinsed under water to remove the soil. Extracted seeds were enumerated, dried and stored at room temperature until viability tests could be carried out. Seeds which germinated whilst in storage, and which could be identified as the sampled species, were recorded as viable seeds.

The proportional viability of seeds from the different species and depth classes were determined by using a tetrazolium-chloride stain test (Porter et al., 1947). The seeds were cut longitudinally, and one half of each seed submerged overnight in a 2% solution of 2,3,5-triphenyl-tetrazolium chloride. Visibly stained seeds were enumerated. The different habitat types in which the sampled trees occurred served as replicates with 10-50 seeds (depending on availability of seeds extracted from soil cores) tested per habitat type per species x depth class combination aiming for a total of 100 seeds to be tested per species x depth class combination. Samples where no seeds were obtained in particular species x depth class combinations, in some habitat types, reduced the number of replicates available for statistical testing.

Data analysis

The effects of species and depth class on seed bank density were tested. The data did not conform to the assumptions of normality and homogeneity of variance, and were log(x+1) transformed (Barlett, 1947). The transformed data were analysed as a two-way factorial analysis of variance (ANOVA), testing for the effects of species and depth (STATISTICA v.13, Dell Inc., 2015). Factors showing significant effects were further analysed with Tukey post-hoc tests. To compare seed bank densities recorded in this study with those reported in the literature, seed counts were converted to seed number m^{-2}.

The effects of species and depth class on seed viability were tested and expressed as a proportion of the total number of seeds tested per replicate of species x depth class combinations. The proportions did not conform to assumptions of normality and homogeneity of variance and were subjected to a rank transformation. The ranked and unranked data were tested using factorial ANOVA, which yielded comparable results. Test results from the unranked data were therefore regarded valid, as the assumptions for ANOVA were reasonably satisfied (Montgomery, 2013).

To obtain estimates of viable seed bank densities, we multiplied the proportional viability with the seed count data for each species x depth class combination. The derived data on viable seed bank densities were then subjected to the same statistical tests as the original seed bank density data to assess for the effects of species and soil depth class.

RESULTS

Seed bank densities differed significantly among species ($F_{(2,81)} = 26.88$; $p < 0.001$) with all three species differing significantly from one another ($p < 0.006$). *Acacia mearnsii* had the highest seed bank density, followed by *V. divaricata* and *A. melanoxylon.* The average seed bank density in the sampled soil profile of the three species was 2 936 seeds m^{-2} with large variation (ranging from ~100 to several thousand seeds m^{-2}) evident in all species (Table 1). Seed bank densities did not differ significantly between soil depth classes ($F_{(2,81)} = 1.62$; $p = 0.205$) although all three species (and *A. melanoxylon* in particular) had fewer seeds in the litter layer than in the shallow layer, and comparable numbers of seeds in the shallow and deep layers (Figure 2). In terms of the reliability of soil-stored seed banks, *V. divaricata* and *A. mearnsii* appeared to maintain seed banks more consistently (with 22% and 20% of sample plots per depth class yielding no seed, respectively) than *A. melanoxylon* (63%).

Table 1: Seed bank densities (seed m^{-2}) and viability (%) of *Virgilia divaricata*, *Acacia mearnsii*, and *A. melanoxylon* recorded in this study and compared to seed bank densities reported in literature.

Species	Seed bank density (seeds m^{-2})		Seed viability (%)	
	Current study mean (range)	Literature	Current study	Literature
V. divaricata[*]	938 (170-3 406)	15-685[e]; 500-2 000[f]	88	90-99[f]
A. mearnsii	7 596 (57-35 060)	5 314[a]; 38 340[c]	91	92[b]
A. melanoxylon	274 (0-1 262)	2 860-94 420[d]	87	70[c]; 90[d]

[a] Pieterse (1997); [b] Garner (2007); [c] Milton and Hall (1981); [d] Donald (1959) cited in Milton and Hall (1981); [e] Geldenhuys (1994); [f] Phillips (1926); [*] *V. capensis* was also included in literature searches as *V. divaricata* and *V. oroboides* were both referred to as *V. capensis*, prior to taxonomic revision.

Seed viability did not differ significantly between the study species ($F_{(2,20)} = 0.83$; p = 0.452) and was high in all three species (*A. mearnsii* 91%, *V. divaricata* 88%, and *A. melanoxylon* 87%). Seed viability did not differ significantly between depth classes ($F_{(2,20)} = 3.01$; $p = 0.072$). For *V. divaricata*, viability was highest in the litter layer, whereas in the acacias (*A. melanoxylon* in particular), viability was highest in the shallow layer (Figure 3).

Estimates of viable seed bank densities differed significantly among species ($F_{(2,81)} = 27.33$, $p < 0.001$), with all three species differing significantly from one another ($p < 0.004$). Average viable seed bank densities were estimated at 6 916 seeds m^{-2} for *A. mearnsii*, 826 seeds m^{-2} for *V. divaricata*, and 247 seeds m^{-2} for *A. melanoxylon*.

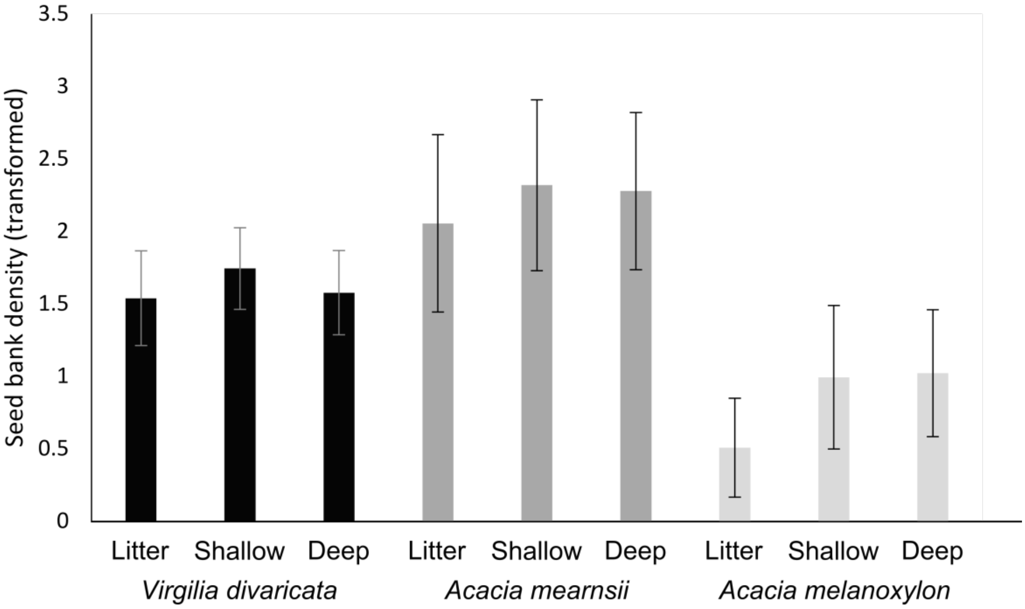

Figure 2: Seed bank densities (means ± 95% confidence limits of log(x+1) transformed data) of *Virgilia divaricata*, *Acacia mearnsii*, and *A. melanoxylon* in litter, shallow, and deep soil layers.

