
What do seedlings die from and what are the implications for evolution of seed size?

Angela T. Moles and Mark Westoby, Dept of Biological Sciences, Macquarie Univ., NSW 2109, Australia (amoles@bio.mq.edu.au).

Plants face a fundamental trade-off between producing many small seeds, each with a low probability of successfully establishing as a seedling and producing fewer, better provisioned seeds with higher establishment probabilities (reviewed in Leishman et al. 2000, Westoby et al. 2002). In the absence of frequency-dependent interactions between seedlings, this trade-off is predicted to result in a single optimum seed mass in a given environment (Smith and Fretwell 1974). However, plant communities usually contain species whose seed sizes span 5–7 orders of magnitude (Leishman et al. 2000).

Theory to explain the wide range of seed mass strategies coexisting in plant communities invokes frequency-dependent processes. Consider, for example, the game-theoretical seed-size/number trade-off model (developed by Geritz 1995 and extended to track population and evolutionary dynamics by Rees and Westoby 1997). Under this model, a large-seeded strategy can be invaded by a small-seeded strategy because small-seeded strategies have greater seed output and therefore reach a proportion of living-sites that are not reached by larger-seeded strategies. However, small-seeded strategies can be invaded by large-seeded strategies because seedlings from large seeds are able to outcompete the relatively poorly-provisioned seedlings produced by small seeds. Thus neither strategy excludes the other and a range of strategies can co-exist.

Two assumptions of this model are 1) that small seeded species produce more seeds from a given ground area occupied and in this sense are better colonisers than large-seeded species and 2) that large-seeded species win sites through superior competitive ability. There is strong evidence for the first: small-seeded species do produce more seeds for a given amount of effort (Greene and Johnson 1994, Jakobsson and Eriksson 2000, Aarssen and Jordan 2001, Henery and Westoby 2001). This higher fecundity should give small-seeded species a greater number of colonising opportunities (empirically

demonstrated in some, but not all situations; evidence reviewed in Leishman 2001). Evidence for the second assumption is not as strong. A positive relationship has often been found between seed size and competitive ability across species (Eriksson 1997, Turnbull et al. 1999, Leishman 2001). However, there is debate as to whether the competitive hierarchies observed are strong enough to maintain a range of coexisting strategies (Coomes and Grubb 2003). Further, as Leishman (2001) pointed out, competition between seedlings might not be important in deciding species composition in most real vegetation.

Almost all studies of seedling–seedling competition have been performed at artificially high densities achieved through seed supplementation or seedling planting. Our field observations have led us to suspect that natural populations of seedlings seldom occur at high enough densities for seedling–seedling competition to be a major cause of seedling mortality. Evidence that seedling survival is dependent on competition under natural conditions and at natural densities is sparse. Silvertown and Bullock (2003) reported both frequency- and density-dependent mortality among seedlings establishing in experimentally created gaps in calcareous grassland in Oxfordshire, England and concluded that the evidence supported the assumptions of the seed-size/number trade-off model. Coomes et al. (2002) studied spatial patterning among annuals establishing on sand dunes in Britain. They found negative associations between two large-seeded species and smaller-seeded species at a small spatial scale (interpreted as evidence for local exclusion of small-seeded species by large-seeded species), but only in one year out of the three studied, when seedling densities were particularly high. These authors concluded that the frequency of competitive interactions between species was low enough that competition was unlikely to be a major determinant of community structure. Moles and Westoby (in press)

found that drought and herbivory were the major causes of seedling mortality in sclerophyll vegetation in Sydney, with seedling–seedling competition affecting only one of the 29 species studied. Like Coomes et al. (2002), these authors suggested that most seedlings were too widely spaced for competitive interactions to be a major selective force. The results of each of these studies can only be interpreted as site-specific. Thus, the major aim of the present study was to compile available evidence across a range of different ecosystems to quantify the generality and relative importance of seedling–seedling competition as a determinant of seedling mortality. A secondary aim was to quantify the density of seedlings emerging in natural environments, in order to assess the likelihood of direct interactions between seedlings.

