



Research note

Comparing germination stimuli of two alien invasive species and a native analogue: Towards sustainable management of invasives



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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 (chipped (manually), hot water exposure, dry heat pulse, smoke, and no treatment) at two temperature regimes (winter ~12 °C and summer ~20 °C) to explore how their germination requirements may be used to favour *V. divaricata* in areas cleared of the invasives. Chipped 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 stimulus–temperature 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 that have been chipped or exposed to hot water in areas cleared of the invasives of which the seeds would not have received stimuli.

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1. Introduction

Plant species use various strategies to increase the 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 stimulus 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 (de Wit et al., 2001; Richardson and Van Wilgen, 2004) and intensive management is often required to restore ecological functioning (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 between plant species, including between native and invasive species. The outcome of such competition is often condition and situation dependent. However, it is possible for native species to outperform invasives where they co-occur in space and time (Daehler, 2003). Understanding how different stimuli affect both invasive and native plant species may offer potential for more effective management of IAPs through the manipulation of environmental conditions (often referred to as 'habitat management') to favour the germination of native species over that of the invasive species. 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 direct stimuli when heat ruptures the testa (Brown and Botha, 2004) or through the presence of germination and growth

Abbreviations: IAP, invasive alien plant.

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stimulating chemicals in the smoke (de Lange and Boucher, 1990). Fire also provides indirect stimuli involving increased light intensity and resource availability resulting from removal of aboveground plant biomass, as well as the reduction of soil pathogens and allelopathic compounds (Ahlgren, 1974; Botha and Le Maitre, 1992; Melkiana, 1992; Rosenzweig, 1995). Physical scarification resulting from trampling and other disturbances also breaks seed dormancy (Baskin and Baskin, 2001; Bradbeer, 2013) through removal of the seed testa/endocarp to allow water into the seed (imbibement).

We investigated whether the application of different germination stimuli could aid the management of invasive alien plants 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 and elsewhere that are particularly difficult to manage (Van Wilgen et al., 2012). The third species is an ecologically analogous, but indigenous species (*Virgilia divaricata* Adamson) which is a pioneer tree with seed ecology similar to that of the invasive species. In its native range, it plays an important role after fire (~disturbance) in the ecotone of forest and fire-prone fynbos shrublands (Geldenhuys, 1994). All three species are fast-growing, nitrogen-fixing trees that maintain long-lived (>50 years) soil-stored seed banks displaying water-impermeable seed coat dormancy (Geldenhuys, 1994; Milton and Hall, 1981; Praciak et al., 2013). 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 invasive species.

2. Materials and methods

2.1. Study area

The study area is the south-eastern part of the Cape Floristic Region (South Africa), known for its high levels of biodiversity and endemism, which are threatened by IAPs amongst other disturbances (Baard and Kraaij, 2014; Goldblatt and Manning, 2000). The vegetation comprises fire-prone fynbos shrublands and fire-sensitive southern afro-temperate forest (Mucina and Geldenhuys, 2006; Rebelo et al., 2006). The region has year-round rainfall (~800 mm per annum) with summer and winter temperatures averaging 20 °C and 12 °C, respectively (Tyson and Preston-Whyte, 2000). Natural disturbances occur regularly in the form of floods (Russell and Kraaij, 2008) and fires (at 10–30 year intervals; Kraaij et al., 2013).

2.2. Trial design and data analysis

Undamaged seeds were extracted from seed pods collected (November 2015) from the canopies of approximately ten trees per species interspersed in the study area. 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 (in the dark) at room temperature and enumerating stained (i.e. viable) seeds (Porter et al., 1947).

The germination trial comprised of a factorial design ($3 \times 5 \times 2$) 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 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 5-cm-diameter petri dish on top of a sheet of filter paper, which was moistened with 2 ml 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 h, as per product instruction. Dry heat pulse stimulus was applied

by soaking the seeds in a 70% isopropyl alcohol solution for 1 min, removing all the seed from the alcohol and igniting the mass and extinguishing it after 3 s (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 h (Pérez-García and González-Benito, 2006). Hot water exposure and dry heat pulse are representative of the temperature range during an average fire in the top 2 cm (80 to 120 °C) and deeper 2 cm (20 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 treatment (measured after 3 sec, 10 s, 1 min and 3 min of submersion) and dry heat pulse (measured directly after extinguishing the flames, and every 10 s for 1 min). Seed temperature measured directly after alcohol flame exposure ranged between 65 and 90 °C (with flame temperatures ranging from 120 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 and 65 °C (irrespective of the time submerged) 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 and 20 °C, representative of winter and summer conditions (calculated as the average temperature over 24 h 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.

Germination count was determined as the total number of seeds per replicate that have germinated by the end of the trial. 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).

3. Results

Seed viability was high (93%) in all three species, i.e. 94% in *V. divaricata*; 99% in *A. mearnsii*; and 88% in *A. melanoxylon*. Differences in germination counts between the three 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, 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). Amongst the different stimuli, control and smoke were comparable, but differed significantly from the other stimuli, while the other stimuli also differed significantly amongst one another (Fig. 1; Supplementary S1). Chipped resulted in the highest mean germination (97%) across all three species (95% in *V. divaricata* 95%; 100% in *A. mearnsii*; and 95% in *A. melanoxylon*), comparable to the viability test results. 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

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