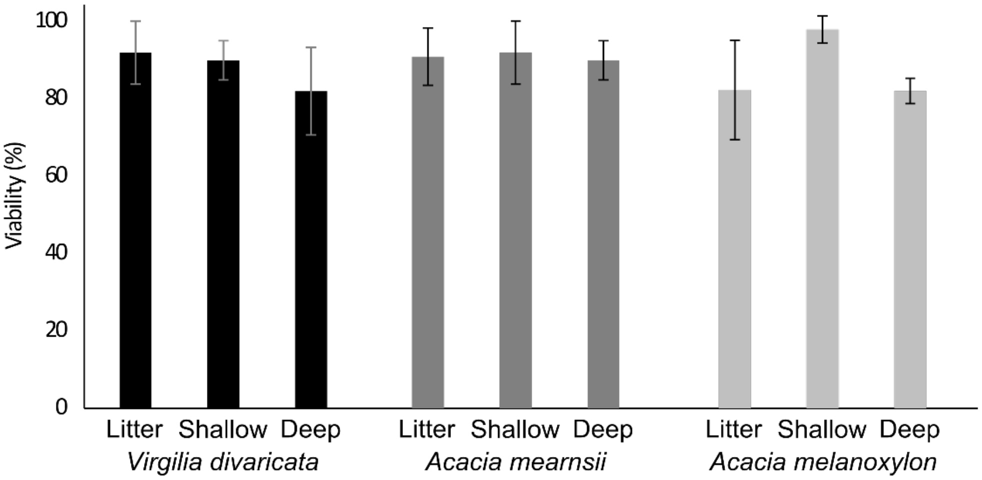

Figure 3*:* Percentage viability (means ± 95% confidence limits) of seeds of *Virgilia divaricata*, *Acacia mearnsii*, and *A. melanoxylon* in the litter, shallow, and deep soil layers.

DISCUSSION

Seed bank densities differed significantly among the study species. *Virgilia divaricata* had smaller seed banks than *A. mearnsii*, but larger than *A. melanoxylon.* The seed bank densities observed for *V. divaricata* and *A. mearnsii* generally corresponded with those reported in the literature (Table 1). *Acacia melanoxylon*, however, showed a large discrepancy with literature, being 10-345 times smaller than the only other published study on this species (Donald, 1959 cited in Milton and Hall, 1981). However, Donald (1959) obtained samples from *A. melanoxylon* infestations as well as plantations whereas our sampled trees occurred in densities ranging from solitary to small groups, which may explain some of the discrepancy. The low seed bank densities generally observed for *A. melanoxylon* in our study may have resulted from combined effects of bird dispersal (Richardson and Kluge, 2008), a seed-boring weevil, *Melanterius acacia* Lea, that was introduced in the study area as a biological control agent in 1986 (Dennill and Donnelly, 1991), and the low densities in which sampled trees occurred. In contrast high seed densities were recorded for *A. mearnsii*. Although a seed-boring weevil (*M. maculatus* Lea) (Impson et al., 2009) and flower-galling midge (*Dasineura rubiformis* Kolesik) (Impson et al., 2008) have been introduced for this species, these introductions have been more recent (1993 and 2001, respectively; Impson et al., 2011), and may therefore not have reduced seed production to the same extent as in the case of *A. melanoxylon.* When comparing our findings to seed bank densities of other invasive acacias in South Africa (Milton and Hall, 1981; Richardson and Kluge, 2008), the range for *A. mearnsii* falls within a moderate to high density (similar to *Acacia longifolia* (Andr.) Willd. and *Acacia saligna* (Labill.) H.L.Wendl.), whereas *V. divaricata* showed a low to moderate density (similar to *Acacia cyclops* A.Cunn. ex G.Don) and *A. melanoxylon* showed densities similar to the lowest densities observed for the other acacias.

Seed bank densities within species were largely comparable between soil depth classes, with all species displaying a trend of fewer seeds in the litter layer than in the shallow and deep layers (most pronounced in *A. melanoxylon*) (Figure 2). Seed density in the litter layer depends on variability in seed rain, lateral seed drift, and predation (Holmes, 1990; Richardson and Kluge, 2008), whereas seed density within the soil profile would mostly be affected by germination events and pathogens or decay (Holmes, 1988; Pierce and Cowling, 1991) and thus expected to be less variable in time. The similarity in seed bank densities between the shallow and deep layers in all three study species may be accounted for by the deep layer representing twice the volume of soil that the shallow layer represents, suggesting that at equivalent volumes, deep soil would yield fewer seed than shallow soil. Alternatively the similarity between deep and shallow soil seed bank densities which we observed may relate to the particular depth at which one differentiates between the shallow and deep seed banks. In a review of the seed ecology of invasive Australian acacias, Richardson and Kluge (2008) regarded this interface to be at a depth of approximately 8 cm, after which seed bank densities rapidly declined. Seed banks do extend deeper in the soil profiles, especially those that consist of loose sand (Holmes, 2002; Milton and Hall, 1981). The interface between shallow and deep seed banks in our study was arbitrarily chosen at a depth of 5 cm, suggesting that a large component of our deep layer could be considered part of the shallow layer when using a different differentiation (thus rendering our results more comparable with other studies).

Between the study species, *A. mearnsii* had the highest overall viability and most constant viability throughout the soil profile. *Virgilia divaricata* was more similar to *A. mearnsii* than *A. melanoxylon*, with the latter species having larger differences between the three layers. Viability observed in the two acacias corresponded well with ranges reported in the literature (Donald, 1959 cited in Milton and Hall, 1981; Garner, 2007; Milton and Hall, 1981), and in *V. divaricata* was slightly lower than that reported by Phillips (1926). When compared to studies in South Africa on other invasive acacias, the seed viability for all three of our study species were comparable to those observed for *A. cyclops*, *A. longifolia*, and *A. saligna* (Milton and Hall, 1981; Richardson and Kluge, 2008). Seed viability differed only marginally between depth classes, but trends in terms of this aspect differed among the species. Seed viability for *V. divaricata*, unlike the acacias, was highest in the litter layer, which may be due to the presence of the biocontrol agents on the acacias (the difference being more pronounced in *A. melanoxylon*). All three species displayed higher seed viability in the shallow layer than in the deep layer, in accordance with the general assumption that seed in the deeper layers would be older and thus less viable (Smith and Berjak, 1995).

Persistent, soil-stored seed banks are a major challenge to the management of IAPs as multiple and large germination events may occur in response to appropriate germination stimuli (chapter 2), requiring numerous and costly follow-up treatments to prevent recolonisation (van Wilgen et al., 2016). In this regard, the higher seed bank densities and high seed viability throughout the sampled vertical soil profile displayed by *A. mearnsii* suggest that this species would pose a greater management challenge than *A. melanoxylon*. *Acacia mearnsii* has been classified (Richardson and Kluge, 2008) as having a ‘Type A’ seed ecology, whereby the seed testa’s impermeability to water persists and only small proportions of the seed bank germinate at any given time, whereas the seed testa of *A. melanoxylon* (‘Type B’) does not have persistent impermeability and the majority of seeds will germinate at a given time (as a result of digestive processes in animals, particularly birds, or aging; Milton and Hall, 1981). The substantial decrease of viability between the shallow and deep layers in *A. melanoxylon*, as opposed to *A. mearnsii* and *V. divaricata*, may thus be explained by its ‘Type B’ seed ecology. *Virgilia divaricata* appears to also have a ‘Type A’ seed ecology, as it has been observed that the proportion of seeds that germinated from the soil-stored seed bank after a single disturbance event (fire) was comparable between *V. divaricata* (mean proportion ± 95% confidence interval = 0.2 ± 0.13) and *A. mearnsii* (0.14 ± 0.06) (unpublished data). Seeds with more persistent impermeability would have lower moisture content over longer periods than in seeds with lower impermeability, retaining their viability for longer (Roberts, 1974) and would thus be able to move deeper down the soil profile over time.

