Plant survival in relation to seed size along environmental gradients: a long-term study from semi-arid and Mediterranean annual plant communities

Johannes Metz[1], Pierre Liancourt[1,2], Jaime Kigel[3], Danny Harel[4], Marcelo Sternberg[4] and Katja Tielbörger[1]*

[1]*Department of Plant Ecology, University of Tübingen, Auf der Morgenstelle 3, 72076 Tübingen, Germany;*
[2]*Department of Biology, University of Pennsylvania, 322 Leidy Labs, Philadelphia, PA 19104-6018, USA;*
[3]*Robert Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, Rehovot Campus, 76100 Rehovot, Israel; and* [4]*Department of Plant Sciences, Tel Aviv University, 69978 Tel Aviv, Israel*

Summary

1. A positive relationship between seed size and subsequent offspring survival is a key assumption in ecological theory concerning life-history strategies. Yet, this relationship is uncertain in respect to lifetime survival because sound evidence only exists for early seedling stages. Furthermore, the effect of environmental variation in space and time, and of contrasting plant functional groups, on this relationship has been scarcely examined.

2. Here, we investigated survival and between-year variation therein. We tested for both whether their relationship to seed size (i) is maintained up until reproduction, (ii) changes along environmental gradients and (iii) differs between functional groups (grasses, legumes, forbs).

3. Survival was monitored from established seedlings to reproductive plants in 49 annual species under natural conditions during 7 years in three sites along a steep rainfall gradient. We then related average survival per species and between-year variation in survival to seed size, site along the gradient and functional group.

4. Larger seed size was associated with higher survival and lower between-year variation. Across the rainfall gradient, we detected no difference in the seed size–survival relationships; however, variation between years was lowest in the most mesic site where no relationship for between-year variation with seed size was observed. Legumes showed lower survival and higher between-year variation than grasses.

5. Our findings indicate that larger seed size provides survival advantages beyond seedling establishment up until reproduction among annual species. Larger seed size also provides a bet-hedging strategy in temporally unpredictable environments. Increased abiotic favourability along environmental gradients may have little effect on survival rates but reduces survival variation between years and thus reduces the bet-hedging benefit of larger seed size. We suggest that the contrasting response of legumes and grasses may partly result from their disparity in seed dormancy.

6. *Synthesis*. Current plant life-history theory can be refined by accounting for both benefits of larger seed size, higher survival rates and bet-hedging. Studies along environmental gradients are needed to generalize findings across ecosystems and to predict patterns of plant traits and plant performance under changing environmental conditions.

Key-words: annuals, bet-hedging, dormancy, grasses, legumes, seed size, seedlings, survival

Introduction

Plant species within the same community often differ greatly in their survival rates, presumably owing to differences in their specific set of traits for coping with environmental conditions (Tevis 1958; Loria & Noy-Meir 1980; Verkaar & Schenkeveld 1984; Kelly 1989). Among the array of traits that may determine survival rates, seed size was studied intensively and is considered of particular importance at early seedling stages (Leishman *et al.* 2000; Coomes & Grubb 2003). There is strong evidence that the surplus resources of larger seeds render

*Correspondence author. E-mail: katja.tielboerger@uni-tuebingen.de

young seedlings more resistant to hazards like drought, shade or herbivory during the early stage of seedling establishment, as reviewed in Leishman *et al.* (2000) and supported by a recent data synthesis (Moles & Westoby 2004). Based on this evidence, a positive relationship between seed size and survival has been commonly assumed and has crucially shaped life-history theory, e.g. about trade-offs between seed size and seed number or between competition and colonization (Venable & Brown 1988; Turnbull, Rees & Crawley 1999; Jakobsson & Eriksson 2000; Leishman 2001; Coomes & Grubb 2003; Falster, Moles & Westoby 2008).

However, seed size–survival relationships have been scarcely examined beyond the very early stage of seedling establishment, i.e. the advantage of large seeds for lifetime survival remains unclear. Information on survival at later stages of the plant life cycle stems from only few studies, often with a small number of species, that yielded contradicting results (e.g. Loria & Noy-Meir 1980; Lloret, Casanovas & Peñuelas 1999; Moles & Westoby 2004; Baraloto, Forget & Goldberg 2005). A reason for this scarcity may be that studies often focused on long-lived species, where survival monitoring is difficult. Therefore, it remains controversial whether surplus seed resources during seedling establishment can also translate into higher survival up to reproduction. On one hand, it has been argued that the survival advantage with increased seed size is a direct consequence of additional resources and vanishes when seed resources are depleted (Saverimuttu & Westoby 1996; Walters & Reich 2000). This view was supported by the synthesis of Moles & Westoby (2004) who detected no correlation between seed size and survival from emergence to reproduction, in contrast to survival at early stages. On the other hand, some evidence exists for higher survival rates associated with larger seed size beyond early establishment, namely for saplings of tropical tree species (Moles & Westoby 2004; Baraloto, Forget & Goldberg 2005) and Mediterranean shrub species (Lloret, Casanovas & Peñuelas 1999), with the latter study attributing the higher survival to better initial root establishment. Another possible advantage is that larger seed size improves competitive ability due to its strong correlation with subsequent plant size (Gross 1984; Leishman 2001). This size advantage may translate into survival advantages at later, more density-dependent stages (Baraloto, Forget & Goldberg 2005; Falster, Moles & Westoby 2008).

