# Seed mass and summer drought survival in a Mediterranean-climate ecosystem

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**Abstract** We related seed mass to summer drought survival in a Mediterranean-climate ecosystem. Previous experimental evidence linking seed mass and survival under drought is limited and at times contradictory. We tracked summer drought survival among four families/subfamilies at a restoration site in southwestern Australia. We coupled these observations with a glasshouse experiment assessing the growth and root morphology of *Acacia* and *Eucalyptus* species, with a range of seed masses, under mild and severe drought compared with a well-watered control. Summer drought survival in the field increased with seed mass across all four families/subfamilies. Seedling root biomass and length increased with seed mass consistently across five harvests over 60 days. Initial survival of seedlings in the glasshouse increased with seed mass and decreased with drought, but there was no interaction between the two. Greater absolute root investment provides a mechanism for both short and longer-term drought survival. Within-species variation in root growth may also affect the relative versus absolute survival advantage of large-seeded species. The benefits of large seed mass for establishment under environmental hazards are often considered to be temporary. Our results show that seed mass was correlated with other traits, including root length, which in turn, increased longer-term drought survival. Traits correlated with seed mass should therefore be considered in explanations of the ecological effect of seed mass variation.

**Keywords** *Acacia · Eucalyptus · Corymbia* · Plant establishment · Restoration · Southwestern Australia

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## Introduction

This study addresses the longer-term benefits of large seed mass for drought survival in a Mediterranean-climate ecosystem. Most ecosystems contain species with a wide range of seed masses (Leishman et al. 2000). This range has traditionally been considered the result of a tradeoff between seed size and seed number: a plant can either invest its resources in a few large seeds each with a high probability of establishment or in many small seeds with lower individual establishment rates (Salisbury 1942). Under certain conditions of environmental stress this

balance may shift (Westoby et al. 2002). For example, under light limitation the carbon reserve in large seeds improves their establishment rates relative to small seeds (Leishman and Westoby 1994a; Paz and Martinez-Ramos 2003). Similarly, in low nutrient systems the nutrient stores in large seeds has been documented to provide them a greater relative survival advantage (Stock et al. 1990; Milberg and Lamont 1997).

Because the advantage of a large seed can change with environmental conditions, spatial and temporal heterogeneity have increasingly been coupled with the original seed success/seed number model to explain observed ranges in seed mass (Coomes and Grubb 2003; Turnbull et al. 2007). Even under harsh conditions, however, the initial survival advantage afforded by large seeds would have to be unrealistically high to compensate for the greater number of seeds produced by small-seeded species (Moles and Westoby 2004; Moles and Westoby 2006). As a result, focus has shifted to consider not only the relationship between seed mass and initial seedling survival, but also the relationship between seed mass and survival to adulthood and reproductive maturity (Falster et al. 2008). We explore the relationship between seed mass and drought survival within this context.

Mediterranean-climate ecosystems (MCEs) are characterised by a mild and wet winter and spring followed by a prolonged hot, dry summer. High variability in rainfall timing means that young seedlings might be exposed to short droughts soon after recruitment in winter and spring (Miranda et al. 2009). Large seeds typically result in large seedlings (Jurado and Westoby 1992a), and a greater absolute root investment might allow large-seeded species to avoid these short springtime droughts (Padilla et al. 2007). Large seeds might also allow seedlings to invest in greater root mass relative to total biomass, further facilitating drought avoidance (Lloret et al. 1999). The relevance of this relationship would likely vary with the yearly rainfall pattern. The long summer drought, however, is a primary filter to establishment in MCEs (Herrera et al. 1994). If a positive relationship between seed mass and root investment continued throughout the summer, large seeds might confer a drought survival advantage beyond the phase in which seedlings are primarily reliant on seed resources.

Climate-change scenarios predict hotter and drier conditions in MCEs in the future (Hewitson and Crane 2006; CSIRO 2007; Klausmeyer and Shaw 2009). Rainfall decline since the 1970s has already been documented in southwestern Australia (Nicholls 2006), where our study was conducted. At the same time, efforts to restore vegetation are becoming more frequent (McDonald and Williams 2009), resulting in a practical need to understand the traits that may govern plant establishment under climate change. Correlative studies indicate a tendency for large-seeded species to be associated with low-rainfall (drought-prone) conditions (Baker 1972; Wright and Westoby 1999; Peco et al. 2009). Yet, experimental evidence linking seed mass and seedling survival under drought is limited (Moles and Westoby 2004) and at times contradictory. For example, Leishman and Westoby (1994b) observed that establishment rates of large-seeded species were less affected by drought than those of small-seeded species under glasshouse, but not field conditions.