Germination-inducing management schemes, such as fire (Brown and Botha, 2004; Holmes et al., 1987; see chapter 2), may thus be more effective at reducing the upper seed bank in *A. melanoxylon* than in *A. mearnsii* since the majority of the former species’ seed bank would germinate, necessitating fewer follow-up efforts to clear seedlings. In addition to depleting the soil-stored seed bank by stimulating germination, fires destroy most of the seeds in the litter layer (Pieterse and Boucher, 1997). Although germination-inducing management schemes may be less effective (requiring more rotations) in *A. mearnsii* than in *A. melanoxylon*, it may serve to control the timing of germination and the area in which it takes place, allowing for organised follow-up management. Soil solarisation is another method that may be employed to deplete soil-stored seed banks, which may be appropriate for the management of very high seed bank densities at localised scales where native biodiversity is already severely compromised. The method involves the covering of the soil with mulch underneath a polyethylene sheet, causing temperature increases (to 75-80°C) in the upper 12 cm of the soil over extended periods and thereby killing the majority of seeds of both alien and native species (Cohen et al., 2013). The ability of *A. melanoxylon* to resprout vigorously from the base of the stem and from root suckers, as well as its seeds being dispersed by birds, present different management challenges. Bird dispersal of seeds is likely to result in more widespread recruitment of new infestations of this species albeit at lower densities.

In our assessment of propagule pressure as a measure of plant competitive performance, *A. mearnsii* would be the strongest competitor when considering seed bank density, followed by *V. divaricata* and *A. melanoxylon*, respectively. However, estimated seed longevity in *V. divaricata* (230 years; Geldenhuys, 1994) exceed that in the acacias (at least 50 years; Richardson and Kluge, 2008), suggesting that *V. divaricata* may outcompete the acacias in terms of propagule pressure over time. Programmes aimed at the management of the invasive acacias should combine approaches of reducing acacia seed banks whilst supplementing the seed bank of *V. divaricata* with locally obtained seeds, especially in forest margins and degraded areas where there is no threat of *V. divaricata* outcompeting sensitive fynbos species. The use of germination-inducing techniques (fire) would promote germination of all three species (if present in the seed bank), after which the seedlings of the acacias could be removed or thinned to allow the seedlings of *V. divaricata* to establish more readily and compete with subsequently germinating seedlings of the acacias (chapter 4).

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CHAPTER 4 - Comparing growth performance between two invasive alien species (*Acacia mearnsii* and *A. melanoxylon*) and an indigenous analogue (*Virgilia divaricata*)

ABSTRACT

The success of an invading alien plant species depends largely on the performance of the newly established individuals in the novel environment. The probability of an invasion decreases as the number of niches that an invasive species may occupy becomes unavailable due to analogous, indigenous species. An understanding of the competition between co-occurring native and invasive species may allow for management to focus efforts on promoting the success of native species that would result in the exclusion of the invasive species from the area. We assessed growth performance in seedlings and saplings (and how it is affected by competition) of two invasive species, *Acacia mearnsii* and *A. melanoxylon*, and an indigenous analogue, *Virgilia divaricata*, on the southern Cape coast of South Africa. *Virgilia divaricata* outperformed *A. mearnsii* in the seedling stage, in terms of growth in height and total dry mass produced. Individual performance of saplings of the three species was generally comparable and the extent of competition appeared to have no negative effect on the growth of *V. divaricata* or *Acacia* saplings. This suggests that *V. divaricata* may be used in integrated management of the invasive acacias along with other management strategies such as the removal of the invasive species and the introduction of biocontrol agents. Additionally, the effects of sowing stimulated *V. divaricata* seeds in areas cleared of the acacias (not having received stimuli) could be investigated, as *V. divaricata* would be provided with adequate time during which it may form a dense stand, facilitating native forest species establishment.

INTRODUCTION

All plants require resources such as light, space, nutrients, and water for growth, leading to intra- and inter-specific competition between individuals for these resources within the same area (Booth et al., 2010). As competition occurs, the available resources decrease, with the strongest competitor potentially outcompeting weaker competitors (Goldberg, 2012). Two main factors can determine the outcome of plant competition, namely directionality and symmetry. Directionality relates to the direction of the competition between the competitors, and can be either one-way or two-way (te Beest et al., 2013). For one-way competition, the weaker competitor is impacted more than the stronger competitor, whereas in two-way competition both competitors are affected equally, relative to their 'size' (te Beest et al., 2013; Vaugh and Young, 2015). One-way competition is mostly observed where one species outperforms (outcompetes) another and excludes it from the local community, whereas two-way competition can be considered as co-existence, and is most often observed when the two competitors occupy different niches (Firbank and Watkinson, 1990; Schulze et al., 2005). The symmetry of competition relates to how the competitors affect each other relative to their size (Schwinning and Weiner, 1998). Symmetric competition occurs when both competitors are of relatively equal size and the competition for resources is also equal (Schwinning and Weiner, 1998). Asymmetric competition is when an individual uses proportionally more resources than its competitors in relation to its size (Freckleton and Watkinson, 2001; Schwinning and Weiner, 1998).

For invasive alien plants (IAPs) to become established, they need to overcome several barriers, including competition posed by native species (Theoharides and Dukes, 2007). An ecologically intact landscape is less likely to be invaded by IAPs, as most of the niches remain occupied with high levels of competition from established plants (Kennedy et al., 2002). Areas that undergo frequent natural or unnatural disturbance are therefore more likely to be invaded, as native species still experience stress and competition from their local ecosystem, reducing the competition that IAPs experience (Hobbs and Huenneke, 1992; Jauni et al., 2015). IAPs often have fewer biological factors that can affect them negatively than native species, such as pathogens and specialised predators (Lake and Leishman, 2004; Wolfe, 2002). Native species that are ecologically and functionally similar to the alien species have been shown to compete well due to the occupation of niches that the IAP would occupy (Dietz and Edwards, 2006). The competition between native and alien species has been well documented (see Daehler, 2003; Vilà and Weiner, 2004), but has been studied more extensively in grasses and herbaceous species than in larger woody plants (Funk et al., 2008). However, the use of native species as a tool in the management of IAPs has not been well documented. Of the 16 studies on native-alien competition reviewed by Daehler (2003), 11 showed that native species competed equally with or outcompeted the alien species. One of these studies assessed competition in the seedling stage between a native species (*Virgilia oroboides* (Berg.) Salter) and two invasive aliens (*Albizia lophantha* (Willd.) Benth. and *Acacia longifolia* (Andr.) Willd) in South Africa and found that the native species was the strongest competitor. That suggests that if the environment was to be manipulated correctly in favour of the indigenous species that it could potentially be used to suppress the two invasive species (McDowell and Moll, 1981). However, this study was limited to the seedling stage, and the effectiveness of such an approach would have to be explored across all life stages. In another study, however, it was found that seedlings of a native protea, *Protea repens* (L.) L., could only compete well with seedlings of the invasive *Acacia saligna* in low nutrient conditions (Witkowski, 1991). However, it should be noted that in the latter study, there is less similarity between the study species than in the aforementioned study.

