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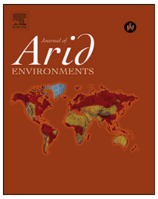

Interactions between seed functional traits and burial depth regulate germination and seedling emergence under water stress in species from semi-arid environments

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ABSTRACT

Ecological restoration presents many challenges, particularly in semi-arid environments, where large volumes of seeds are required. Here, we hypothesized that two key seed functional traits, namely seed mass and speed of germination, would affect overall germination and emergence: heavier-seeded and faster-germinating species would display greater germination and emergence under water stress. We also hypothesized that seed burial would ameliorate this stress. Using eight native coexisting taxa from five families, we investigated the interaction of seed mass, water stress and sowing regime (seed burial and surface sowing) under laboratory and field conditions. From the laboratory experiments, most lighter seeds rather than heavier seeds had higher germination and emergence in dry conditions. Species that showed faster germination, displayed higher germination proportions under water stress. Seed burial did not increase germination but seedling emergence was significantly greater from depth compared to surface sowing, particularly for heavier-seeded species. Under field conditions, few seedlings emerged, which was attributed to high soil mechanical impedance and lack of rainfall. This study highlights the complex interplay between water stress and seed traits and how these factors regulate emergence of species required for semi-arid restoration.

1. Introduction

In semi-arid regions, plant community recovery following disturbance is often slow and erratic and, consequently, active restoration is of particular importance (James et al., 2011). Restoration of degraded environments (e.g. post mining and retired agricultural land) commonly relies on supplementary seeding, which requires large volumes of limited and expensive seed resources (Mortlock, 2000; Merritt and Dixon, 2011). However, for all the quantities of seed typically used, seedling emergence in most semi-arid land restoration programs from supplementary seeding is often low (<10%) (Turner et al., 2006; James et al., 2011; Commander et al., 2013). Therefore, to efficiently restore biodiversity it is important to understand recruitment constraints when using additional seed resources.

Seed germination and seedling emergence are critical processes in the plant life cycle which underpin recruitment and establishment success (Forcella et al., 2000; James et al., 2011). Seeds germinate under environmental conditions that enhance the chances of seedling survival. Consequently, their germination is strongly influenced by environmental factors such as light, temperature and soil moisture (Bell, 1999). The ability of seeds to germinate under low moisture conditions may enable species to recruit in semi-arid environments (Flores and Briones, 2001; Arnold et al., 2012). Functional traits comprise trade-offs that determine the ecological role of the species. For example, seed mass would be an indicator of the trade-off between the number of seeds produced and the size of each individual seed (Wright et al., 2006) which may have consequences for seedling survival (Moles and Westoby, 2002). However, there is a limited understanding of how germination functional traits (e.g., water potential thresholds and speed of germination) contribute to long-term population

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processes at the community level, which has drawn recent attention (Huang et al., 2016; Jiménez-Alfaro et al., 2016).

Since species from semi-arid environments often germinate rapidly in response to relatively low amounts of intermittent moisture, these species are likely to germinate under lower water potentials (i.e. increased water stress). Taxa from higher rainfall environments tend to germinate more slowly highlighting the resilience of species from low moisture environments (Jurado and Westoby, 1992; Abbott and Roundy, 2003; Kos and Poschlod, 2010). These observations may also be applicable to co-occurring species subjected to the same environmental stresses, which would suggest a tangible link between the speed of germination, sensitivity to moisture stress and local environmental conditions.

Many studies have linked the ability to germinate in drier soil with larger seed mass, as the greater endogenous seed resources potentially increase survival time and the ability to resist and recover from environmental stress (Kidson and Westoby, 2000; Moles and Westoby, 2002; Daws et al., 2008; Huang et al., 2016). Larger food reserves theoretically enable a seed to germinate and emerge from greater soil depths, thereby reducing extreme environmental stressors (e.g. wind and water erosion, seed predation and desiccation), to which seeds at the soil surface are generally more exposed (Montalvo et al., 2002; Turner et al., 2006). However, other studies have reported that lighter seeds within the same species germinate faster or to higher percentages, which may be due to a reduced seed coat thickness and consequent reduction of dormancy (Stamp, 1990; Zhang, 1993).

Plant community composition is determined in part by the distribution of soil moisture available for plants (Breshears and Barnes, 1999). Since soil drying occurs more quickly at the soil surface, seed burial may increase germination and emergence under drier conditions, however this may vary with other soil properties such as soil crusting, texture, and structure. At present, the relative importance of these factors is largely unknown for species required for semi-arid land restoration which has clear implications for achieving good restoration outcomes (Abbott and Roundy, 2003; James et al., 2011).