We hypothesised that large-seeded species would be able to invest in greater root growth, resulting in higher seedling survival during the long summer drought. In addition, we predicted that increasing seed mass would be associated with decreasing variation within individual seedling root investment, because small-seeded species depend on patchy environmental resources whereas large-seeded species have reliable seed reserves (Jurado and Westoby 1992b; Milberg et al. 1998). As a consequence, we expected a lasting and more consistent benefit of increasing seed mass beyond the probable life of the seed reserves. To test these predictions, we first related seed mass to summer drought survival at a restoration site in the Mediterranean-climate ecosystem of southwestern Australia. Then, for a select subset of species, we determined the relationship between seed mass, seedling survival and root investment under drought conditions in the glasshouse.

## Materials and methods

### Restoration site

We selected two sampling locations 1 km apart (named Barlow and Payne) in the Gnangara ex-pine

plantation, a restoration site situated on the Swan Coastal Plain, 20 km north of Perth, Western Australia. Prior to the establishment of the pine plantation and groundwater abstraction for the public water supply, the natural vegetation at the site was *Banksia* woodland atop a large, shallow unconfined aquifer (Groom et al. 2000). The sandy soils of the coastal plain have limited capacity to retain water, and so there is virtually no water available within the top few metres of the soil profile during the summer drought (Zencich et al. 2002). Both sampling locations were on Bassendean sands with a field capacity of 4%. We determined field capacity by suspending water in a column of soil for 24 h, weighing a sample of the wet sand and comparing this value to the sample's dry weight.

The climate at the restoration site is Mediterranean, with mild wet winters (June–August) and hot dry summers (December–February). Long-term average annual rainfall for the climate station nearest the restoration site that collects both rainfall and temperature data is 729 mm (1993–2010); total rainfall for 2008 and 2009 was 808 and 607 mm, respectively (Bureau of Meteorology, unpublished data). The sites were direct seeded by the Western Australian Department of Environment and Conservation in August 2008 with the same mix of 21 *Banksia*-woodland species in the Myrtaceae and Proteaceae families, and Fabaceae, which includes the Mimosoideae and Faboideae subfamilies. After seeding there were short springtime droughts and a long summer drought associated with successive high-temperature days at the restoration site (Fig. 1).

To establish, seedlings must tolerate and survive their first summer drought (Groom 2002). Although our study focused on abiotic site conditions, seedling establishment may also be affected by biotic factors such as competition and herbivory. Invasive plants were not present in the seeded furrows, however, and the young seedlings were sparsely distributed and so competition among them was probably minimal. We found no evidence of western grey kangaroos (*Macropus fuliginosus*) browsing on seedlings, although they were present at the restoration site. This is likely due to the availability of grass swards near to the site, which these kangaroos prefer over the woody species that grow in *Banksia* woodland (Wann and Bell 1997).

Field survey

In November 2008 we established 50 evenly spaced 1 m × 1 m plots at each location within the restoration site. We recorded the species and position of all recruits within the plots and in April 2009, after the summer drought, we recorded their survival. Eighteen of the 21 planted species recruited and were used in subsequent analysis (Table 1). The number of recruits within a species and site ranged between 1 and 301 (Table 1). To obtain seed masses we averaged the masses of 50 individual seeds per species, except for the small-seeded Myrtaceae, which we weighed in batches of 10. The wide inter-specific variation in seed masses (0.16–95 mg; Table 1) spanned the range for *Banksia*-woodland species and allowed us to meaningfully explore the relationship between seed mass and seedling recruitment.