To further explore this concept of using an indigenous species to suppress (outcompete) IAPs, we assessed the competitive performance of one indigenous species and two alien species in terms of growth rates at different life stages. The three study species are fast-growing, small to large trees from the Fabaceae (legume) family (Coates Palgrave et al., 2002; Louppe et al., 2008; Praciak, 2013; Searle, 1997). *Acacia mearnsii* De Wild and *Acacia melanoxylon* R.Br. are serious invaders in South Africa and elsewhere and difficult to manage (van Wilgen et al., 2012), while *Virgilia divaricata* Adamson is an indigenous, ecologically analogous species that fulfils an important ecological role after fires (~disturbance) in the ecotone of fire-prone fynbos shrublands and forests (Geldenhuys, 1994). We assessed seedling growth and resource allocation in a nursery study, and sapling growth (and how that is affected by the extent of competition experienced) in 'naturally' seeded populations in the field. Competition in this study was generally compared between *V. divaricata* and *A. mearnsii*, with *A. melanoxylon* as an additional study species. It was envisaged that improved understanding of the competitive performance of *V. divaricata* in relation to that of the invasive species in both the seedling and sapling stages of growth could be applied to inform management and rehabilitation of areas cleared of the invasives.

METHODS

Study area

The study area was along the southern Cape coast of South Africa. The site for the nursery study was located within an enclosed plot (to exclude large herbivores) on the George Campus of Nelson Mandela Metropolitan University (33° 57.830’ S, 22° 32.0’ E). The field study was undertaken within the Garden Route National Park at Farleigh (33°52.988’ S, 22°52.655’ E) and Millwood (33° 53.181’ S, 23° 0.697’E). The climate of the study areas is temperate with year-round rainfall (800 mm annum^{-1}), peaking in April and October, with summer and winter temperatures averaging 20°C and 12°C, respectively (Tyson and Preston-Whyte, 2000). All field sites were situated in former commercial pine plantations where the final rotation had been harvested three to five years prior to the study, and where the vegetation (indigenous and alien) was left to recover naturally. Prior to conversion to plantation, the vegetation at the field sites would have been ecotonal between Southern Afrotemperate forest and fynbos shrublands, depending on the frequency and severity of past fires (Mucina and Geldenhuys, 2006; Rebelo et al., 2006). Due to the history of disturbance associated with plantation management, high densities of *A. mearnsii* and some *A. melanoxylon* occurred among patches of fynbos and forest species.

Data collection

Seedling performance: nursery study

Seeds of *V. divaricata* and *A. mearnsii* (1 500 seeds species^{-1}) were subjected to a smoke and heat treatment. Seeds were placed in a metal sieve and suspended within smoke generated by leaf material on a metal plate over a fire (Poggenpoel, 1978). Seeds of both species were planted at the beginning of the cold season in 2014. The seeds were planted 1 cm deep, with the two species interspersed randomly but spaced 5 cm apart in order for germinants to be unaffected by competition amongst one another (Midgley et al., 1989) The exclosure plot was exposed to full sun (receiving shade from nearby trees only in the late afternoon) as would be present after a major disturbance event (i.e. fire). Above-ground heights of germinants (‘seedlings’) were measured one (T_1) and three months (T_2) after planting of seeds. Seedlings were harvested three months after planting, and dried in paper bags at 60°C for 48 hours. The above and below-ground parts of each plant (referred to as 'shoots' and 'roots', respectively) were weighed separately to determine their respective dry masses, and root:shoot (mass) ratios calculated.

Sapling performance: field study

Circular study plots of 2 m radius were located where at least one individual of *V. divaricata* (considered to be the reference species) occurred interspersed within stands of co-occurring *A. mearnsii* and *A. melanoxylon* individuals and little other vegetation. Being situated in areas where plantations were clear-felled three to five years prior to the study, plots contained saplings ranging in size from 0.2 - 8.0 cm groundline diameter (GLD; stem diameter measured 8 cm above ground level). Saplings of such sizes are likely to display rapid, and thus detectable, growth rates over a short period (Kozlowski, 1971). All saplings of the three study species with heights greater than 50 cm were marked and numbered. The first measurements (T_1) were taken during August-September 2015. Data collected for all the marked saplings included GLD (cm), height (cm), and distance from the plot centroid. Additional variables recorded for each plot included coordinates, slope and aspect. The second measurement (T_2) taken in June 2016, included GLD and height. A total of 18 study plots (nine at Farleigh and nine at Goudveld) were surveyed, with a total of 1 252 individual saplings (34 of *V. divaricata*; 1 138 of *A. mearnsii*; 80 of *A. melanoxylon*).

Data analyses

Seedling performance

As the root and shoot dry masses, and root:shoot ratios of seedlings did not conform to assumptions of normality and homogeneity of variance, between species comparisons were made using Mann-Whitney U tests. Height increment (i.e. absolute change in height) was calculated by subtracting the first measurement from the second measurement (T_2-T_1). The relationship between height increment and initial seedling height (at T_1) was explored, to determine whether this relationship (termed 'relative growth rate') differed among species. A general linear model (GLM) was used with initial seedling height and species (dummy variable with *V. divaricata* as reference species) as explanatory variables.

Sapling performance

For all marked saplings in the study plots, growth increment (between T_2 and T_1) in terms of height, GLD, and biomass index 'BI' (calculated as GLD squared multiplied by height; Eccles et al., 1997) were calculated. GLMs were used to explore whether the relationship between growth increment and initial size (at T_1) differed among the three species, with initial size and species (dummy variables with *V. divaricata* as reference species) as explanatory variables. These analyses were conducted for height, GLD, and BI, respectively.

To assess the competitive performance of individual saplings (of the three study species) in relation to competition collectively exerted by other saplings in the vicinity, a subset of marked saplings was first identified as focal saplings. This included saplings occurring within the central one metre radius portion of the (two metre radius) study plot (21 for *V. divaricata*; 331 for *A. mearnsii*; 33 for *A. melanoxylon*). The performance of each of these focal saplings was assessed in relation to the competition collectively exerted by the remainder of all the saplings within the two metre radius plot. Competition was expressed on a plot basis in terms of BI, which was calculated as the sum for all saplings (excluding the focal sapling), using the average BI between T_1 and T_2 (as an indication of each sapling's average 'biomass' during the study period). Relative growth rate in BI $\left(\frac{T_2-T_1}{T_1}\right)$ was used as the measure of growth for the focal saplings, since the relationships between BI increment and initial BI did not differ among species (investigated previously). To explore how the relative growth rate for BI of the focal saplings was affected by the extent of competition (~plot biomass) and whether this differed among species, a GLM was conducted on the relative growth rate in BI of the focal saplings as a dependent variable, with plot biomass and species (using dummy variables with *V. divaricata* as reference species) as explanatory variables.

As the primary focus of this study was on differences in competitive growth among species, the GLM slope coefficients (as opposed to intercept coefficients) relevant to species comparisons were interpreted (Tables 1 and 2; comprehensive GLM outputs in Appendix 1).

RESULTS

Seedling performance

Root dry mass (Z=-11.767; p<0.001), shoot dry mass (Z=-10.914; p<0.001), and root:shoot ratios (Z=-9.625; p<0.001) of seedlings harvested at 2-3 months of age differed significantly between species. *Virgilia divaricata* had greater average root (132 mg) and shoot (98 mg) dry masses, and root:shoot ratios (1.48) when compared to *A. mearnsii* (8 mg, 15 mg, and 0.63, respectively) (Figure 1). *Virgilia divaricata* displayed a significant negative linear relationship between growth (in terms of height increment) and initial seedling size. This relationship for *A. mearnsii* was also negative, and not significantly different to the relationship for *V. divaricata* (Table 1; Figure 2). Growth rate of seedlings relative to their size declined during the two to three months following germination. Average seedling height at two to three months of age for *V. divaricata* and *A. mearnsii* was 5.3 cm and 1 cm respectively, with maximum heights being 9.8 cm and 1.5 cm respectively.

