

## Effect of water supply on the germination of seven exotic and seven native species in Western Australia

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**Summary** The germination of seven common weeds and seven common species native to southwestern Australia was studied at three sites where they co-occur and in the laboratory. Under field conditions, final germination of the exotic species was much higher than that of the native species, and the number of days to reach 50% of final germination was lower. For some of the germination period, soil moisture was lower than expected after 48 h without rain, with one dry period lasting 10 days. Overall, germination rose with increasing wetness of the three sites, especially among the weeds. Most exotic species germinating under laboratory conditions needed less than 10 days to reach 50% of final germination which was further delayed by two days when seeds were removed from their moist substrate and allowed to dry out (air-drying) for 48 h before rewetting. Most native species took 10–35 days, with a mean delay of seven days after 48 h of air-drying. Total germination of the weeds was close to 100% and was little affected by periods of air-drying. Germination of the native species was more variable and greatly reduced by air-drying in two species. We conclude that water availability as it varies through time and space is significant in controlling germination even during the wet season. The quicker and greater responses of weed seeds to moisture may contribute towards the superior ability of weeds to colonise disturbed habitats. Differences in life form, seed size, flatness, presence of appendages, and ability to absorb or retain water only partially explain these results.

**Keywords** Weeds, drought, exotic species, germination, native species, soil water content.

### INTRODUCTION

A number of exotic herbaceous species has spread over vast areas in Mediterranean southwestern Australia, rapidly invading bare areas following soil disturbance (Higgins *et al.* 1996) at the expense of native species (Milberg and Lamont 1995). Some of the possible reasons for the superior invasive attributes of some exotic species include their high fecundity (Holmes *et al.* 1987), and their ability to survive in harsh environments (Witkowski 1991). High tolerances of tempera-

ture and soil moisture fluctuations are also regarded as possible attributes that explain superior germination of many weeds (Martínez-Chersa *et al.* 1997).

In south-western Australia recruitment of both herbaceous and woody life forms is usually restricted to disturbed substrates following land clearing or fire (Milberg and Lamont 1995). Despite possible great differences in rate of maturation and final plant size, germination and establishment occurs in the same wet season. Thus, there is likely to be intense competition for resources at the recruitment stage in disturbed vegetation.

Seed imbibition is the starting point leading to germination; its rate and extent may be governed by the surrounding water levels and in general there is a decrease in seed imbibition and germination rate with a decrease in soil water potential (Evans and Etherington 1990). Changes in soil water potential are accompanied by changes in soil water conductivity and seed-soil contact area. In south-western Australia, most rain falls in sporadic rainfall events during winter and spring. In these environments, most seeds remain at the soil surface or are only shallowly buried (Lamont *et al.* 1993). As part of the explanation for the ability of non-natives to establish at the expense of native species, we proposed that exotic weedy species are better able to utilise water in the surface soil for germination; and also regain germinability faster when air dried following imbibition. We compared total and rate of germination among seven common weed species and seven common native species in the coastal sandplain vegetation of south-western Australia. The study was carried out under both laboratory and field conditions and the results compared.

### MATERIALS AND METHODS

**Field experiment** A field experiment was conducted in *Banksia* woodland in the Perth Coastal Plain at three sites: the Field Trial Area at Curtin University, Jandakot Airport and Kings Park. Two sites had been 'opened up' by fire 18 months before while the third was cleared by hand to create a disturbed substrate conducive to colonisation. This experiment was designed to compare the germination of seven exotic

(*Hypochaeris radicata* L., *Urospermum picroides* (L.) Scop. ex F.W.Schmidt, *Gladiolus caryophyllaceus* (N.L.Burman) Poir., *Petrorhagia velutina* (Guss.) P.W.Ball & Heywood, *Briza maxima* L., *Avena barbata* Pott. ex Link and *Ursinia anthemoides* (L.) Poir.) and seven native species (*Allocasuarina humilis* (Otto & Dietr.) L.Johnson, *Eucalyptus todtiana* F.Muell., *Banksia attenuata* R.Br., *Acacia pulchella* R.Br., *Bossiaea eriocarpa* Benth. *Gompholobium tomentosum* Labill. and *Podotheca gnaphalioides* R.A.Graham) under field conditions where seeds were usually able to use water available in the upper 5 mm of soil (Lamont *et al.* 1993). The experiment was carried out in winter, the season that provides the best temperature and humidity conditions for seed germination in the Southern Hemisphere.

At each site, three plots of 210 cm by 100 cm subdivided into sub-plots of 30 cm by 50 cm were established. All seeds were soaked for a period of 24 hours prior to sowing. No other treatment was applied to the seeds, with the exception of the three legumes, *Acacia pulchella*, *Bossiaea eriocarpa* and *Gompholobium tomentosum*, which were pre-soaked for eight hours in boiling water and immediately allowed to cool to room temperature to break their innate dormancy. This was to simulate the effect of fire, which is the usual way that dormancy is broken in these species (Bell *et al.* 1993). Germination, as measured by seedling emergence, was recorded over a period of 50 days. At the three field sites, soil water content was also monitored. An initial control soil sample was taken at the surface (upper 5 mm). Three soil samples were randomly taken at the soil surface, after watering and the same was done after 12, 24 and 48 h. Moisture content on a wet weight basis of the samples was assessed by weighting soil samples before and after heating at 105 °C for 48 h.