**Fig. 1** Daily rainfall and maximum temperatures at the restoration site after seeding in August 2008. Seedling establishment may be influenced by both short springtime droughts and the longer summer drought
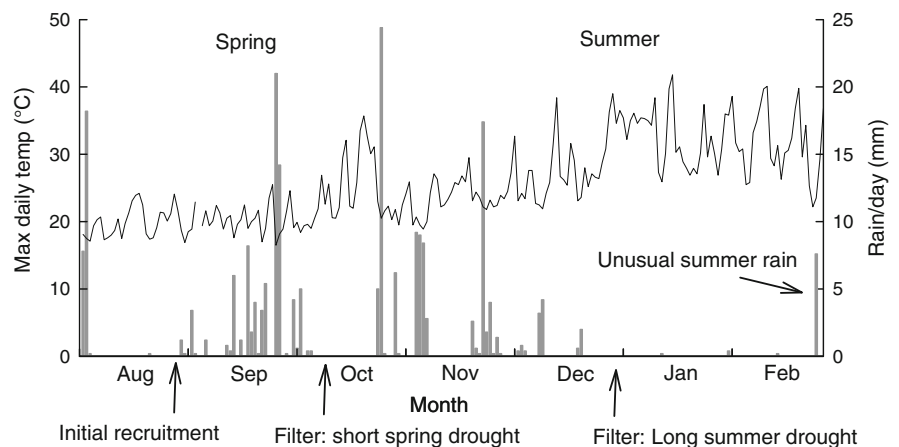
**Table 1** Seed mass, life form, number of recruits by field site and study in which each species was included

| Species | Family/subfamily | Seed mass (mg) | Life form | No. of field recruits (Barlow, Payne) | Study |
|---|---|---|---|---|---|
| *Calothamnus quadrifidus* | Myrtaceae | 0.16 | Erect shrub | 142, 301 | Field |
| *Kunzea glabrescens* | Myrtaceae | 0.16 | Erect shrub | 101, 163 | Field |
| *Melaleuca systena* | Myrtaceae | 0.19 | Erect/spreading shrub | 153, 169 | Field |
| *Eucalyptus decipiens* | Myrtaceae | 0.54 | Mallee or tree | 2, 4 | Both |
| *Eremaea pauciflora* | Myrtaceae | 0.94 | Erect/spreading shrub | 160, 87 | Field |
| *Acacia sessilis* | Mimosoideae | 1.9 | Diffuse shrub | 72, 66 | Both |
| *Jacksonia calcicola* | Faboideae | 2.3 | Erect/spreading shrub | 55, 65 | Field |
| *Jacksonia furcellata* | Faboideae | 5.2 | Prostrate shrub | 54, 72 | Field |
| *Eucalyptus marginata* | Myrtaceae | 5.6 | Tree | 41, 45 | Both |
| *Eucalyptus todtiana* | Myrtaceae | 6.3 | Mallee or tree | 47, 50 | Both |
| *Acacia pulchella* | Mimosoideae | 9.7 | Shrub | 176, 129 | Both |
| *Jacksonia sternbergiana* | Faboideae | 15 | Shrub or tree | 45, 49 | Field |
| *Acacia huegelii* | Mimosoideae | 18 | Semi-prostrate shrub | 4, 1 | Field |
| *Acacia saligna* | Mimosoideae | 23 | Dense shrub | 70, 53 | Both |
| *Acacia cyclops* | Mimosoideae | 25 | Dense shrub | N/A | Glasshouse |
| *Hakea prostrata* | Proteaceae | 49 | Shrub | 57, 51 | Field |
| *Corymbia calophylla* | Myrtaceae | 78 | Tree | N/A | Glasshouse |
| *Banksia menziesii* | Proteaceae | 86 | Tree or shrub | 55, 49 | Field |
| *Banksia attenuata* | Proteaceae | 92 | Tree or shrub | 48, 49 | Field |
| *Banksia grandis* | Proteaceae | 95 | Tree or shrub | 40, 22 | Field |

Species nomenclature follows Paczkowska and Chapman (2000)

## Glasshouse experiment

Of the species seeded at the restoration site, those within the Mimosoideae subfamily and Mytraceae family displayed a greater range of seed mass than the Proteaceous species and a stronger relationship between seed mass and seedling survival than those in the Faboideae subfamily, and so were the focus of our glasshouse experiment. We selected four *Acacia* (Mimosoideae) and three *Eucalyptus* and one *Corymbia* (Myrtaceae) species, representing a range of seed masses (Table 1). All eight species are commonly used in restoration and are native to Bassendean sands in southwestern Australia. Three *Acacia* and three *Eucalyptus* species used in the glasshouse experiment were present at the restoration site (Table 1).