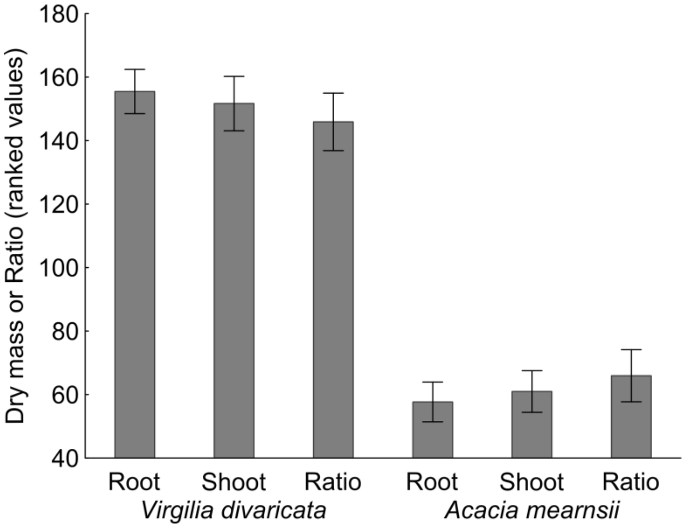

Figure 1: Root and shoot dry masses, and root:shoot ratios (mean ranks ± 95% confidence limits) of *Virgilia divaricata* and *Acacia mearnsii* seedlings harvested three months after planting of seeds.

Sapling performance

Saplings of all three species displayed a positive relationship between growth increment and their initial sizes (in terms of height, GLD, and BI) (Figure 2). This relationship was not significant for *V. divaricata* in terms of height. The relationship for *A. mearnsii* was significantly stronger than that of *V. divaricata*, and for *A. melanoxylon* the relationship did not differ significantly from that of *V. divaricata* (Table 1). The positive relationship between initial GLD and GLD increment was significant for *V. divaricata* and the relationship for *A. mearnsii* did not differ significantly from that of *V. divaricata*. The relationship for *A. melanoxylon* was significantly weaker than that of *V. divaricata.* The relationship between BI increment and initial BI was significant for *V. divaricata* and did not differ from those of the acacias. The extent of competition (summed competitor BI) had no effect on growth (relative growth rate in BI) of focal saplings of all three species (Table 2; Figure 3).

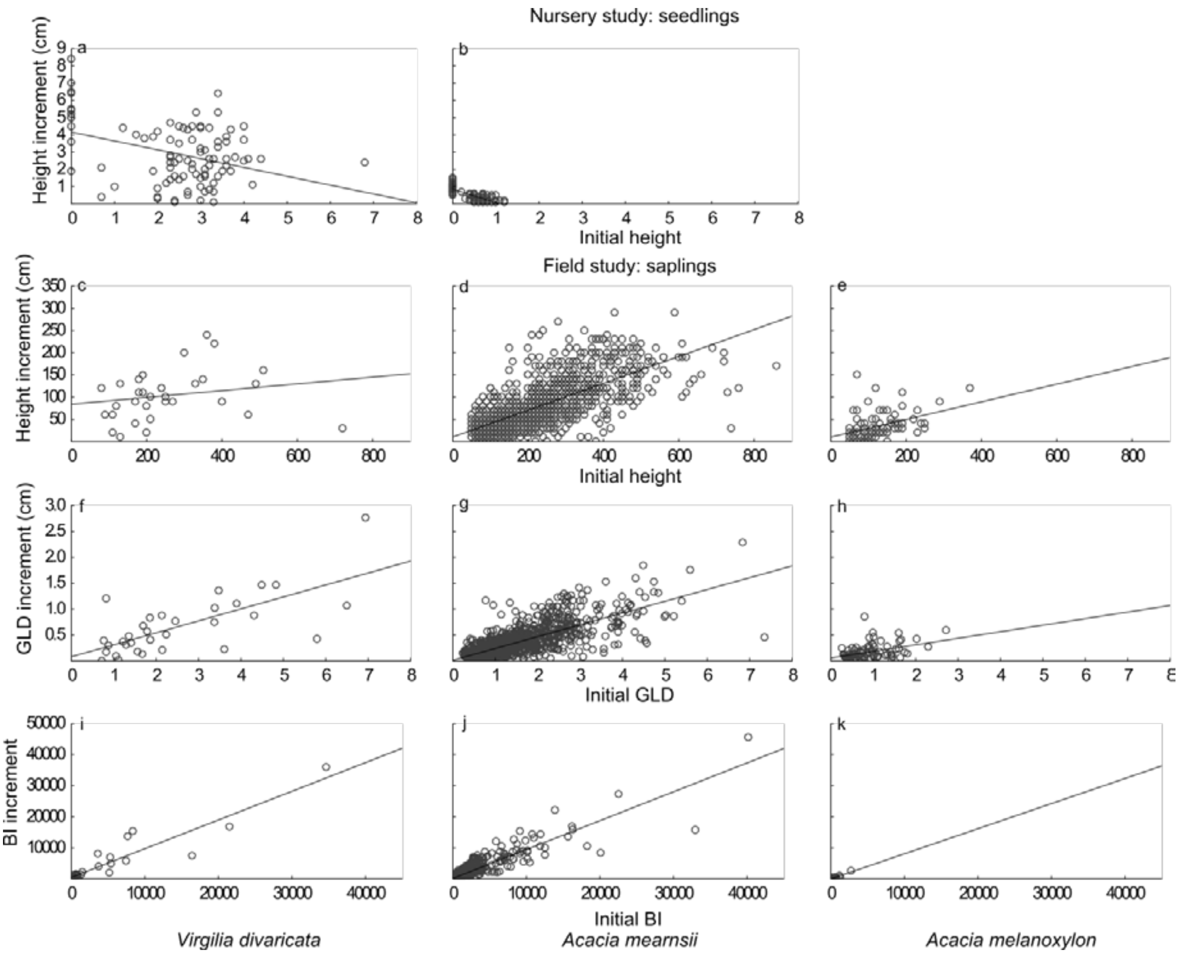

Figure 2: Relationships between growth increment and initial size for height of seedlings of *Virgilia divaricata* and *Acacia mearnsii* (nursery study), and height, groundline diameter (GLD), and biomass index (BI) for saplings of *V. divaricata*, *A. mearnsii*, and *A. melanoxylon* (field study).

Table 1: Results of general linear models exploring the relationships between seedling or sapling growth (expressed as increment in height, ground line diameter 'GLD', and biomass index 'BI', respectively) and initial size (in terms of the same measures, respectively) and how these differ between *Virgilia divaricata* (reference species) and *Acacia mearnsii* and *A. melanoxylon*.