The available information on seed size–survival relationships is also limited because the effect of temporal variation in survival has rarely been investigated. For instance, survival rates of species can strongly differ between years, especially in highly variable environments such as arid or Mediterranean ecosystems (Mott & McComb 1974; Loria & Noy-Meir 1980; Kelly 1989; Lloret, Casanovas & Peñuelas 1999). Such temporal variation may render results from only a single study season misleading. Multiyear studies are therefore vital to evaluate the generality of seed size–survival relationships, but are largely missing in the literature (but see Lloret, Casanovas & Peñuelas 1999). Specifically, if seedlings from small-seeded species are altogether more vulnerable, then they should show lower survival chiefly in unfavourable but not in favourable

years, resulting in larger between-year variation with a higher chance of zero survival in particularly severe years. Larger seed size may reduce this inter-annual variation in survival at the cost of lower seed number and was therefore suggested as a bet-hedging strategy against temporal environmental variation (Venable & Brown 1988; Pake & Venable 1996).

Furthermore, spatial variation in abiotic environmental conditions, as across resource or stress gradients, may affect seed size–survival relationships in complex ways. Specifically, higher resource availability in favourable sites should reduce mortality caused by water or nutrient shortage, possibly with stronger relief for small-seeded species and thus diminishing the survival advantage of large-seeded species. Yet, this effect may be counteracted by higher mortality due to increased competition intensity that is associated with increased abiotic favourability (Grime 1974; Holzapfel *et al.* 2006; Liancourt & Tielbörger 2009), probably also with stronger negative impact on smaller and thus small-seeded species. Despite this complexity, numerous studies implicitly assumed that survival is generally lower in harsh environments, such as studies that tested whether seed sizes are larger in these areas (Baker 1972; Mazer 1989; Pluess, Schütz & Stöcklin 2005). However, this implicit assumption was barely tested and could not yet be confirmed in the field (Moles *et al.* 2004). It thus remains unknown whether survival rates generally increase or decrease along environmental gradients and also whether the survival advantage of larger seed size changes alongside them in a predictable way.

Seed size–survival relationships may also differ between functional and taxonomic groups with contrasting life-history strategies. For instance, various ecological studies distinguished between grasses, legumes and forbs due to several distinct characteristics such as nitrogen fixation in legumes or basal meristems in grasses, and demonstrated differential performance between these groups (e.g. Grünzweig & Körner 2003; Zavaleta *et al.* 2003; Suttle, Thomsen & Power 2007; Petrů & Tielbörger 2008; Xia & Wan 2008). Moreover, grasses, legumes and forbs differ also in seed dormancy, which is another important bet-hedging strategy in temporally unpredictable environments besides large seed size (Cohen 1966, 1967; Valleriani 2005). In Mediterranean and arid environments, legumes commonly possess high dormancy and build up long-lasting seed banks, whereas grasses show very low dormancy and forbs often act intermediately (Young *et al.* 1981; Jain 1982; Gulmon 1992; Kigel 1995; Sternberg *et al.* 2003; Petrů & Tielbörger 2008). This difference is of particular interest because theoretical studies predicted a trade-off between seed size and dormancy as alternative bet-hedging strategies (Venable & Brown 1988), with large seed size mainly helping to withstand unfavourable conditions and seed dormancy rather helping to escape them. Based on this difference, we hypothesized that the functional groups grasses, legumes and forbs may exhibit distinct seed size–survival relationships.

In summary, the available empirical evidence on seed size–survival relationships is still limited. Information is scarce beyond early seedling stages and is usually based on single study years and single environments, without the consideration

of environmental variation in space and time. In the present study, we aimed to address these open questions, focusing on annual species. We monitored the survival of established seedlings to reproduction under natural conditions in 49 common annual species, separated into grasses, legumes and forbs, and related their survival to seed size. Our data set covered seven distinct years and three sites ranging from semi-arid to mesic-Mediterranean conditions, and thus spanned large temporal and spatial environmental variation. We tested the following hypotheses. (1) Survival from established seedlings to reproduction increases and inter-annual variation in survival decreases with increasing seed size. (2) Along our gradient of increasing rainfall, survival increases, inter-annual variation in survival decreases and the relative survival advantage of large-seeded species decreases. (3) Functional groups differ in survival and in inter-annual variation in survival at comparable seed sizes.