We acquired all seeds from Nindethana Seed Company based in Albany, Western Australia. We stimulated germination for the smaller *Acacia sessilis* and *A. pulchella* seeds by hand scarifying them with sandpaper. We chemically scarified *A. saligna* and *A. cyclops* seeds for 1 h in a bath of 18 M sulphuric acid. *Eucalyptus* and *Corymbia* seeds were smoke treated for 12 h. To avoid fungal growth we bathed all seeds in 0.5% sodium hypochlorite solution for 10 min. We were interested in seedling growth after germination, and so we germinated seeds in Petri dishes prior to planting.

In March 2008 we transferred seeds to pots in a temperature controlled glasshouse within 24 h of radicle emergence. We planted three seeds per pot at depths of 1–5 mm. Pots were 21 cm deep and 17 cm wide and we filled them with Bassendean sand collected from the restoration site. The soil was sieved through a 4 mm screen, and then steam sterilised for 72 h and dried at 40°C before use. We arranged pots within three replicate benches (blocks). To limit evaporation we covered pots with a 1 cm layer of alkathene polyethylene beads (Qenos Pty Ltd, Altona, Victoria, Australia). We watered pots daily with de-ionised water until the cotyledons

emerged on the seedlings (generally 5 days after planting). At this time, we removed two seedlings and randomly applied one of three treatments to each pot containing one seedling: two pulsed drought treatments, a mild drought in which we watered pots to field capacity every 3 days and a severe drought which we watered to field capacity every 6 days, and a control that we watered to field capacity daily. Mortality was recorded. To ensure adequate replication (i.e., at least three replicates of each treatment), senesced individuals were replaced in the control and mild treatments. The same planting procedure was applied for the replacement pots. As a result, the final harvests were staggered and based on individual seedling age rather than time since the experiment commenced. All replacements were completed within the first 3 weeks of the experiment. Mortality was consistently high under the severe drought treatment and so we did not replace individuals in this treatment.

To track growth over time we harvested three replicates at 12-day intervals, five times (thus, the oldest seedlings were 60 days old). We did not continually harvest replicates of the severe drought treatment; instead we tracked their survival and harvested all remaining individuals at 60 days. We measured soil moisture with a TDR probe (Hydrosense 12 cm rod, Campbell Scientific Australia Pty Ltd) prior to the final watering, thus, at the driest point in the watering cycle. Soil moisture decreased with increasing severity of the drought treatment (Proc GLM, $F_{2,95} = 50.7$, $P < 0.0001$). The average ($\pm$SE) values for soil moisture at the driest point of the watering cycle were: control $= 3.4\% \pm 0.05$, mild drought $= 2.9\% \pm 0.04$, severe drought $= 2.4\% \pm 0.08$.

To measure overall growth we separated root and shoot biomass, dried them for at least 48 h at 60°C, and weighed them to the nearest 0.001 g. We scanned root samples from the 36–60 day harvests prior to drying them to assess root morphology. We analysed root scans with WinRhizo software (Regular V.4.1., Regent Instruments Inc, Chemin Sainte-Foy, Quebec, Qc), quantifying total root length and root length within five diameter classes (0–1, 1–2, 2–3, 3–4, and >4 mm). We could not score rooting depth because despite using large deep pots, the roots were longer than the depth of the pots at harvest.

Seedling mortality was high enough that we were able to conduct a subsidiary analysis of initial

survival based on seed mass and treatment. Seedling survival was assessed as a comparison of number of individuals that survived compared with the total number of individuals that recruited within a treatment and species. Because we ceased replacements after sufficient replication was achieved, sample sizes were larger for species with higher mortality. Sample sizes therefore varied between three and 15 individuals per species and treatment.

Analysis

For all analyses we used SAS statistical software (SAS version 9.1.3, SAS Institute, Inc.) and set significance levels at $|Z| \leq 1.96$ for logistic analysis and $P \leq 0.05$ for other analyses. Seed mass and growth measurements were log-transformed prior to analyses. To determine the importance of seed mass on summer survival in the field we conducted a multiple logistic regression with survival as the binary dependent variable, seed mass a continuous predictor and site and family/subfamily as categorical predictors (Proc LOGISTIC). The predictor 'family/subfamily' encompassed differences among species other than seed size that might influence seedling survival.