Study component	Dependent variable	Explanatory variables	Species	Coefficient	p
Nursery (seedlings)	Height increment	Initial height	*V. divaricata*	-0.511	<0.001
			A. mearnsii	-0.285	0.389
Field (saplings)	Height increment	Initial height	*V. divaricata*	0.076	0.111
			A. mearnsii	0.226	<0.001
			A. melanoxylon	0.123	0.151
	GLD increment	Initial GLD	*V. divaricata*	0.231	<0.001
			A. mearnsii	-0.004	0.86
			A. melanoxylon	-0.105	0.034
	BI increment	Initial BI	*V. divaricata*	0.924	<0.001
			A. mearnsii	0.006	0.844
			A. melanoxylon	-0.115	0.737

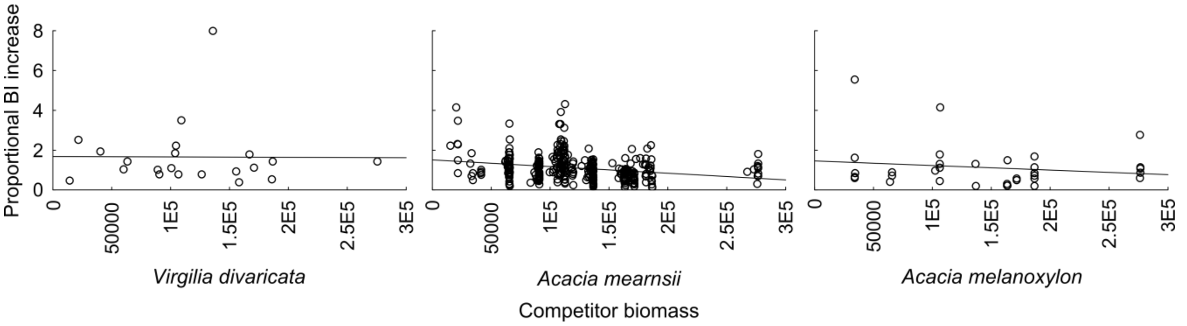

Figure 3: Relationship between proportional biomass index (BI) increase of focal saplings of *Virgilia divaricata*, *Acacia mearnsii*, and *A. melanoxylon* and summed competitor biomass.

Table 2: Results of general linear model exploring the relationship between sapling growth (expressed as relative increase in biomass index 'BI') of focal saplings and the extent of competition (expressed as summed BI of competitors), and how this differs between *Virgilia divaricata* (reference species) and *Acacia mearnsii* and *A. melanoxylon*.

Explanatory variable	Species	Coefficient	p
Summed BI of competitors	*V. divaricata*	-1.9E^{-7}	0.943
	A. mearnsii	-3.1E^{-6}	0.276
	A. melanoxylon	-2.1E^{-6}	0.522

DISCUSSION

Virgilia divaricata generally outperformed *A. mearnsii* during the seedling stage in terms of root and shoot dry masses, and growth in height, with *V. divaricata* having invested more resources in root development relative to aboveground development than *A. mearnsii* (Figure 1). The negative relationship observed for increase in height relative to initial height is supported by literature, as a decrease in growth rates over time is related to factors such as self-shading and soil resource depletion (Rees et al., 2010). Results from the germination study (see Chapter 2) suggest that *A. mearnsii* germination response and seedling performance was suppressed in the cool season compared to the warm season, which was apparent in the superior performance of *V. divaricata* seedlings in the nursery study. The overall superior performance of *V. divaricata* may also be related to its seed ecology. *Virgilia divaricata* produces larger, but fewer seeds than *A. mearnsii*, which allows for the formation of larger cotyledons (a larger initial photosynthetic surface area) and more rapid hypocotyl extension due to increased seed reserves (Leishman et al., 2000).

In all three species, larger saplings grew more than smaller saplings (relative to their initial size) over an equivalent period of time. This corresponds with the literature, where larger saplings of all species tend to grow more than smaller saplings over an equivalent period of time (Kozlowski, 1971). *Acacia mearnsii* outperformed *V. divaricata* in terms of relative height increases, whereas *A. melanoxylon* showed similar performance to that of *V. divaricata*. *Virgilia divaricata* had similar performance in relative GLD increases as *A. mearnsii*, and performed significantly better than *A. melanoxylon*. The relationship between increase in BI and initial BI was significant for *V. divaricata* and did not differ from the relationships of the acacias. It is apparent that different growth strategies are used by the three study species. For example, *A. mearnsii* allocated more resources into height growth than roots (during the seedling stage) and stem diameter growth during the sapling stage than did *V. divaricata*. The measures of height and GLD thus give different results when comparing species. BI incorporates both height and GLD, therefore equalising the differences in life strategies between species, and noticeably reducing the variation in the data (Figure 2).

Competitor biomass did not have a significant negative effect on relative growth for BI in focal saplings of any species. Considering that the majority of competitors in this study (and thus competitor biomass) consisted of *A. mearnsii*, this result suggests that

A. mearnsii does not have an apparent negative effect on growth of *V. divaricata* saplings, even at high densities. Competition directionality could, in this instance, be considered as two-way (equal) between *A. mearnsii* (the strongest competitor in terms of biomass) and *V. divaricata*. The symmetry of competition was more difficult to interpret, as neither small nor large saplings were affected significantly by their counterpart. The directionality may even be considered as asymmetrical, as smaller saplings were equally competitive as larger ones. Daehler (2003), in a review of studies on plant competition, showed that IAPs largely did not outperform their native counterparts in the invaded habitats. This effect was particularly true when the native and invasive species were phenotypically similar, as there would be a degree of niche overlap, or an absence of appropriate niches for the IAPs to colonise (Funk et al., 2008). Our study species are functionally similar in having rapid growth rates, atmospheric nitrogen fixing capabilities, and often functioning as pioneers for climax vegetation types such as forests and woodlands (*A. melanoxylon* fulfilling the pioneer role less often). In cases where IAPs outperform native species, the differences in performance can be attributed to differing life strategies, such as the native species being less shade tolerant than a faster growing IAP (Grotkopp et al., 2002), or that only the IAP can fix atmospheric nitrogen (Vitousek and Walker, 1989). The near-zero slope coefficients for the effects of competitor biomass on all three of our species may not be adequately explained in this study. High densities of a single tree species have been shown to result in intense intraspecific competition in other pioneer species, causing self-thinning (Hjálten et al., 1993; Peet and Christensen, 1987; Yeaton, 1978), which was not observed for *A. mearnsii* in this study.

A factor which was not investigated in this study that affects invasive species success in relation to native species, is enemy release. Exotic plants are often exempt from their specialist predators and pathogens in their adopted environment, providing them with a competitive advantage over native species (Keane and Crawley, 2002). A species of pathogenic fungus affecting native trees in the southern Cape, *Ceratocystis tsitsikammensis* Kamgan & Jol. Roux, have been found to produce similar symptoms (i.e. stem lesions) in *A. mearnsii* (Nkuekam et al., 2008; Van der Colff et al., 2016). The relatively good performance of *V. divaricata* in presence of its pathogens and predators, in addition to the strong competition from *A. mearnsii*, raises the question whether it may become weedy when introduced artificially outside its native range. This has been recorded in numerous European species where approximately 28% of alien plants originate from within the continent (Lambdon et al., 2008). Further autecological studies need thus be conducted on *V. divaricata* to determine habitats into which the species may be introduced without risk of becoming weedy.