Causes of seedling mortality

Data were compiled through a search of BIOSIS and current contents for any papers in English containing the words “seedling survival” and “germination” published between 1969 and week 38 of 2002. We aimed to compile information on populations of seedlings establishing under ‘natural’ conditions. Therefore, studies in habitats recently subjected to major unnatural disturbances (such as mines, pastures in recently cleared tropical rainforests and cropping systems), highly successional environments (e.g. sites recently affected by landslides, hurricanes or volcanism and glacier forelands), or sites undergoing rapid changes in species composition (such as grasslands being colonised by woody species and areas experiencing biological invasion); studies using seed supplementation (addition of any seed to the system) or seedling transplants and studies that artificially reduced plant mortality (e.g. with herbicides, fencing or supplementary watering) were all excluded. Control treatments of experiments were included if they fit the other criteria. Studies were only included if they began following seedlings from the time they first emerged from the soil. A minimum sample size was also required: species were excluded if the cause of mortality was known for less than 20 individuals, or if the total number of seedlings studied was less than 50. This left 20 species for which cause of death had been quantified under ‘natural’ conditions (Table 1).

Across all species, herbivory (38%), drought (35%) and fungal attack (20%) were the most frequently recorded causes of mortality (Table 1). Physical damage (4.6%) and competition with established vegetation (1.3%) killed only a small proportion of the seedlings. Interestingly, seedling–seedling competition was responsible for only 1.6% of known seedling deaths, all of which occurred in one species.

As eight of the 20 species were from one study, we also investigated the cross-study average mortalities. The

cross-study means were slightly different to the cross-species means (Table 1), with a higher proportion of species dying as a result of drought and fungal attack and a lower proportion of seedlings recorded as being killed by herbivores. However, seedling–seedling competition represented a very minor component of seedling mortality, whether taken cross-species (1.6%) or cross-study (0.5%).

Are natural seedling densities high enough for competition to be important?

The advantages of large-seededness are transient (evidence compiled in Westoby et al. 2002). Therefore, in order for seed mass to be correlated with the expected outcome of seedling–seedling competition, seedlings would have to reach a size where they were encountering and competing with, other seedlings early enough that the large-seeded species were still advantaged by their greater maternal resources. Moreover, neighbours would need to be present on two to three sides, else the seedling would simply lean away (or grow roots into areas free from neighbours).

In order to assess the likelihood of this circumstance, we compiled data on the number of seedlings emerging per square metre. We searched BIOSIS for papers that contained the term “seedling emergence” and were published in English between 1969 and 2002. As in the previous search, we aimed to compile data for populations of seedlings establishing under natural conditions, using the exclusion criteria described above. Because seedling densities change rapidly with post-emergence mortality, we excluded studies in which seedling emergence was monitored less frequently than fortnightly. Only seven studies fulfilled all these criteria and provided estimates of the total density of emerging seedlings (Table 2). However, these studies spanned a range of vegetation types, on a number of continents.

Seedling densities ranged from 2084 to less than four seedlings m^{-2} . If these seedlings were randomly distributed, each would have between five and 2590 cm^2 in which to establish (mean distances between nearest-neighbour seedlings of 1.1 and 25.4 cm respectively; Cottam and Curtis 1956). Thus, seedling–seedling competition is plausible only at the highest end of the range of observed densities. Furthermore, it is possible that seedlings avoid canopy overlap even at the highest observed density. An exact calculation of the amount of space required per seedling cannot be made without data on seedling size and the amount of clustering in their spatial distribution. However, large seeds tend to produce large seedlings (Ganade and Westoby 1998), so high densities of seedlings are likely to be correlated with small seedling sizes. A study of 50 Australian species showed that seedling “canopy areas” of species with