Materials and methods

STUDY SITES

We conducted field work at three sites in Israel that differ primarily in average annual rainfall and its inter-annual variation (Table 1), representing a steep favourability gradient for plant growth and reproduction (Aronson & Shmida 1992; Holzapfel *et al.* 2006). We will henceforth refer to the sites as semi-arid (location: Lahav, Northern Negev desert, N 31°23′, E 34°54′), Mediterranean (location: Matta, Jerusalem Mountains, N 31°42′, E 35°03′) and mesic-Mediterranean (location: Ein Yaacov, Galilee Mountains, N 33°0′, E 35°14′). All sites are semi-natural shrublands with predominantly annual vegetation in the inter-shrub matrix. They share the same general Mediterranean-type climate with mild, rainy winters and hot, rainless summers and have similar annual mean temperatures (17.7–18.4 °C). Main growth season is from autumn to spring (November–May) and it is shorter in the drier sites. All sites are located on southern slopes of the same type of calcareous bedrock, and were fenced against livestock grazing prior to the beginning of the experiment. A detailed description of the sites is given in Holzapfel *et al.* (2006).

Our study spanned seven consecutive seasons of strongly varying rainfall, thus covering a wide range of temporal environmental variability (Table 1). Rainfall was measured directly at the sites with automatic rain gauges.

SURVIVAL MONITORING

At each field site, 50 permanent quadrats of 20 × 20 cm were set up in 25 random pairs before the onset of rainfall in October 2001 and monitored until the end of the 2007/2008 growing season. For each pair, one quadrat was located under the canopy of the dominant shrub species, *Sarcopoterium spinosum* (L.) Spach (Rosaceae), a hemispherical dwarf-shrub. The other quadrat was placed nearby in the inter-shrub matrix. In this way, we accounted for the major source of small-scale heterogeneity in annual plant abundance and performance in our study system (Holzapfel *et al.* 2006).

All permanent quadrats were monitored twice per growing season. In the first census at the beginning of the season, the number of germinated seedlings per species was recorded. In the second census at the end of the season, the number of individuals that had reached reproduction was recorded per species. Survival fraction was then estimated for each species as the ratio between the second and first census.

Seedlings were monitored approximately in December; i.e. *c.* 1 month after the initial rain events had triggered the main germination wave from the soil seed bank. Multiple counting in 3 years for a subset of quadrats indicated that there was one major germination event and later cohorts were negligible. At the time of the census, dicot seedlings had one to two leaves and grass seedlings had unfolded at least their first blade. Previous studies had shown that seed resources are used up at first-leaf stage (Saverimuttu & Westoby 1996) or 2 weeks after germination (Grime & Jeffrey 1965) for species of similar and even larger seed size than those in our study. We thus assumed that subsequent survival was not affected anymore by undepleted seed resources.

The second census was carried out *c.* 3 months (semi-arid site) and 4–5 months (Mediterranean and mesic-Mediterranean sites) after the first census, depending on the season's rainfall pattern. By this time, all annual species were at least flowering and most of them fruiting. Each individual that was flowering or fruiting was considered as a survivor.

Some closely related species could not be unequivocally distinguished at the seedling stage. Those species were treated as one single species: the individuals were pooled and the average seed size (see below) was used. In the analyses, we included only species with at least 10 seedlings counted in each season to ensure reasonable sample size for survival estimates. The final data set included 21 species in the semi-arid site, 33 in the Mediterranean and 21 in the mesic-Mediterranean site, and covered 49 species altogether. For a list of species and their seed size, see Table S1.

SEED SIZE

We used primarily seed mass data published by Osem, Perevolotsky & Kigel (2006). For additional species not listed there, we randomly collected in our sites 10 individuals and measured the mass of 10 seeds per individual to the nearest 0.1 mg and subsequently calculated the mean seed weight. Seed mass included the seed coat and tissues adhered to it, but no additional parts of the dispersal unit. In legumes, the seeds were released from indehiscent fruits. In grasses, the caryopsis was weighed and in composites the achene.

Table 1. Seasonal rainfall (in mm) at the three study sites along a natural rainfall gradient in Israel

Site	Average 1977–2008	2001/2002	2002/2003	2003/2004	2004/2005	2005/2006	2006/2007	2007/2008
Semi-arid	300 (±32%)	323	352	235	377	196	262	182
Mediterranean	540 (±29%)	654	799	461	558	521	609	421
Mesic-Mediterranean	780 (±26%)	833	963	775	635	631	687	482

Presented are long-term averages (±coefficient of variation) and rainfall during each of the seven study seasons.

FUNCTIONAL GROUPS

We distinguished chiefly between grasses (Poaceae) and legumes (Fabaceae) and aggregated all other species as forbs. Among several other characteristics, these groups differ in between-year seed dormancy. In annuals from Mediterranean and arid environments, grasses commonly possess low dormancy and legumes high dormancy, whereas forbs have heterogeneous, but often intermediate, dormancy (Young *et al.* 1981; Jain 1982; Gulmon 1992; Kigel 1995; Sternberg *et al.* 2003; Petrů & Tielbörger 2008). This pattern was confirmed for species from our study sites by parallel investigations on soil seed bank composition (D. Harel & M. Sternberg, unpublished data) and germinability of seeds under greenhouse conditions (K. Tielbörger, unpublished data) respectively.