Whilst competition between native and invasive species has been well studied (see Daehler, 2003; Vilà and Weiner, 2004), the potential use of native tree species in aid of the management of IAPs and re-establishment of indigenous vegetation, has not been fully investigated, but the method is often suggested. Under natural growing conditions, as was present in our field study, *V. divaricata* saplings appear to perform comparably to those of *A. mearnsii* and *A. melanoxylon* (comparison with the latter being less meaningful, due to inadequate representation of size classes), and does not seem to be affected negatively by high densities of *A. mearnsii* in its vicinity. *Virgilia divaricata* seedlings furthermore performed better than those of *A. mearnsii* in the first few months of growth in the nursery study, even with below-average precipitation during the study period. *Virgilia divaricata* may thus have a competitive advantage over the acacias if combinations of active and passive management are incorporated to assist in its establishment and proliferation. Active management may include the killing of acacias through manual removal and chemical means, in conjunction with the sowing of pre-treated seeds (see chapter 2) of *V. divaricata*. Purposeful establishment of populations of *V. divaricata* should preferably take place in areas where the species would normally form stands (i.e. forest edges), or in degraded areas where there is no threat of *V. divaricata* outcompeting sensitive fynbos species. Passive management may involve the introduction of a rust fungus, *Uromycladium acaciae* (Cooke) P. Syd. & Syd., severely affecting the growth and survival of *A. mearnsii* (McTaggart et al., 2015). Other introduced biological control agents that damage flower and seeds may further assist management by reducing further seed-set in acacias that do manage to reach reproductive age. Given enough time in habitat suitable for forest establishment, the formation of a closed canopy by colonizing native forest species will also prevent the majority of *A. mearnsii* seedlings from establishing due to shade intolerance often observed in pioneer species (Fargione and Tilman, 2012). *A. melanoxylon*, in contrast, is more tolerant of shade and may remain in the understory until a gap in the canopy has formed (Medhurst et al., 2003).

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APPENDIX 1: GLM output tables

GLM output of the difference in relationship between growth in height and initial height of seedlings of *Virgilia divaricata* and *Acacia mearnsii.*

Effect	Coefficient	p
Intercept	4.159	<0.001
Initial height	-0.512	<0.001
Acacia mearnsii	-3.299	<0.001
Initial height**Acacia mearnsii*	-0.285	0.389

GLM output of the differences in relationships between growth in height and initial height of saplings of *Virgilia divaricata*, and *Acacia mearnsii* and *A. melanoxylon*.

Effect	Coefficient	p
Intercept	84.045	<0.001
Initial height	0.076	0.111
Acacia mearnsii	-73.842	<0.001
Acacia melanoxylon	-74.331	<0.001
Initial height**Acacia mearnsii*	0.226	<0.001
Initial height**Acacia melanoxylon*	0.123	0.151

GLM output of the differences in relationships between growth in groundline diameter (GLD) and initial GLD of saplings of *Virgilia divaricata*, and *Acacia mearnsii* and *A. melanoxylon*.

Effect	Coefficient	p
Intercept	0.08	0.189
Initial GLD	0.231	<0.001
Acacia mearnsii	-0.067	0.285
Acacia melanoxylon	-0.022	0.776
Initial GLD**Acacia mearnsii*	-0.004	0.868
Initial GLD**Acacia melanoxylon*	-0.105	0.034

GLM output of the differences in relationships between growth in biomass index (BI) and initial BI of saplings of *Virgilia divaricata*, and *Acacia mearnsii* and *A. melanoxylon*.

Effect	Coefficient	p
Intercept	498.989	0.026
Initial BI	0.924	<0.001
Acacia mearnsii	-347.011	0.126
Acacia melanoxylon	-500.552	0.061
Initial BI**Acacia mearnsii*	0.006	0.844
Initial BI**Acacia melanoxylon*	-0.115	0.737

GLM output of the differences in relationships between relative rate in BI and competitor biomass of focal saplings of *Virgilia divaricata*, and *Acacia mearnsii* and *A. melanoxylon*.

Effect	Coefficient	p
Intercept	1.682	<0.001
Competitor biomass	$-1.9E^{-7}$	0.943
Acacia mearnsii	-0.171	0.654
Acacia melanoxylon	-0.225	0.629
Competitor biomass**Acacia mearnsii*	$-3.1E^{-6}$	0.276
Competitor biomass**Acacia melanoxylon*	$-2.1E^{-6}$	0.522

CHAPTER 5 - Synthesis and conclusions

SUMMARY OF MAJOR FINDINGS

Acacia mearnsii and *A. melanoxylon* are two invasive tree species with high incidence in the southern Cape of South Africa (Baard and Kraaij, 2014). These species have numerous negative impacts, such as the alteration of fire regimes, reduction in catchment water yield, and reduction of local biodiversity (de Wit et al., 2001; Le Maitre et al., 2011). The acacias have rapid growth rates, and can produce large quantities of seed that may persist in the soil for at least 50 years (Richardson and Kluge, 2008). Both species have the capability to resprout from the base of the stem following damage (Praciak, 2013; Searle, 1997), with *A. melanoxylon* being able to resprout from root suckers as well (Praciak, 2013). These traits complicate the management of the acacias as a stand is able to regenerate from the seed bank and resprout from the stump or roots of felled trees (van Wilgen et al., 2016). Improper herbicide application after tree felling and the occurrence of fires or other disturbances after clearing operations will result in the re-establishment of alien stands. This requires additional follow-up treatments which increases the cost of clearing operations (van Wilgen et al., 2012). An alternative strategy, which has not been investigated extensively, is the use of habitat management in the control of invasive alien plants (IAPs). Using an ecologically analogous native species, if known to compete well with or outcompete IAPs (Daehler, 2003; Vilà and Weiner, 2004), may not only assist with the management of IAPs, but assist with the re-establishment of native vegetation. We investigated *Virgilia divaricata*, which is indigenous to the southern Cape coast of South Africa and ecologically analogous to the acacias, as a competitor for the acacias. Three aspects related to the competitive performance of these plants were investigated. Firstly, the germination of the three species were compared in response to five stimuli at two temperature regimes (representative of summer, 20°C, and winter, 12°C). The germination stimuli investigated were chipping, hot water exposure, dry heat pulse (igniting alcohol-soaked seeds), smoke (aqueous smoke solution), and control (no stimulus). Secondly, the soil-stored seed bank densities and seed viability under mature trees were compared among the species, as well as the variation of density and viability with depth in the soil profile. Lastly, comparisons of performance, in terms of growth, were made among the three species for seedling (*V. divaricata* and *A. mearnsii*) and sapling stages (all three species). The effect of competitor density (at a stand level) on sapling performance (increase in biomass index) was also compared among the species.

In terms of germination stimuli, chipping resulted in the highest germination for all three species, at both temperatures, followed by hot water exposure. Dry heat pulse resulted in moderate germination for all three species, with *V. divaricata* performing marginally better at 20°C. Smoke and the control resulted in very poor germination for the three species at both temperatures. *Acacia melanoxylon* did display a slight increase in germination response at 20°C to all the stimuli. Within each stimulus and temperature combination, none of the species showed superior performance over the other. The similarities observed between the species in their responses to germination stimuli were attributed to their water-impermeable seed coat dormancy.

In terms of the seed bank study, *Acacia mearnsii* had the highest average seed bank density (7 596 seeds m^{-2}), followed by *V. divaricata* (938 seeds m^{-2}) and *A. melanoxylon* (274 seeds m^{-2}). No differences were observed among the three soil depth classes within each of the species. Seed bank densities of each species were comparable between the depth classes. Seed viability was high (87-91%) in all three species and comparable among the study species. A marginal non-significant difference in seed viability was observed among depth classes (which was most evident for *A. melanoxylon*).

In terms of competition in seedling growth, *V. divaricata* displayed superior individual performance to *A. mearnsii* during the first three months of growth. This occurred despite or perhaps due to the cold conditions during the study. The average height and total mass of *V. divaricata* seedlings were five and ten times that of *A. mearnsii*, respectively. Saplings of *V. divaricata* and *A. mearnsii* displayed comparable performance in terms of growth, although *A. mearnsii* performed slightly better in terms of height. *Acacia melanoxylon* displayed poor performance in terms of all growth measures investigated. The performance of individual saplings was not significantly affected by the summed biomass (as determined using a biomass index) of competitors (which consisted mostly of *A. mearnsii*) in their vicinity.