Table 1. Percentages of attributable deaths due to each of major mortality agents in studies of seedling establishment (details of selection criteria in text). Nine further studies gave a qualitative estimate of the dominant cause of mortality (competition with established vegetation (1), drought (6) and herbivory(2)).

| Species | Cause of death | | | | | | | Timespan | Location | Vegetation type | Reference |
|--|--------------------------------------|-------------------------------------|--------------------|------------------|---------------------------------------|---------|-------------------|--------------------|-------------------|---------------------------------------|---|
| | seedling- seedling competition | shading from adult vegetation | physical damage | fungal attack | herbivory (incl. below- ground) | drought | unknown/ other | | | | |
| <i>Pistacia lentiscus</i> | | | | | | 63.8 | 36.2 | 1 growth season | Spain | sclerophyllous shrublands | Garcia-Fayos and Verdu 1998 |
| <i>Phillyrea latifolia</i> | | | 2.8 | 1.0 | 2.8 | 64.0 | 29.3 | 1 year | Spain | mediterranean-type montane forest | Herrera et al. 1994 |
| <i>Pinus banksiana</i> | | | | 26.4 | 59.6 | 6.9 | 7.0 | 2 years | Minnesota, USA | needle-leaved evergreen forest | LeBarron 1944 |
| <i>Picea mariana</i> | | | 3.4 | 17.3 | 59.7 | 4.1 | 15.2 | 2 years | Minnesota, USA | needle-leaved evergreen forest | LeBarron 1944 |
| <i>Alnus glutinosa</i> | | | | | 22.0 | 26.0 | 52.0 | 1 growth season | England | temperate wetlands (fens) | McVean 1956 |
| <i>Symphoricarpos occidentalis</i> | | | | 18.9 | 32.8 | 29.9 | 18.4 | 1 growth season | Minnesota, USA | shrubs in grazed pasture | Pelton 1953 |
| <i>Olea europea</i> | | | | 5.8 | 10.0 | 70.0 | 14.2 | 1 year | Spain | Mediterranean scrubland | Rey and Alcantara 2000 |
| <i>Acer mono</i> | | 4.3 | 32.2 | 31.5 | | | 31.9 | 1 growth season | Japan | temperate deciduous forest | Seiwa 1998 |
| <i>Viola lanceolata</i> | | | | | 10.0 | 74.0 | 16.0 | 1 year | USA | temperate old fields | Solbrig et al. 1988 |
| <i>Banksia</i> spp. | | | 7.7 | 3.8 | 61.5 | 7.7 | 19.2 | 1 year | Australia | sclerophyll woodland | Moles and Westoby in press |
| <i>Acacia</i> spp. | | | | | 46.3 | 4.9 | 48.8 | 1 year | Australia | sclerophyll woodland | Moles and Westoby in press |
| <i>Viminaria juncea</i> | | | 5.8 | 3.8 | 7.7 | 23.1 | 59.6 | 1 year | Australia | sclerophyll woodland | Moles and Westoby in press |
| <i>Aotus ericoides</i> | | 9.5 | 4.8 | 3.2 | 4.8 | 22.2 | 55.6 | 1 year | Australia | sclerophyll woodland | Moles and Westoby in press |
| <i>Phyllota grandiflora</i> | | | 8.1 | 6.5 | 6.5 | 25.8 | 53.2 | 1 year | Australia | sclerophyll woodland | Moles and Westoby in press |
| <i>Gonocarpus teucrioides</i> | | 7.4 | 7.4 | 3.7 | 14.8 | 9.9 | 56.8 | 1 year | Australia | sclerophyll woodland | Moles and Westoby in press |
| <i>Allocasuarina distyla</i> | | | 8.3 | 1.7 | 23.3 | 30.0 | 36.7 | 1 year | Australia | sclerophyll woodland | Moles and Westoby in press |
| <i>Hibbertia riparia</i> s.l. | 20.8 | | | | 78.7 | 0.6 | | 1 year | Australia | sclerophyll woodland | Moles and Westoby in press |
| <i>Platypodium elegans</i> | | | | 86.8 | | | 13.2 | 3 months | BCI, Panama | semi-deciduous tropical rainforest | Augspurger 1983 |
| <i>Tachigalia versicolor</i> | | | 8.4 | 28.1 | 32.0 | | 31.6 | 2 months | BCI, Panama | semi-deciduous tropical rainforest | Kitajima and Augspurger 1989, Kitajima 1992 |