STATISTICAL ANALYSIS

Survival per species was calculated, for each year and site separately, as the ratio of all surviving individuals divided by all seedlings, both summed up over the 50 quadrats. From these seven single-year values, we calculated the mean, indicating the average survival to reproduction across temporal environmental variability (henceforth, mean survival), and the coefficient of variation, indicating between-year variation in survival rates (henceforth, CV-survival).

Mean survival and CV-survival were analysed separately with linear models, using for both $\log_{10}$-transformed seed size as continuous predictor plus site and functional group as fixed factors. We interpreted significant effects of seed size as an overall relationship between seed size and mean survival or CV-survival respectively (Hypothesis 1). Changes in the slope of that relationship along the spatial gradient were indicated by significant site × seed size interaction, whereas significant effects of site alone indicated that mean survival or CV-survival generally differed between sites (Hypothesis 2). Overall differences between functional groups in mean survival or CV-survival were indicated by a significant functional group effect, whereas significant seed size × functional group interactions showed that the slope of the relationship of mean survival or, respectively, CV-survival with seed size differed between functional groups (Hypothesis 3).

Tukey's HSD test was applied for identifying pairwise differing factor levels. Mean survival data were arcsine square root-transformed prior to the analysis to meet homoscedasticity (Sokal & Rohlf 1995). All analyses were carried out with JMP 5.0.1 (SAS Institute 2002).

Results

Mean survival from established seedlings to reproduction ranged from 40% to 80%, including all species in all sites. Across all sites, mean survival was positively related to seed size, i.e. larger-seeded species showed higher mean survival (Table 2, Fig. 1a–c). The slope of this relationship was similar among sites, as indicated by the non-significant seed size × site interaction (Table 2). Mean survival did not generally differ between sites despite a gentle decrease towards more mesic sites (Table 2, Fig. 1a–c). Functional groups differed in mean survival, with grasses showing higher mean survival compared to both forbs and legumes (Table 2, Fig. 1a–c). The slope of the relationship between mean survival and seed size showed no difference between functional groups.

Table 2. Results of linear models testing the effects of seed size, site (semi-arid, Mediterranean, mesic-Mediterranean) and functional group (grasses, legumes, forbs) on mean survival to reproduction and coefficient of variation in survival for the most common annual species along a rainfall gradient in Israel

Source of variation	d.f.	Mean survival*		CV-survival†	
		F	P	F	P
Seed size	1	20.78	**< 0.0001**	7.81	**0.0071**
Site	2	2.25	0.1145	3.87	**0.0266**
Functional group	2	8.37	**0.0006**	4.56	**0.0146**
Seed size × site	2	1.02	0.3639	4.17	**0.0205**
Seed size × functional group	2	0.48	0.6233	2.22	0.1177
Site × functional group	4	0.94	0.4470	4.51	**0.0031**
Seed size × site × functional group	4	0.76	0.5538	1.89	0.1243
Error	57				

Bold indicates significant *P*-values ($P < 0.05$).
*R^2 of the full model: 0.57.
†R^2 of the full model: 0.59.

CV-survival was overall negatively related to seed size, indicating larger between-year variation in survival for small-seeded species (Table 2, Fig. 1d–f). However, this relationship was missing in the mesic-Mediterranean site and resulted in a significant seed size × site interaction (Table 2). Also the general level of CV-survival differed among sites and was significantly higher in the semi-arid than in the mesic-Mediterranean site (Table 2, Fig. 1d–f). Regarding functional groups, CV-survival was generally higher for legumes than for grasses, whereas forbs were not distinguishable from either of the two (Table 2, Fig. 1d–f). Moreover, particularly high CV-survival for legumes in the semi-arid site resulted in a significant site × functional group interaction. The slope of the relationship between CV-survival and seed size showed no difference between functional groups (Table 2, Fig. 1d–f).

Discussion

Our results showed a clear positive relationship between seed size and survival from established seedlings to reproduction in annual plant communities. This pattern was consistent for three sites differing strongly in annual rainfall, where 49 species were monitored during seven consecutive years.