IMPLICATIONS FOR MANAGEMENT

An integrated approach would be required if *V. divaricata* were to be used for the management of the acacias. Using *V. divaricata* to compete directly with acacias (with management intervention) may be a viable management strategy as its performance was not affected negatively by competitor biomass. The significantly larger seed banks of *A. mearnsii* and the similar responses of the study species to germination stimuli exclude the use of fire or other disturbances to favour *V. divaricata* germination and growth over that of the acacias. *V. divaricata* seedlings significantly outperformed those of *A. mearnsii*, however performance during the period between seedlings at three months of age and saplings of a few years of age is not yet known. It is possible that all three species may germinate simultaneously after disturbance events and remain in equal competition after the seedling stage, depending on the seed bank size prior to the disturbance. The dense seed banks occurring underneath mature trees of *A. mearnsii* would inevitably result in much denser recruited stands compared to *V. divaricata*. *Acacia melanoxylon*, however, had small seed banks compared to the other two species, although seeds may be dispersed over greater distances by birds. Subsequent to clearing operations, new recruitment of *A. melanoxylon* therefore needs to be monitored over larger areas than in the case of *A. mearnsii*. It is likely that the strong resprouting abilities of *A. melanoxylon* may require alternative management to effectively kill individuals.

Management generally prioritises young and/or sparse infestations, which decreases ecological impacts and cost of management (Higgins et al., 2000; Hobbs and Humphries, 1995; Moody and Mack, 1988). In young/sparse infestations, seed banks may not have formed yet, rendering the management of subsequent recruitment less problematic. Sowing pre-treated *V. divaricata* seeds into areas cleared of the acacias (where *V. divaricata* would occur naturally) and preventing fire (and other disturbances), may give *V. divaricata* seedlings sufficient time to establish a dense canopy that may prevent further large-scale establishment of acacias due to strong competition. The leaf litter of *V. divaricata* may also play a role in the prevention of *Acacia* seed germination, as was observed by McDowell and Moll (1981) where *A. longifolia* germination was reduced under *V. oroboides* litter but not *vice versa*. In dense, older stands of acacias the prevention of stand expansion is more economically viable than attempting to clear the entire stand. The accumulation rate of *Acacia* seed into seed banks, and the spreading of seed to adjacent areas, may be decreased through the use of biocontrol agents already present in some areas. The seed boring weevils (*Melanterius acacia* and *M. maculatus*) and flower-galling midge (*Dasineura rubiformes*) should reduce the rate of seed accumulation within the seed bank. The trees in dense old stands can then be left standing, to sustain a source of biocontrol agents for spreading to new recruits. A small, young infestation that has not reached reproductive age may be cleared and the area monitored for subsequent germination. If a persistent seed bank of *A. mearnsii* is present and the area has undergone severe ecological degradation, it can be reduced through the use of fire, or in smaller areas, soil solarisation. Where native ecosystems still function, germination stimuli could be withheld, and the area supplemented with stimulated seeds of *V. divaricata* and other native species to promote the formation of a closed canopy, where appropriate in forest-fynbos ecotones. Assisting in the spread of the wattle rust fungus (*Uromycladium acaciae*), which may have been present in the country since the introduction of *A. mearnsii* (but only recently became prevalent in the eastern parts of the country), may increase the efficiency of management strategies directed at the control of *A. mearnsii*, as it can be particularly detrimental to seedlings and saplings (McTaggart et al., 2015). In an area where *U. acaciae* is active, *V. divaricata* may be used to compete with remaining individuals of *A. mearnsii* as they will have reduced vigour.

STUDY CONTRIBUTIONS AND LIMITATIONS

This study contributed towards the understanding of the competitive interactions of a co-occurring native and two alien plant species, and its potential use for the management of the invasive species (of which the studied acacias are some of the worst globally, nationally, and regionally) as well as subsequent rehabilitation of forest-fynbos ecotones or areas that would have been forest. Furthermore, it expanded on the limited knowledge of the seed banks and seed viability of all three species. Aspects of this study can be used as points from which further studies can be initiated, focussing on particular aspects in more detail. The diverse approach used in this study (lab experiment, nursery trial and field studies) provided valuable insight into multiple facets of plant competition (germination requirements, seed bank densities and viability, growth, and competition) and how these compare between an analogous native and two alien species.

The biggest limitation in this study was the length of the study period, particularly in terms of the competition chapter (chapter 4). Three months were inadequate to capture growth trends of the entire seedling phase. The sapling growth study also occurred over too short a period, not completely capturing all the phases in one growth season. Time constraints, and uncertainty of whether growth would be detectable over shorter periods of four to five months, resulted in only two measurements taken of saplings, and calculation of a single growth increment, whereas several measurements should have allowed for trends in growth rates to become apparent. Alien clearing operations scheduled by the management agency at the study sites (chapter 4) precluded the opportunity for recording follow-up measurements. A lack of availability of sites wherein all three species occurred at more comparable densities, was also a limitation. *A. melanoxylon* was underrepresented in terms of density and size classes.

RECOMMENDATIONS FOR FUTURE STUDY

To address the majority of limitations experienced in this study, a more controlled and long-term approach is recommended for studying competition among the study species. Pre-germinated seeds may be planted at predetermined spacing and varying densities in plots to reduce the inequality of densities within and among species observed in our competition study. This will also allow for an investigation of the effect of species dominance on competitive interactions (i.e. having a dense stand of *V. divaricata* with interspersed acacias). This study may be conducted over a period that would allow for competition to be assessed during all the life stages (i.e. seedling, sapling, and adult). Disparate competition should also be investigated wherein seedlings of acacias are planted underneath saplings of *V. divaricata*, to simulate the scenario advocated earlier whereby treated *V. divaricata* seed are sown and an acacia seed germinates after the establishment of a highly competitive stand of *V. divaricata*. To obtain a clearer understanding of the interactions between *V. divaricata* and the acacias, and whether their presence has a negative effect on its performance, *V. divaricata* performance should also be investigated in conditions where it competes with native trees with the native-invasive and native-native competitive performances compared (Vilà and Weiner, 2004). Investigating the effects of the various germination stimuli on subsequent vigour of seedlings may also provide further insight into managing the species at a landscape level. A study on three indigenous fynbos species reported that smoke treatment significantly improved seedling vigour in all three species, although it did not have a significant effect on germination percentage (Sparg et al., 2005). Other studies also reported improved seedling vigour where smoke treatment was used (Baxter and van Staden, 1994; Brown, 1993). The large discrepancy between seed banks of *A. melanoxylon* observed in this study and in the literature needs further investigation. In this respect, one should also consider that *A. melanoxylon* is less of a pioneer than the other two species and may be less mature when comparing similar size classes. Seed production in the presence and absence of biocontrol should furthermore be quantified as it was shown to differ substantially in other invasive acacias in South Africa (Moran et al., 2013). The effectiveness of multiple successive, short-rotation burns on depleting the seed banks of *A. mearnsii* should also be investigated (*cf* Lonsdale and Miller, 1993; Pieterse and Cairns, 1988) in localised areas with old, monospecific stands (where biodiversity has already been severely compromised). Lastly, the effect of recurring coppicing (due to mechanical damage) on resource partitioning, and thus reproductive vigour, should also be investigated in the acacias.

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