**Laboratory experiment** Seeds were soaked in water for 24 h. Seeds of the three legumes, *A. pulchella*, *B. eriocarpa* and *G. tomentosum*, were scarified by soaking them in boiling water as above. Following the soaking treatment, seeds were placed on dry filter paper in an air-blown cabinet and left to dry for various intervals (12, 24, 48 h) until transferred to germination conditions. Imbibition and drying treatments were carried out at 23°C and relative humidity of 55% in the cabinet.

Batches of three replicates of 50 seeds per species were placed in Petri dishes of 90 mm diameter for germination immediately after the initial soaking period. At intervals of 12, 24 and 48 h of air-drying, separate batches of each species were placed in Petri dishes for germination. Germination tests were car-

ried out in 1% water agar in an incubator at constant temperature of 15°C and a photoperiod of 12 h light and 12 h darkness. Germination was recorded daily for a period of 50 days.

**Statistical analyses** Nested ANOVA was used to test differences in **level** (total by 50 days) and **rate** (time to 50% of final) of germination between native and exotic species in the field, as well as to compare levels and rates of germination of native and exotic species after 0 and 48 h of air-drying in the laboratory. The effect of origin of species (native vs. exotic) and drought periods (0 and 48 h) on germination were tested for significance by two-way ANOVA. Tukey's multiple range test was used to examine differences in level and rate of germination between species within each group (exotic and native) and between drying periods and species.

## RESULTS

**Overall field germination** Final germination of the exotic species was higher than that of the native ones with two exceptions, the exotic *Urospermum picroides* which was similar to some native species, and *Banksia attenuata* which was near the average of the exotic species (Figure 1). The number of days to reach 50% of final germination for the native species was considerably greater than that of the weeds, with the exception of *Gladiolus caryophyllaceus* and *B. attenuata*.

**Soil water content and germination** Field level of germination of both exotic and native species increased with increasing moisture content, with Kings Park being much wetter than the other two sites. Exotics germinated better than the natives and they were more sensitive to water availability. The overall rate of germination of the native species was slower than that of the exotic species at the three sites and the final level increased with increasing soil moisture.

**Germination in the laboratory** Final germination in the absence of a drying treatment of exotic seeds was close to 100% and significantly higher than the native species with the exception of *Eucalyptus todtiana* (Table 1). There was no significant differences in final germination percentage between exotic species under the four drying treatments. Final germination among the native species was lower at 48 h drying (61.1%) than at 0 h (80.7%). The number of days to complete 50% of final germination was lower (5.9 vs 18.6 days and 8.1 vs 25.8 days after 0 h and 48 h drying respectively) in seeds of the exotic species at both 0 and 48 h drying. Significant differences were detected between native and exotic species as well as between

species within each group. The multiple range test detected significant differences between desiccation treatments in all species except *Ursinia anthemoides* and *Allocasuarina humilis* (Table 1).