Positive relationships between seed size and survival have played a major role in shaping ecological theory about life-history strategies (Venable & Brown 1988; Coomes & Grubb 2003; Falster, Moles & Westoby 2008). However, previous evidence was restricted mainly to early seedling survival, a stage still dependent on seed resources (Leishman *et al.* 2000; Moles & Westoby 2004). Our findings thus demonstrate that larger seed size ensures higher survival also at later stages, and that this advantage can be maintained up until reproduction among annual species. The strongest claim against such a long-lasting survival advantage with larger seed size came from the synthesis of Moles & Westoby (2004) who compiled data from the
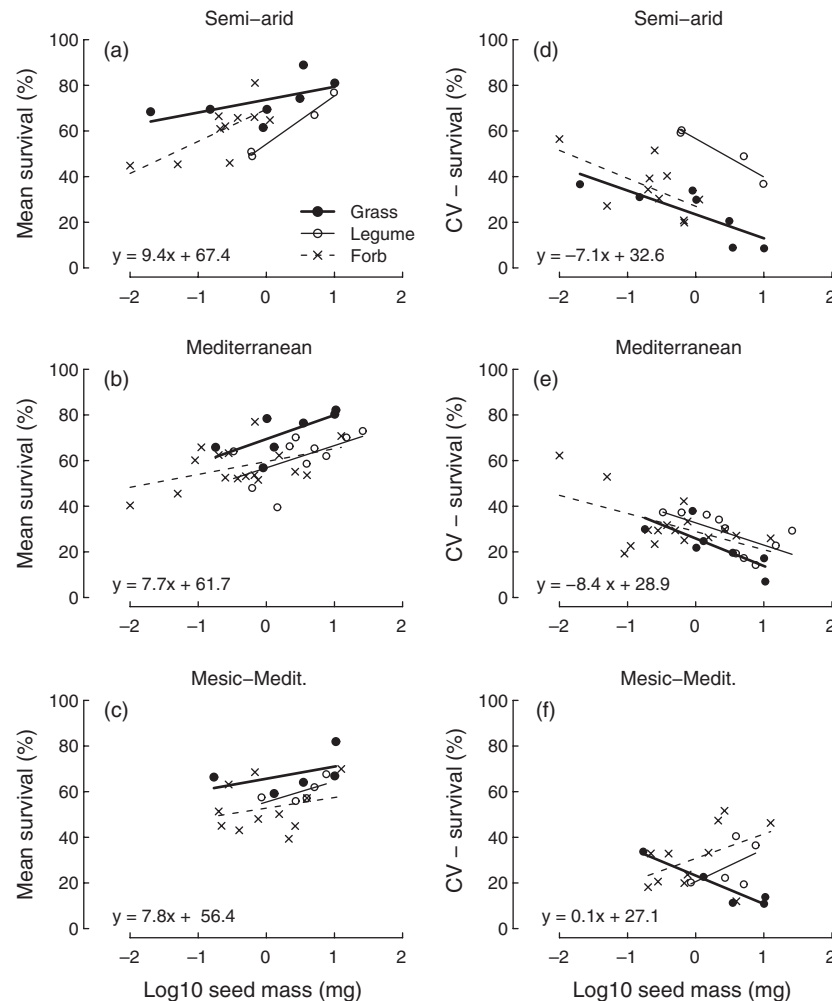
Fig. 1. Relationship between $\log_{10}$-transformed seed size and mean survival from established seedlings to reproduction (a–c) and coefficient of variation in survival (d–f) for the most common annual species along a rainfall gradient in Israel. Species were separated into functional groups (grasses, legumes, forbs) and trend lines are presented for each group. Note that the single trend lines were not tested for significance to avoid multiple comparisons given the small sample size within functional groups per site. To further ease interpretation of the figure, correlation equations are presented separately for each site, calculated across all species regardless of functional group. See Table 2 for statistical analysis.

global literature indiscriminate of habitat type, life-form and time to reproduction. The authors, however, remarked that the power of this analysis was possibly limited by small species number. They also added in a later paper that survival negatively covaries with time to reproduction and suggested additional work within single ecosystems to provide more controlled tests (Moles & Westoby 2006). In line with this suggestion, several studies with species of only one life-form and ecosystem are consistent with our findings, showing a positive relationship between seed size and survival beyond early establishment (Lloret, Casanovas & Peñuelas 1999; Moles & Westoby 2004; Baraloto, Forget & Goldberg 2005; but see Loria & Noy-Meir 1980). Moreover, contradicting results in the literature may in part originate from between-year variation in survival, as expressed by CV-survival in our study, which may mask general seed size–survival relationships in single years.

Survival across the whole life cycle may be subdivided into several stages (Moles & Westoby 2004, 2006). Our study addressed the scarcely examined later stage between estab-

lished seedlings and reproduction. Although this limits conclusions about entire lifetime survival, the advantage of large-seeded species documented here should clearly contribute to lifetime survival and further enlarges their well-documented advantage during early seedling stage (Leishman *et al.* 2000; Moles & Westoby 2004). Uncertainty regarding survival across the whole life cycle remains primarily because mortality of seeds before germination, i.e. the impact of post-dispersal seed predation and storage in the soil, is difficult to assess and no consensus exists on its relationship to seed size (Hodkinson *et al.* 1998; Thompson *et al.* 1998; Moles & Westoby 2006; Traba, Azcarate & Peco 2006).

Altogether, survival from established seedlings to reproduction was remarkably high and differences between species were rather small. Survival ranged from 40% to 80% for species that differed roughly a 1000-fold in seed size, which is comparable with survival rates during the first week after germination (Moles & Westoby 2004). There is intense recent debate about how such survival differences scale with numerical advantages

that small-seeded species potentially accrue during seed production and, moreover, how this interacts with other life-history characteristics such as adult plant size, time span to reproduction and reproductive lifespan (Moles & Westoby 2006; Rees & Venable 2007; Falster, Moles & Westoby 2008; Venable & Rees 2009).