We excluded the severe drought treatment from growth analyses due to insufficient replication. Total plant biomass increased over time within all species ($P < 0.0001$, slope $\geq 0.98$) except for *E. marginata* ($P = 0.94$, slope $= -0.014$; Proc REG). Consequently, we excluded *E. marginata* from the growth analyses. To determine the influence of seed mass on seedling growth over time we conducted an ANCOVA with seedling biomass as the dependent variable, seed mass a continuous predictor and harvest time, drought treatment and genus as categorical predictors (Proc GLM). We repeated this model with root biomass, root:total biomass, total root length and root length within diameter classes each as dependent variables.

To determine if increasing seed mass was associated with decreasing individual variation we focused on total root length. We calculated the coefficient of variation (CV) of total root length first among individuals with the same seed mass, treatment and harvest period and ran the same model with CV as the dependent variable. To increase the sample size we next calculated the CV of total root length among all individuals of a species regardless of treatment or harvest period and conducted an ANCOVA treating

CV as the dependent variable, seed mass a continuous predictor and genus as a categorical predictor. Finally, we assessed initial seedling survival in the glasshouse through multiple logistic regression with seed mass a continuous predictor and drought treatment as a categorical predictor (Proc LOGISTIC).

## Results

### Seedling summer survival increased with seed mass

Summer survival of seedlings increased with seed mass across all four families/subfamilies (logit regression coefficient $= 0.61 \pm 0.08$, $Z = 7.54$), although the strength of this relationship varied among families/subfamilies ($Z = 5.49$, Fig. 2). Seedling survival also varied with location ($Z = 11.9$) and family/subfamily ($Z = 12.5$), with highest survival among the Myrtaceae and lowest survival among the Mimosoideae (Fig. 2). The model had a pseudo-$R^2$ value of 0.25.

### Seedling size increased with seed mass

Total seedling biomass increased with seed mass ($F_{1,154} = 320.1$, $P < 0.0001$, slope $= 0.36$) and over time ($F_{4,154} = 45.8$, $P < 0.0001$). Mild drought did not significantly affect total biomass ($F_{1,154} = 1.29$, $P = 0.28$). The model was significant ($F_{39,154} = 26.75$, $P < 0.001$) with an $R^2$ of 0.87. A similar ANCOVA with root biomass as the dependent variable was significant ($F_{39,155} = 18.4$, $P < 0.0001$, $R^2 = 0.82$). Root biomass increased with seed mass ($F_{1,155} = 251.4$, $P < 0.0001$, slope $= 0.43$) and over time ($F_{4,155} = 25.87$, $P < 0.0001$; Fig. 3), and was insensitive to the mild drought treatment ($F_{1,155} = 1.54$, $P = 0.21$).

Both genera invested early in root growth, with highest root:total biomass in the first 24 days ($F_{4,154} = 6.36$, $P < 0.0001$; model $F_{39,154} = 2.94$, $P < 0.0001$, $R^2 = 0.43$, Fig. 4). Root:total biomass was also greater among *Acacia* than it was among *Eucalyptus/Corymbia* species ($F_{1,154} = 4.10$, $P = 0.045$, Fig. 4). Root:total biomass was not significantly affected by seed mass ($F_{1,154} = 0.63$, $P = 0.42$) or treatment ($F_{1,154} = 0.59$, $P = 0.44$).
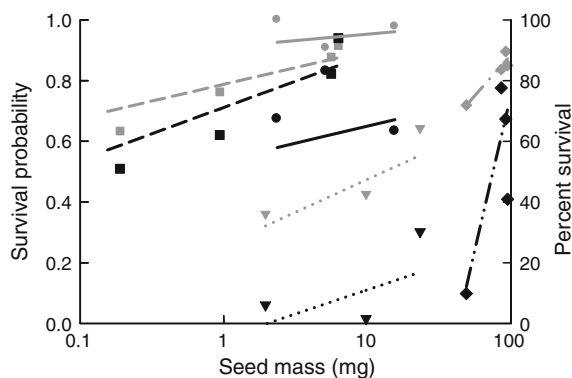


