

Colonization, tolerance, competition and seed-size variation within functional groups

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Ecologists interested in seed size have generally contrasted functional groups of plants but, recently, some have focussed on explaining the large range of seed size found within a functional group. A potentially important theoretical advance was the idea that seed number–seedling survival tradeoffs could explain the coexistence of species, in particular colonization–competition tradeoffs where smaller-seeded species are superior colonizers and larger-seeded species are superior competitors. However, recent models have placed limits on the potential of this approach, chiefly by showing that the asymmetry of competition must be strong. Also, although there is evidence from studies within functional groups that seed size does trade off against number of seeds and dispersal of those seeds, and that seed size is correlated with competitive ability among seedlings and tolerance of hazards during establishment, the available evidence suggests that SNSS tradeoffs do not make possible long-term coexistence without other forms of niche differentiation.

Ever since E.J. Salisbury published his seminal work of 1942 [1], the significance of seed size has fascinated ecologists [2–4]. Most ecologists have contrasted functional groups, such as shade-tolerators and light-demanders or bird- and mammal-dispersed species, but some ecologists have begun to focus on explaining the range of seed size found within functional groups, such as particular groups of annuals, or of rainforest trees [5–13]. The range of mean seed size among species within a functional group is commonly much greater than the difference between the means of contrasted groups. For example, in tropical lowland rainforests, the mean seed dry mass of shade-tolerant tree species is 10–100 times greater than that of light-demanding tree species [14], whilst the smallest and largest mean values within both these groups differ by 10^5 – 10^6 .

At the most basic level, seed mass is considered to be pivotal to the fitness of a plant because of its influence on two key components of life history [4]. First, the seed mass of a plant is negatively correlated with the number of seeds that it can produce. Consequently, smaller-seeded species are considered to be superior colonizers. Second, seed mass is positively associated with seedling survival, because

larger seeds generally develop into larger seedlings, which are potentially better able to withstand either lack of resources (light or nutrients) or the various hazards that face them (dry spells, partial damage, etc). Therefore, smaller- and larger-seeded species differ in their life-history strategies as a result of a seed number versus seedling survival tradeoff.

A simple mathematical model that incorporates the seed number–seedling survival SNSS tradeoffs predicts that, under the forces of natural selection, a single seed size should evolve in a given habitat. However, when appropriate biological details are included in mathematical models, they start to reproduce something of the patterns observed in real communities. Specifically, the performance of a seedling is not simply correlated with seed size, but varies in response to environmental heterogeneity, the effects of established vegetation, and competition with surrounding seedlings. Also, the ability of a species to reach suitable regeneration sites does not depend only on how many seeds it produces, but also on how well the seeds are dispersed. We start by considering these issues in turn, seeing how their inclusion influences the predictions of models, and illustrating our major points with recently published examples. Then we consider for a few contrasted functional groups, whether the available evidence supports the idea that SNSS tradeoffs occur, and whether they maintain coexistence of species.

Seedling responses to environmental heterogeneity

The strongest case for an advantage of greater seedling size is the tolerance of hazards faced by young seedlings, reviewed most recently by Leishman *et al.* [4]. Large seeds usually produce large seedlings, which produce deeper roots and are more likely to survive dry spells; they are also likely to be better anchored in the face of frost-heaving or disturbance by animals. They have a better chance of pushing down through or up through a layer of litter and of surviving partial destruction by herbivores or falling plant parts. The greater tolerance of larger-seeded species would not be enough to promote coexistence in homogeneous environments (Box 1). However, in spatially and temporally varying environments, mixtures of species can persist provided that each species is fittest under some circumstances, and each species can disperse propagules to sites where conditions are optimal (Box 1).

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Box 1. Tradeoff between seedling survival and seed number

Simple reasoning suggests that a single seed size should evolve under natural selection in a given habitat. The Smith and Fretwell (SF) model proposed that two opposing selective forces act on seed size [61]. Assuming that plants do not vary the amount of resources available for reproduction (R), then a larger-seeded plant will produce fewer seeds than will a smaller-seeded plant (Fig. 1a). However, the larger seedlings produced by larger-seeded plants will stand a greater chance of surviving the hazards associated with establishment (Fig. 1b).

Assuming that per capita seed production is given by $N = R/m$, where m is seed mass, and probability of survival to reproductive maturity is a smooth convex function $f(m)$, then a mother's fitness is given by (Eqn I):

$$W = f(m)R/m$$
 [I]

The model predicts a single peak in fitness, and therefore a globally optimal seed size (Fig. II) [61].

The SF model amalgamates many components of life history. For example, seed size is likely to have its greatest influence during establishment, but have a much weaker influence on plant performance after establishment.