Along our steep rainfall gradient, we detected no difference in the seed size–survival relationship. In contrast to our hypothesis, survival rates were not generally higher or lower in any of the sites and the survival advantage of larger-seeded species (i.e. the slope) was also similar. Our gradient is characterized by decreasing drought stress and increasing standing biomass with associated competition intensity (Holzapfel *et al.* 2006; Schiffers & Tielbörger 2006). Under both conditions larger seed size was suggested to be advantageous for survival (Lloret, Casanovas & Peñuelas 1999; Baraloto, Forget & Goldberg 2005; Falster, Moles & Westoby 2008; Liancourt *et al.* 2009). We argue that along our gradient, decreasing mortality by drought may be counterbalanced by increasing mortality by competitive exclusion. This would lead to overall similar survival rates among sites and also to similar survival advantages for larger-seeded species. Larger seed size may therefore be a response to both competition and stress that provides comparable survival advantages along environmental gradients. Furthermore, local adaptation to specific site conditions probably contributed to balancing up survival rates along the gradient. Namely, for species from our study region, it was reported that plants from dry habitats adapted to drought at the expense of competitive ability, whereas plants from more mesic sites are better competitors but less drought-tolerant (Petrů *et al.* 2006; Liancourt & Tielbörger 2009). Nonetheless, the result of similar survival rates along the gradient was surprising, because previous studies had often implicitly assumed that survival is generally lower in more stressful environments (Baker 1972; Mazer 1989; Pluess, Schütz & Stöcklin 2005). Our finding, however, is consistent with a latitudinal compilation on early seedling survival from tropic to temperate environments (Moles *et al.* 2004) and may thus stand for a more general pattern.

Another key finding of our study is that larger seed size was associated with lower variation in survival between years. This supports theoretical models proposing larger seed size as a bet-hedging strategy in temporally unpredictable environments (Venable & Brown 1988), an idea that has so far only rarely been confirmed in the field (Pake & Venable 1996). The advantage of larger seed size lies therefore not only in higher average survival rates but also in ensuring rather constant survival and avoidance of zero success in particularly severe years (Venable & Brown 1988; Pake & Venable 1996). This bet-hedging effect should be especially important for annual plant species, because they are more susceptible to reproductive failure in single years.

Interestingly, the relationship of reduced variation in survival with larger seed size was not observed in our wettest site, where variation in survival was also generally lower. We know of no similar studies testing inter-annual variation in survival or other fitness traits along environmental gradients to judge the generality of this finding. However, an analogous trend of reduced bet-hedging with increasing habitat stability was reported for seed persistence in the soil (Thompson *et al.* 1998). This suggests that the bet-hedging effect of larger seed size may be less important in sites where environmental conditions are generally more favourable and predictable. This interpretation is in line with our earlier suggestion that competitive exclusion and not drought stress is the dominant cause for mortality in our wettest site. Unlike drought stress, competitive exclusion should cause rather constant mortality among years, leading to generally lower variation in survival and with no relation to seed size, as it is consistent with our findings in this site.

Another salient finding of our study was that seed size–survival relationships varied between functional groups. Legumes expressed lower survival rates and higher between-year variation than grasses. Despite the extensive use of functional groupings in ecological research (e.g. Grime 1974; Hodgson *et al.* 1999; Mc Intyre & Lavorel 2001; Voigt, Perner & Jones 2007), this approach has found little attention in studies on survival. We cannot unequivocally explain the distinct response of legumes and grasses, because they differ in a whole array of traits that may affect their performance. However, we suggest that the contrast between high seed dormancy in legumes and low dormancy in grasses may contribute to their distinct behaviour in both survival and its inter-annual variation. High dormancy provides a greater ability to escape unfavourable years. Accordingly, high-dormant species probably evolved fewer adaptations for coping with unfavourable conditions and specialized instead on years with large resource availability (Venable & Brown 1988). They should thus suffer high mortality predominantly in unfavourable years, resulting in lower average survival and higher between-year survival variation. This is consistent with the general pattern for legumes in our study and also with the particularly high survival variation for legumes in our driest, most variable site. Analogous to these findings, studies on Sonoran desert annuals showed that high-dormant species have higher variation in reproductive success (Pake & Venable 1996; Venable 2007). This indicates that the effect of larger seed size may be counteracted by increased seed dormancy, as is in line with previous studies that suggested a trade-off between dormancy and large seed size as alternative bet-hedging strategies (Venable & Brown 1988; Pake & Venable 1996).