**Fig. 2** Percentage summer survival in the field according to seed mass (*symbols*) overlaid by logistic regression of these data within the Myrtaceae (*squares and dashed lines*), Faboideae (*circles and solid lines*), Mimosoideae (*triangles and dotted lines*) and Proteaceae (*diamonds and dash-dot lines*). *Black lines* are for data collected at Barlow, *grey lines* are for data collected at Payne
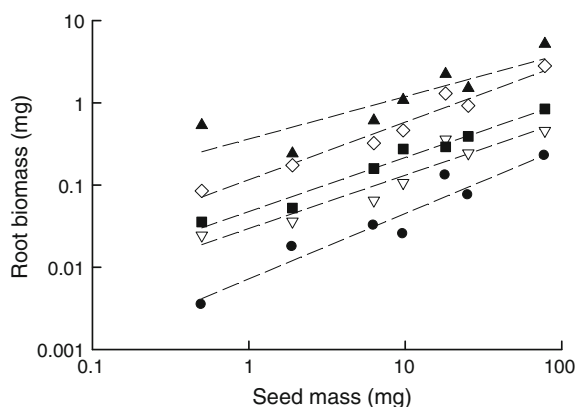


**Fig. 3** Root biomass as a function of seed mass and harvest time for seedlings grown in the glasshouse. *Closed circles* = 12 day, *open triangles* = 24 day, *closed squares* = 36 day, *open diamonds* = 48 day, and *closed triangles* = 60 day harvests

### Root length increased with seed mass

Total root length increased with seed mass ($F_{1,96} = 80.8$, $P < 0.0001$, slope $= 0.32$) and over time ($F_{2,96} = 7.12$, $P = 0.0013$) but decreased slightly under the mild drought treatment ($F_{1,96} = 6.15$, $P = 0.015$; model $F_{23,96} = 7.06$, $P < 0.0001$, $R^2 = 0.63$). Small-seeded species had a higher proportion of thin (0–1 mm thick) roots than large-seeded species ($F_{1,96} = 136.2$, $P < 0.0001$; slope $= -0.016$). On an absolute scale, however, large-seeded
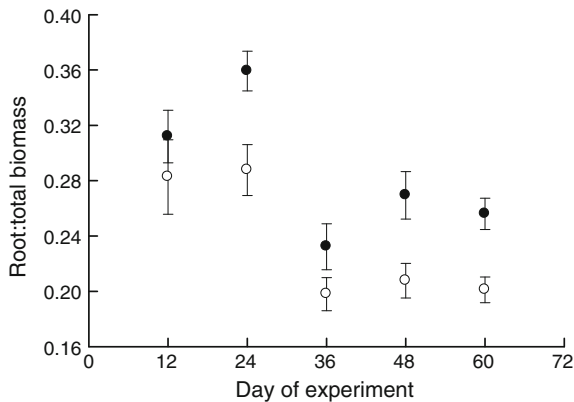
**Fig. 4** Root:total biomass by genus over time for seedlings grown in the glasshouse (mean ± SE). *Acacia* represented by *closed circles*, *Eucalyptus/Corymbia* by *open circles*
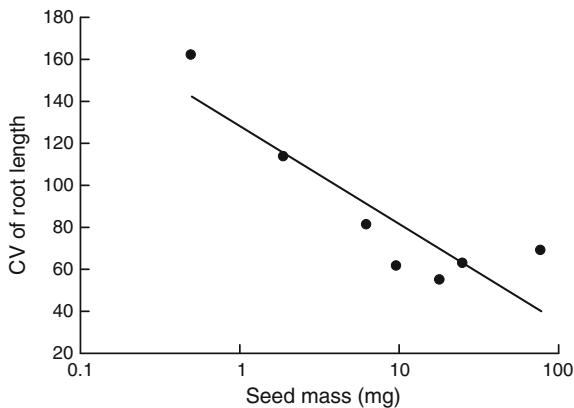


**Fig. 5** Coefficient of variation (CV) of root length across treatments and harvest periods by seed mass for seedlings grown in the glasshouse

species had more roots in all five thickness categories. For example, root length increased with seed mass in both the 0–1 mm ($F_{1,96} = 22.5$, $P < 0.0001$, slope = 0.26; model $F_{23,96} = 3.86$, $P < 0.0001$, $R^2 = 0.48$) and >4 mm categories ($F_{1,96} = 126.6$, $P < 0.0001$, slope = 0.44; model $F_{23,96} = 8.8$, $P < 0.0001$, $R^2 = 0.68$).