Table 1 (Continued)

| Species | Cause of death | | | | | Timespan | Location | Vegetation type | Reference |
|---------------------------|--------------------------------------|-------------------------------------|--------------------|------------------|---------------------------------------|----------|------------|------------------------------|-------------------------|
| | seedling- seedling competition | shading from adult vegetation | physical damage | fungal attack | herbivory (incl. below- ground) | | | | |
| <i>Ocotea endrestiana</i> | | | | 25.6 | | 74.4 | Costa Rica | lower montane rain forest | Wenny and Levey 1998 |
| Cross-species average | 1.6 | 1.3 | 4.6 | 19.9 | 37.9 | 34.8 | | | |
| Cross-study average | 0.53 | 0.17 | 3.33 | 27.9 | 29.5 | 38.5 | | | |

seeds weighing < 10 mg were generally < 1 cm² after 7 days growth (Ganade and Westoby 1998), while the median seed mass in temperate communities is generally around 1 mg (Westoby et al. 2002). Thus the available data suggests that seedlings are much smaller than the amount of space available per seedling, even at 2084 seedlings m⁻². Furthermore, mortality during the first few weeks is often high, so increases in seedling size might be largely offset by reductions in seedling density. These data, though inconclusive, are consistent with field observations of widely spaced-seedlings in natural environments (Coomes et al. 2002, Moles and Westoby in press). It therefore seems likely that the low reporting of seedling-seedling competition as a source of mortality (Table 1) results from natural densities of seedlings being low enough that direct interactions between seedlings are rare.

The self-thinning literature provides ample evidence for the operation of density-dependent population regulation in plants (Yoda et al. 1963, Weller 1987). However, even if these interactions were between individuals of different species, they would only be predicted to lead to coexistence of different seed mass strategies if they occurred while seed mass still affected the outcome (Geritz 1995, Rees and Westoby 1997). Our data suggest that direct interactions between seedlings growing under natural conditions are rare during the first few months of growth. This finding, combined with the temporary nature of the advantage of large-seededness suggests the seed size number trade-off hypothesis is not a major determinant of community composition.

Competition with established vegetation was recorded as the cause of mortality for less than 2% of seedlings in this study. However, established vegetation often significantly reduces seedling recruitment in seed addition experiments (Gross and Werner 1982, Jakobsson and Eriksson 2000, Turnbull et al. 2000, Silvertown and Bullock 2003). The apparent difference in results might be partially due to the fact that the present study measured seedling mortality, while seed addition experiments usually measure recruitment. This distinction would be important in cases where germination is inhibited by the presence of established plants (Gross 1980, Gross and Werner 1982). In this case, fewer seedlings would germinate in situations where competition with established plants was likely to be a cause of mortality and the presence of established vegetation would decrease recruitment without directly affecting seedling mortality. However, the disparity between our results and experimental results might arise partly from under-reporting of deaths due to competition with established vegetation.

Establishing the cause of death of seedlings in the field is difficult. Seedlings can simply vanish, leaving no clue as to their cause of death and in many cases seedlings die as a result of accumulated stress from several factors (for

Table 2. The number of seedlings emerging m^{-2} in relatively natural vegetation (see text for details).