Conclusions

Our study presents clear evidence that larger seed size is associated with higher survival from established seedlings to reproduction among annual species and thus helps to resolve the debate of whether larger seed size is advantageous beyond early seedling establishment (Saverimuttu & Westoby 1996; Lloret, Casanovas & Peñuelas 1999; Moles & Westoby 2004; Falster, Moles & Westoby 2008). Moreover, the surprising finding that this relationship was maintained across a steep rainfall gradient sheds new light on the partly inconsistent results in cross-environmental studies on seed size and survival rates (Baker 1972; Mazer 1989; Moles & Westoby 2004; Moles

et al. 2004; Pluess, Schütz & Stöcklin 2005). Our results also draw attention to the bet-hedging effect of larger seed size, as it was associated with lower variation in survival between years (Venable & Brown 1988; Pake & Venable 1996). Yet, the finding that survival and its inter-annual variation differ between plant functional groups needs future research to evaluate underlying mechanisms. We suggest that the current understanding of plant life-history strategies can be refined by considering both benefits of larger seed size, higher survival rates and bet-hedging effect. We further emphasize that combining this approach with environmental gradients may greatly help to generalize findings across ecosystems and to predict patterns of plant traits and plant performance under changing environmental conditions.

Acknowledgements

References

Aronson, J. & Shmida, A. (1992) Plant species diversity along a Mediterranean-desert gradient and its correlation with interannual rainfall fluctuations. *Journal of Arid Environments*, **23**, 235–247.

Baker, H.G. (1972) Seed weight in relation to environmental conditions in California. *Ecology*, **53**, 997–1010.

Baraloto, C., Forget, P.-M. & Goldberg, D.E. (2005) Seed mass, seedling size and neotropical tree seedling establishment. *Journal of Ecology*, **93**, 1156–1166.

Cohen, D. (1966) Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, **12**, 119–129.

Cohen, D. (1967) Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions a choice has to be made and the subsequent outcome. *Journal of Theoretical Biology*, **16**, 1–14.

Coomes, D.A. & Grubb, P.J. (2003) Colonization, tolerance, competition and seed-size variation within functional groups. *Trends in Ecology and Evolution*, **18**, 283–291.

Falster, D.S., Moles, A.T. & Westoby, M. (2008) A general model for the scaling of offspring size and adult size. *The American Naturalist*, **172**, 299–317.

Grime, P.J. (1974) Vegetation classification by reference to strategies. *Nature*, **250**, 26–31.

Grime, P.J. & Jeffrey, D.W. (1965) Seedling establishment in vertical gradients of sunlight. *Journal of Ecology*, **53**, 621–642.

Gross, K.L. (1984) Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology*, **72**, 369–387.

Grünzweig, J.M. & Körner, C. (2003) Differential phosphorus and nitrogen effects drive species and community responses to elevated CO_2 in semi-arid grassland. *Functional Ecology*, **17**, 766–777.

Gulmon, S.L. (1992) Patterns of seed germination in Californian serpentine grassland species. *Oecologia*, **89**, 27–31.

Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, P.J. & Thompson, K. (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos*, **85**, 282–294.

Hodkinson, D.J., Askew, A.P., Thompson, K., Hodgson, J.G., Bakker, J.P. & Bekker, R.M. (1998) Ecological correlates of seed size in the British flora. *Functional Ecology*, **12**, 762–766.

Holzapfel, C., Tielbörger, K., Parag, H.A., Kigel, J. & Sternberg, M. (2006) Annual plant-Shrub interactions along an aridity gradient. *Basic and Applied Ecology*, **7**, 268–279.

Jain, S.K. (1982) Variation and adaptive role of seed dormancy in some annual grassland species. *Botanical Gazette*, **143**, 101–106.

Jakobsson, A. & Eriksson, O. (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos*, **88**, 494–502.

Kelly, D. (1989) Demography of short-lived plants in chalk grassland. I. Life cycle variation annuals and strict biennials. *Journal of Ecology*, **77**, 747–769.

Kigel, J. (1995) Seed germination in arid and semiarid regions. *Seed Development and Germination* (eds J. Kigel & G. Galili), pp. 645–699. Marcel Dekker, New York.

Leishman, M.R. (2001) Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos*, **93**, 294–302.

Leishman, M.R., Wright, I.J., Moles, A.T. & Westoby, M. (2000) The evolutionary ecology of seed size. *Seeds: The Ecology of Regeneration in Plant Communities* (ed. M. Fenner), pp. 31–57. CAB International, Wallingford.

Liancourt, P. & Tielbörger, K. (2009) Competition and a short growing season lead to ecotypic differentiation at the two extremes of the ecological range. *Functional Ecology*, **23**, 397–404.

Liancourt, P., Tielbörger, K., Bangerter, S. & Prasse, R. (2009) Components of 'competitive ability' in the LHS model: implication on coexistence for 12 co-occurring Mediterranean grasses. *Basic and Applied Ecology*, **10**, 707–714.

Lloret, F., Casanovas, C. & Peñuelas, J. (1999) Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Functional Ecology*, **13**, 210–216.

Loria, M. & Noy-Meir, I. (1980) Dynamics of some annual populations in a desert loess plain. *Israel Journal of Botany*, **28**, 211–225.

Mazer, S.J. (1989) Ecological, taxonomic, and life history correlates of seed mass among Indiana dune angiosperms. *Ecological Monographs*, **59**, 153–175.