### Variation among seedlings decreased with seed mass

Seed mass was the only predictor of CV of total root length, which decreased with increasing seed mass ($F_{1,18} = 12.2$, $P = 0.0026$; slope = −8.5) when CV was calculated among individuals with the same seed mass, treatment and harvest period. The overall

model, however, was not significant ($F_{23,18} = 1.4$, $P = 0.24$, $R^2 = 0.64$). The model was significant when CV was calculated among all individuals with the same seed mass regardless of treatment or harvest period ($F_{3,3} = 10.9$, $P = 0.04$, $R^2 = 0.92$), and CV again decreased with increasing seed mass ($F_{1,3} = 9.25$, $P = 0.05$; slope = −8.8; Fig. 5).

Initial seedling survival increased with seed mass (logit regression coefficient = 0.27 ± 0.06, $Z = 4.87$; model pseudo-$R^2 = 0.24$) and with drought treatment ($Z = 3.87$). There was no interaction between seed mass and drought treatment ($Z = 1.53$).

## Discussion

We hypothesised that seedling survival would increase with seed mass during the long summer drought, a primary filter to seedling establishment in a Mediterranean-climate ecosystem. Seed mass was a significant predictor of seedling survival over the summer drought under field conditions. Root investment remained a function of seed mass throughout the 60-day glasshouse experiment, likely increasing the ability of large-seeded species to avoid drought over time. Accordingly, the initial size advantage provided by a larger seed might improve drought survival even after the seed resources are exhausted.

Seed mass remained a primary correlate of seedling growth and root morphology throughout the experiment. It is well known that large seeds typically result in large seedlings (Buckley 1982; Jurado and Westoby 1992a; Wright and Westoby 1999). In our experiment, however, the strength of this relationship did not decrease during five harvests spanning 60 days. The only exception was *E. marginata*, which is known to have very slow growth rates in low-nutrient soils (Abbott et al. 1989). Small-seeded species are typically associated with faster relative growth rates (Swanborough and Westoby 1996). Among the species used in this experiment, this relationship was not strong enough to alter the initial size advantage provided by a large seed. Moreover, within the range of our treatments, drought did not alter the relationship between seed mass and seedling size. Consequently, despite variable spring conditions, at the onset of the summer drought large-seeded species would have consistently greater absolute root investment than small-seeded species.

Besides differential investment in root growth, specific types of root architecture and morphology may be important for seedling establishment in dry conditions (Wright and Westoby 1999; Nicotra et al. 2002). For example, a thick tap root to maximise rooting depth and thin secondary roots is a strategy to maximise water absorption (Guerrero-Campo and Fitter 2001). Also, faster root elongation is often evident among large-seeded species (e.g. Buckley 1982; Daws et al. 2007). In our glasshouse experiment, larger-seeded species had longer tap and secondary roots at harvest. The root advantage of large-seeded species was true on an absolute but not relative scale; large-seeded species did not invest in higher root:total biomass. This finding was consistent with those of previous glasshouse studies on species from warm temperate, semi-arid and arid ecosystems (Wulff 1986; Jurado and Westoby 1992a; Leishman and Westoby 1994b).

A lasting advantage in absolute root investment is likely the reason we observed seed mass to remain correlated with seedling survival across four families/subfamilies in the field over the long, dry summer. Similar patterns have been documented in other Mediterranean-climate ecosystems. Rooting depth has been correlated with summer survival in a Spanish Mediterranean-climate ecosystem (Padilla and Pugnaire 2007). Survival and seed mass have been similarly correlated in Spanish Mediterranean shrubland, and the strength of this relationship increased in dry years (Lloret et al. 1999). Fire regeneration strategies may also alter survival rates—for species of similar seed size, those that recruit from seeds after fire can have higher survival rates than those that resprout (Enright and Lamont 1989). The fire resprouters at our site, however, also regenerate freely from seeds (e.g. *Eucalyptus marginata*, *Jacksonia furcellata*). Thus, our findings are akin to the conclusions of Bell (2001), who argued that seed size and physiological traits are more important than fire response for seedling establishment in southwestern Australia.