| Loaction | Reference | Vegetation | Seedlings m^{-2} |
|--------------|-----------------------------|-------------------------------|---------------------------|
| California | Moreno and Oechel 1991 | chaparral | 237.4 |
| Panama (BCI) | Dalling and Hubbell 2002 | tropical moist forest | 113.6 |
| Japan | Masuda and Washitani 1990 | floodplain primrose community | 2084 |
| Spain | Garcia-Fayos et al. 2000 | semi-arid badland slopes | 67.6 |
| Japan | Kobayashi and Kamitani 2000 | temperate deciduous forest | 3.86 |
| Europe | Piroznikow 1998 | temperate deciduous forest | 110.2 |
| New Jersey | Leck and Simpson 1994 | tidal marshes | 1101 |

example, most of the seedlings succumbing to fungal pathogens in the wet tropics are growing in extremely low-light understorey environments). Under-reporting of mortality due to competition with established vegetation might arise because this competition does not leave its victims marked in the same way as herbivory, drought or fungal attack. Further, because established vegetation can be ubiquitous in undisturbed environments, experimenters are less likely to attribute it as a source of mortality for particular individuals.

We cannot exclude the possibility that seedling–seedling competition was under-reported in the literature compiled here. However, competition with seedlings seems less likely to be underestimated than competition with adult vegetation, because individual seedlings can be clearly distinguished as having close neighboring seedlings or not. Further, the fact that very few authors even mentioned seedling–seedling competition when discussing causes of seedling mortality, together with its numerical insignificance in this compilation (Table 1) and the evidence that seedlings in natural systems seldom grow densely enough for direct interactions to be prevalent (Table 2) strongly suggest that seedling–seedling competition is not a major force in seedling ecology.

We do not argue that seedling–seedling competition is never an important cause of mortality. There are well-documented cases of seedling–seedling competition in particular situations (e.g. in mast populations of *Acer saccharum*; Taylor and Aarssen 1989). However, the present compilation provides quantitative evidence that seedling–seedling competition kills far fewer seedlings than do processes such as herbivory, drought and fungal attack. Furthermore, even the few situations in which seedling–seedling competition is a major source of mortality most often involve within-species competition. For example, mast-seeding events often produce dense, single-species swards of seedlings, such as those observed in *Eucalyptus regnans* forest in Victoria, Australia (Ashton 1976) and in *Nothofagus* forest in New Zealand (Wardle 1991). In addition, all of the seedlings in Table 1 recorded as victims of seedling–seedling competition died as a result of intraspecific competition Moles and Westoby (in press). The distinction between within-species and between-species competition is important,

as the seed-size/number trade-off hypothesis predicts coexistence of species with a wide range of seed masses only if competition is between seedlings of different species.

Conclusion

The literature compiled here indicates that drought, herbivory and pathogen attack are the major causes of mortality in natural seedling populations, with competition from other seedlings accounting for a relatively small proportion of seedling deaths. These results have implications for game-theoretical models for seed size. We know that seedlings from larger seeds have higher survivorship under many hazards, including drought, defoliation and prolonged periods in deep shade (reviewed by Leishman et al. 2000). However, drought, herbivory by generalists and shading are not likely to operate in a frequency-dependent manner. Attack by specialist herbivores or pathogens might be somewhat density-dependent (Augsburger 1983, Clark and Clark 1985, Augspurger and Kitajima 1992), but these processes account for a relatively small proportion of seedling mortality in the present compilation. An initial period of frequency-independent mortality has been built in to recent versions of the seed-size/number trade-off hypothesis (Geritz et al. 1999). Nevertheless, the model requires frequency-dependent mortality to come into effect while a species' seed mass still influences the outcome of competition. The dominance of frequency-independent mortality in the first season of growth (Table 1) suggests that the seed-size/number trade-off hypothesis is not a convincing explanation for the wide range of seed mass observed in most vegetation types.

Acknowledgements – Supported by an Australian Postgraduate Award to Moles and by Australian Research Council funding to Westoby. Thanks to Daniel Falster for helpful discussion of results and to Michelle Leishman, Peter Vesk and Alison Basden for comments on earlier drafts of the manuscript. Contribution No. 397 from the Research Unit for Biodiversity and Bioresources, Macquarie University.

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