The interactions of water stress, microsite edaphic conditions and seed functional traits related to germination and emergence are often overlooked, yet these insights are essential for improving our understanding of the constraints to re-establishing diverse native floristic communities. Consequently, insights into how these factors interact will aid the development of effective restoration techniques within semi-arid environments (Bochet et al., 2007; Commander et al., 2013). Therefore, this study aimed to gain a better insight into these factors regulating *in-situ* germination and emergence in eight native species from a semi-arid, threatened ecological community (TEC) in southern Western Australia.

The following hypotheses, corresponding to both seed functional traits and microsite conditions, were tested: (1) Heavier-seeded and faster-germinating species will display higher germination and emergence under elevated water stress (lower water potentials); (2) Soil burial of seeds will improve emergence of heavier-seeded species; and (3) the relative advantage of seed burial is greater under drier-soil-conditions than in a wet soil where water is not a limiting factor.

2. Materials and methods

This study examined the hypotheses through three approaches: 1) Germination response to a range of water stresses under incubator conditions, 2) *Ex-situ* germination and emergence from field soil in response to different soil treatments, and 3) *In-situ* emergence following different seed sowing treatments. The two first approaches under laboratory conditions focused on testing the mentioned hypotheses and the third approach aimed to investigate the applicability of laboratory results to a field scale.

2.1. Study site

The study system was located at the Koolanooka mine-site (Sinosteel Midwest Corporation Limited) and adjacent Threatened Ecological Community (TEC), which is located ~ 400 km north-east of Perth, Western Australia. Mining at Koolanooka occurs on a banded ironstone formation (BIF) containing a TEC listed as Vulnerable (DEC, 2007) and thus is of high conservation significance (Beecham, 2002). Seeds from this TEC were used for the laboratory experiments and the field trial was installed at the Koolanooka mine-site. The semi-arid climate of Koolanooka has a mean annual rainfall of 335 mm and areal actual evapotranspiration of 300 mm approx. (Bureau of Meteorology, 2013). Average monthly rainfall peaks during the winter months (June and July), while high wind speeds and temperatures during summer significantly increase evaporation (Bureau of Meteorology, 2013) (Fig. 1).

2.2. Study species and seed preparation

Eight plant species from semi-arid environments that belong to five different families were selected based on differences in seed attributes, seed storage syndrome, taxonomy and plant form (Table 1). Six of these species co-occur within the TEC, with two species (*Acacia microbotrya* and *Maireana tomentosa*) occurring in nearby communities. Three species (*Acacia acuminata, Allocasuarina acutivalvis* and *Melaleuca nematophylla*) are common within the TEC and are an essential requirement of ecological restoration. Fruits and seeds of each species were collected from the TEC between 2011 and 2012. After collection, all seeds were cleaned, air-dried and stored under controlled conditions (15 °C, 15% RH) until required.

Prior to use in experiments, seed fill of each species was determined via X-ray analysis using a Faxitron Specimen Radiography System (MX-20 Cabinet X-ray Unit; Faxitron, Wheeling, IL, USA) and all unfilled and damaged seeds manually removed. Seed mass was determined by weighing of five replicates of 100 seeds (Table 1). Seeds used in experiments were pre-treated to alleviate seed dormancy where required (Table 1). However, for two species a pre-treatment for overcoming dormancy was not known, so the seeds were not treated in any way prior to experimental utilisation (Table 1). After laboratory experiments, seed viability was assessed using a cut test (seeds cut in half and internal contents visually examined for signs of decay) and rated on the presence (viable) or absence (non-viable) of firm, white endosperm and/or embryo (Baskin and Baskin, 1998). Only germinated plus viable non-germinated seeds were considered in the results (i.e. cut test adjusted) (Turner and Merritt, 2009).

2.3. Seed germination and seedling emergence trials

2.3.1. Germination functional traits: seed mass and speed of germination

The seed germination of each species was assessed over a range of water potentials (0, −0.25, −0.5, −0.75, −1.0, −1.25, −1.5 MPa) at 20 °C under (12 h/12 h) light/dark conditions (30-W cool white fluorescent lamps with an average Photosynthetic Photon Flux Density of 30 μmol m^{-2} s^{-1}). Water potential was simulated using Polyethylene glycol (PEG 8000, Aldrich Chemistry, Missouri, USA) with deionised water as the control. PEG solutions were prepared according to the equation of Michel (1983). The actual water potential of the solutions was measured using a psychrometer (WP4C Dewpoint PotentiaMeter, Decagon Devices Inc., Pullman,

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