Previous studies linking seed mass and drought survival have tended to focus on initial seedling survival (Leishman and Westoby 1994b; Schutz et al. 2002). Even in tropical regions young seedlings are likely to experience drought (Engelbrecht et al. 2006), because even a few days without rain can allow the upper soil profile to dry. The Bassendean sands at our Mediterranean-climate restoration site are almost certainly dry in summer (Zencich et al. 2002), and in the glasshouse experiment the surface soils dried under the drought treatments. Survival would presumably increase if a seedling's root tips reached below this layer (Schutz et al. 2002). Root:total biomass allocations were highest in the initial 24 days of establishment among all species, which is likely indicative of the importance of early root investment for avoiding short (springtime) droughts (Padilla et al. 2007). Because large-seeded species resulted in longer root systems, we expected to observe a relatively higher rate of initial survival of large-seeded species in the drought treatments. In fact we observed a consistent pattern of initial seedling survival with seed mass across all drought treatments. It is possible that this finding was the result of the experimental design—our experiment was designed to test the growth mechanisms of summer survival and not initial survival per se—however, other studies expecting a relative survival advantage under drought have also reported equivocal findings (Leishman and Westoby 1994b).

A relative advantage, however, may be dependent on the amount of variation between individuals within a species. Small-seeded species, unlike large-seeded species, are more dependent on environmental resources than seed reserves (Milberg et al. 1998). We observed that variation in individual root investment decreased with increasing seed mass. Consequently, a few small-seeded individuals may still be able to invest in deep roots and survive periods of drought. A lack of a relative survival advantage for large-seeded species under drought therefore does not necessarily mean that seed mass is unimportant for drought survival. Rather, it suggests that small-seeded species may be more reliant on favourable microsites for drought survival than large-seeded species (Winn 1985; Venable and Brown 1988).

The benefit of a large seed for establishment under environmental hazards has been often considered to be temporary; the advantage of a large seed would cease once all seed resources have been deployed (Kidson and Westoby 2000). This framework may be true when seedlings rely directly on seed resources for survival, such as seedlings reliant on seed carbon reserves under deep shade (Saverimuttu and Westoby 1996; Walters and Reich 2000). In the case of drought survival, however, our results indicate that

the initial growth advantage afforded by the nutrient reserves in large seeds (Lamont and Groom 2002) might have lasting consequences for survival. Recent reviews of seed mass literature suggest that seed mass should be considered as part of spectrum of traits influencing plant size, survival and reproductive capacity (Moles and Westoby 2006). In the example of seed mass and drought survival, the resource reserves in large seeds allow subsequent traits, such as long roots, to develop. Thus, when conceptualising seed mass as one in a suite of traits, it is important to consider the traits that might be mediated by seed reserves.

Producing large seeds is an effective bet-hedging strategy in MCEs where the timing and amounts of rainfall are highly variable, both in theory (Venable and Brown 1988) and under field conditions (Metz et al. 2010). On the other hand, small-seeded species are generally better able to take advantage of episodic rainfall due to high seed production (e.g. Rees 1995), rapid germination (Jurado and Westoby 1992b) and perhaps predictable germination (Kos and Poschlod 2010), but in unfavourable years may be restricted to limited microsites (Venable and Brown 1988; Coomes et al. 2002) or remain dormant in the seed bank (Venable and Brown 1988; Jurado and Westoby 1992b).

If the interplay between drought survival and spatiotemporal variation helps to maintain a wide range of seed mass in MCEs, two contemporary factors may alter this balance. First, climate models predict greater rainfall variability and a decrease in rainfall amount in MCEs (Hewitson and Crane 2006; CSIRO 2007; Klausmeyer and Shaw 2009). Accordingly, the length of time between high rainfall years may increase. Second, most restoration practitioners broadcast seeds just once per site, essentially gambling that conditions will be favourable that year. In a continuously regenerating system variation in rainfall can help to increase diversity, but when all individuals recruit in the same year, a drought year would disproportionately affect small-seeded species. Understanding the short and long-term relevance of seed mass for establishment under drought is thus important both for predicting shifts in species assemblages due to climate change and for informing restoration efforts as practitioners work towards establishing communities of large and small-seeded species despite a variable and changing climate.

While our study has focused on a region with a Mediterranean-type climate, observed and predicted increases in rainfall variability in many other systems (Solomon et al. 2007) suggest that our results are likely to be increasingly relevant as more systems experience increased incidence of drought.

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