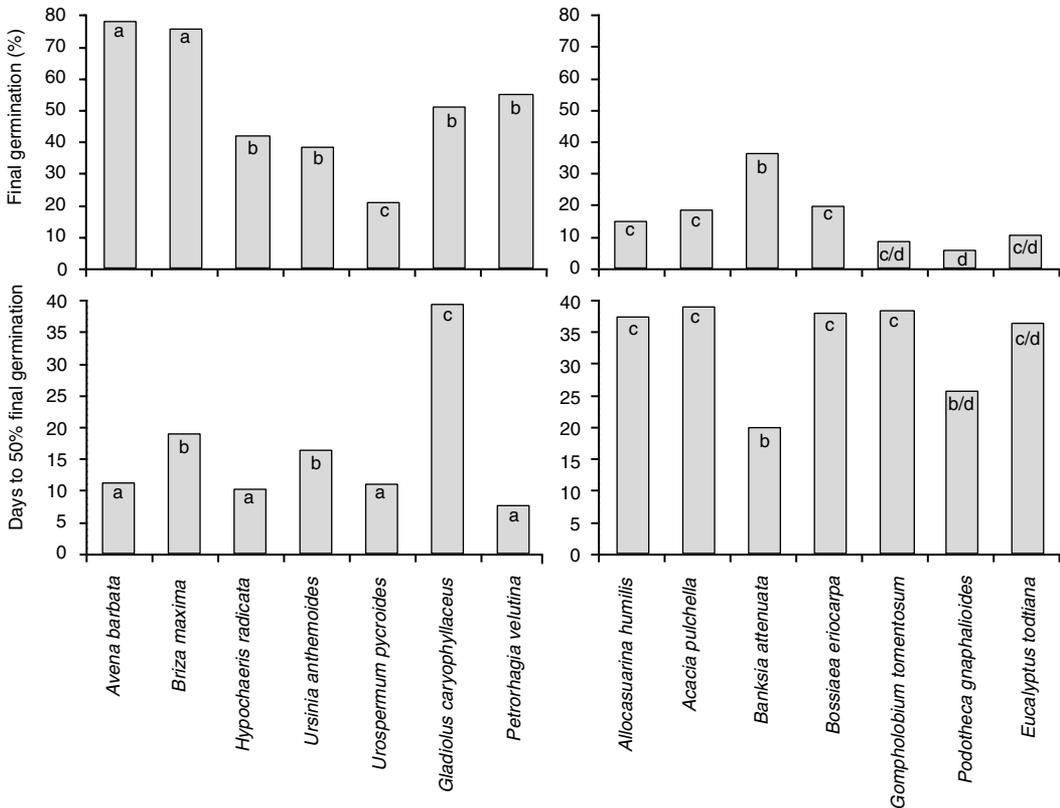
DISCUSSION

Level and rate of germination of exotic species were much greater than native species under both field and laboratory conditions. The weeds germinated proportionately better at higher levels of water availability among the three study sites. They also germinated better than the natives when water supply fluctuated over time. The field experiment showed that soil moisture fluctuated markedly and the sandy soils quickly dried out. Thus, soil moisture plays a major role in regulating germination even during the wet season. The superior ability of weeds to colonise disturbed habitats (Milberg and Lamont 1995) may be due to their capacity to make better use of soil water for germination. This ability is enhanced in coarse-textured soils that dry out rapidly or when there are long intervals between bouts of rain.

Since the weeds germinate faster than native plants once they are wetted they are more likely to avoid subsequent dry periods which would further reduce the rate of germination. Dry periods induce some species (as in the case of the legumes) to adopt a secondary dormancy, which is only readily reversed by improving the water supply (Evans and Etherington 1990). This explains the direct link between rate and level of germination only when water supply fluctuates.

**Table 1.** P values for the nested ANOVA comparing levels and rates of germination of native and exotic species after 0 and 48 h of air-drying in the laboratory.

Attribute	Treatment	Origin (native/exotic)	Species (origin)
Rate of germination	0	0.0329	0.0001
	48	0.0217	0.0001
Level of germination	0	0.0296	0.0334
	48	0.0184	0.0001



**Figure 1.** Level and rate of germination recorded by seeds germinated in the field over 50 days after an 8 h. imbibition treatment.

Such a secondary imposed dormancy may have survival implications by preventing germination in soils that may not be moist enough to support subsequent seedling growth.

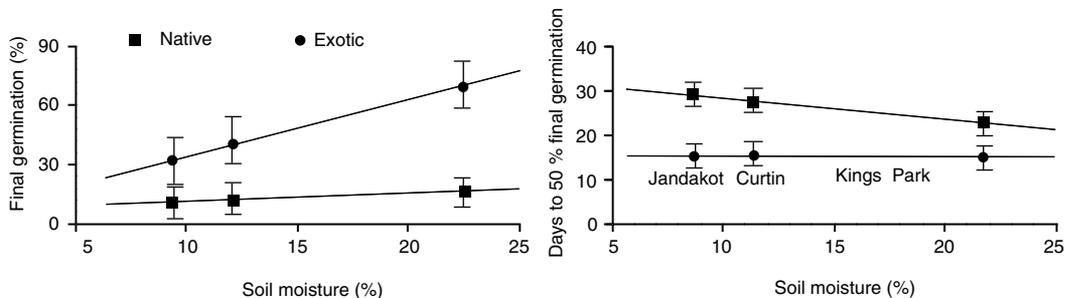
The simplest explanation for the differences in responses of the seeds to varying water availability may lie in their morphology. For example, small or flat seeds, or those with hairs or wings may be better able to absorb water under dry conditions (Peart 1984). The weeds tended to have better developed appendages but there were exceptions, and rate of germination was unrelated to appendage development. In association with the previous explanation, perhaps exotic species are better able to absorb water under wet conditions and/or retain it longer (Martinez-Chersa *et al.* 1997) but our evidence is equivocal.

Data from this study provide evidence that representative exotic species introduced to Western Australia have superior germination properties than representative co-occurring native species that compete for recruitment at the same time following disturbance. Weed establishment is more successful independent of soil moisture levels, but especially when water supply is high or fluctuating during the germination period, compared with native species.

It remains unclear how important this process is in explaining their ability to displace the native flora. It could be critical as early emerging seedlings are more likely to survive and outperform their later appearing competitors. The rapid maturation rate, short life cycles, high fecundity, and ability (in some cases) of weeds to build up a seed bank may give them a numerical advantage over the native species after recurrent fires.

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**Figure 2.** Average level (left graph) and rate (right graph) of germination ( $\pm$  SE) of the two groups of species germinated at Jandakot, Curtin University and Kings Park in relation to mean surface soil moisture, with best fitting lines added.