Mc Intyre, S. & Lavorel, S. (2001) Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *Journal of Ecology*, **89**, 209–226.

Moles, A.T. & Westoby, M. (2004) Seedling survival and sees size: a synthesis of the literature. *Journal of Ecology*, **92**, 372–383.

Moles, A.T. & Westoby, M. (2006) Seed size and plant strategy across the whole life cycle. *Oikos*, **113**, 91–105.

Moles, A.T., Warton, D.I., Stevens, R.D. & Westoby, M. (2004) Does a latitudinal gradient in seedling survival favour larger seeds in the tropics? *Ecology Letters*, **7**, 911–914.

Mott, J.J. & McComb, A.J. (1974) Patterns in annual vegetation and soil microrelief in an arid region of Western Australia. *Journal of Ecology*, **62**, 115–126.

Osem, Y., Perevolotsky, A. & Kigel, J. (2006) Size traits and site conditions determine changes in seed bank structure caused by grazing exclusion in semiarid annual plant communities. *Ecography*, **29**, 11–20.

Pake, C.E. & Venable, D.L. (1996) Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, **77**, 1427–1435.

Petrů, M. & Tielbörger, K. (2008) Germination behaviour of annual plants under changing climatic conditions: separating local and regional environmental effects. *Oecologia*, **155**, 717–728.

Petrů, M., Tielbörger, K., Belkin, R., Sternberg, M. & Jeltsch, F. (2006) Life history variation of an annual plant under two opposing selective forces along a steep climatic gradient. *Ecography*, **29**, 66–74.

Pluess, A.R., Schütz, W. & Stöcklin, J. (2005) Seed weight increases with altitude in the Swiss Alps between related species but not among populations of individual species. *Oecologia*, **144**, 55–61.

Rees, M. & Venable, D.L. (2007) Why do big plants make big seeds? *Journal of Ecology*, **95**, 926–936.

SAS Institute (2002) *JMP 5.0.1*. SAS Institute, Cary, NC.

Saverimuttu, T. & Westoby, M. (1996) Seedling longevity under deep shade in relation to seed size. *Journal of Ecology*, **84**, 681–689.

Schiffers, K. & Tielbörger, K. (2006) Ontogenetic shifts in interactions among annual plants. *Journal of Ecology*, **94**, 336–341.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd edn. W.H. Freeman and Company, New York, USA.

Sternberg, M., Gutman, M., Perevolotsky, A. & Kigel, J. (2003) Effects of grazing on soil seed bank dynamics: an approach with functional groups. *Journal of Vegetation Science*, **14**, 375–386.

Suttle, K.B., Thomsen, M.A. & Power, M.E. (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640–642.

Tevis, L.J. (1958) Variation and adaptive role of seed dormancy in some annual grassland species. *Ecology*, **39**, 688–695.

Thompson, K., Bakker, J.P., Bekker, R.M. & Hodgson, J.G. (1998) Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology*, **86**, 163–169.

Traba, J., Azcarate, F.M. & Peco, B. (2006) The fate of seeds in Mediterranean soil seed banks in relation to their traits. *Journal of Vegetation Science*, **17**, 5–10.

Turnbull, L.A., Rees, M. & Crawley, M.J. (1999) Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology*, **87**, 899–912.

Valleriani, A. (2005) Algebraic determination of the evolutionary stable germination fraction. *Theoretical Population Biology*, **68**, 197–203.

Venable, D.L. (2007) Bet-hedging in a guild of desert annuals. *Ecology*, **88**, 1086–1090.

Venable, D.L. & Brown, J.S. (1988) The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *The American Naturalist*, **131**, 360–384.

Venable, D.L. & Rees, M. (2009) The scaling of seed size. *Journal of Ecology*, **97**, 27–31.

Verkaar, H.J. & Schenkeveld, A.J. (1984) On the ecology of short-lived forbs in chalk grasslands: life-history characteristics. *New Phytologist*, **98**, 659–672.

Voigt, W., Perner, J. & Jones, H.T. (2007) Using functional groups to investigate community response to environmental changes: two grassland case studies. *Global Change Biology*, **13**, 1710–1721.

Walters, M.B. & Reich, P.B. (2000) Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology*, **81**, 1887–1901.

Xia, J. & Wan, S. (2008) Global response patterns of terrestrial plant species to nitrogen addition. *New Phytologist*, **179**, 428–439.

Young, J.A., Evans, R.A., Raguse, C.A. & Larson, J.R. (1981) Germinable seeds and periodicity of germination in annual grasslands. *Hilgardia*, **49**, 1–37.

Zavaleta, E.S., Shaw, R.M., Chiariello, N.R., Thomas, B.D., Cleland, E.E., Field, C.B. & Mooney, H.A. (2003) Grassland responses to three years of elevated temperature, CO_2, precipitation, and N deposition. *Ecological Monographs*, **73**, 585–604.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of annual plant species used in the analyses, their seed mass and occurrence at the study sites (s-a, semi-arid; med., Mediterranean; m-m, mesic-Mediterranean)

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.