Chesson and co-workers [62] have shown that temporal variation can promote coexistence when species differ in their responses to that variation, provided that: (i) species have a long-lived phase of their life cycles, enabling them to persist in years when conditions are unsuitable for their regeneration; (ii) species respond differently to environmental variation, so that the years in which one species can undergo strong population growth are not entirely synchronous with the years when another species responds strongly; and (iii) species exert strong competition effects, and show strong resistance to competition, in years in which they are abundant and when conditions are favourable for them. When all these attributes are in place, species tend to have positive growth rates when rare, promoting coexistence within the community.

Pake and Venable [32] showed the importance of temporal variation in promoting coexistence of annual plant species in the Sonoran Desert (Arizona). The smaller-seeded species in Table I (*Schismus*) produces

many seeds, each of which has a poor chance of surviving to adulthood, and would rise to dominance under homogenous conditions. However, because rainfall is highly erratic in semi-deserts, the reproductive success (average seed set of germinated seed) of species varies tremendously between years. Pake and Venable [32] showed that its fitness varies with environmental conditions, changing with year, sowing density and water supply (Table I). The variation is not entirely synchronous among the species, which have different approaches to minimizing among-year variation in their fitness [33]. All have seed banks, but reproductive success is more variable in smaller-seeded species, and it seems that they compensate for this by increasing the proportion of seed retained in the seed bank (i.e. have lower proportional germination; Fig. III). These species seem to meet the conditions set out by Chesson.

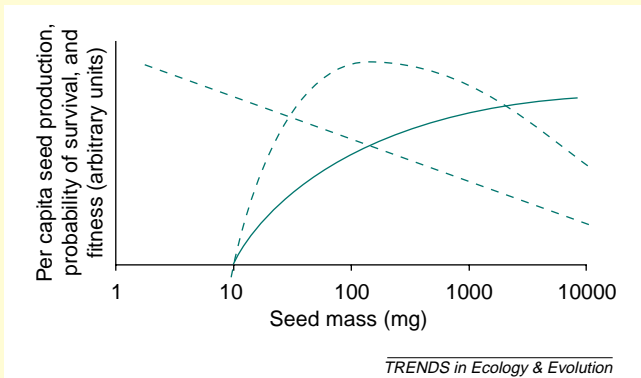


Fig. II. Fitness (dashed line) is the product of per-capita seed production (dotted line) and the probability of survival from seed to maturity (unbroken line); the peak in fitness suggests that a single seed size would evolve under natural selection.

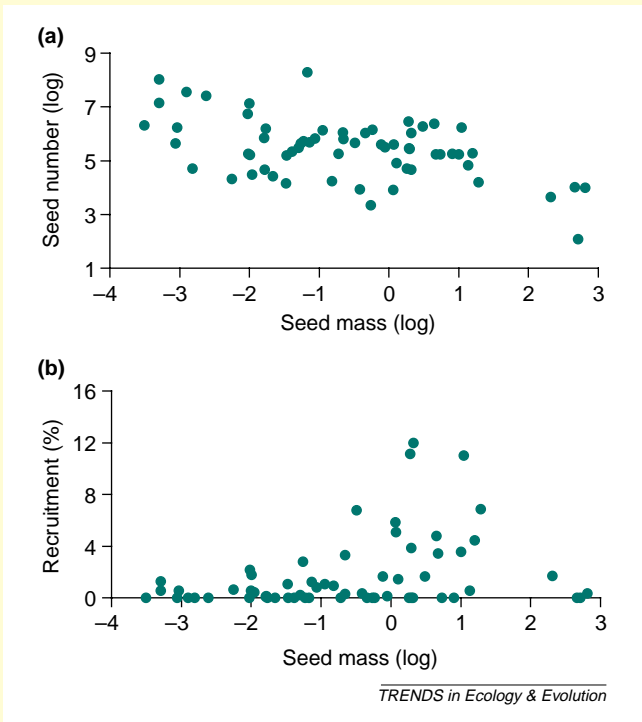


Fig. I. Correlations between seed size and life history components. (a) Strong inverse relationship between seed dry mass and number produced per individual for 62 non-gap-demanding species of semi-natural temperate mesic grassland widespread in north-western Europe, (b) weak positive relationship between seed mass and recruitment probability of a subset of the species (38) sown into established grassland. Data from [29].

Table I. Contrasting properties of two annual species from the Sonoran semi-desert in an experiment run over two years

	<i>Pectocarya</i>	<i>Schismus</i>
Seed mass (mg)	0.95	0.08
Per capita seed output ^a	28	240
Seeds required to make each reproductive adult	18	61
Standard deviation of reproductive success	1.34	1.71
Conditions under which species is fittest (after removing the effects of seed size)	At low seedling density in 1st and 2nd years	At high seedling density in 1st year

^aEstimated by back-transformation.

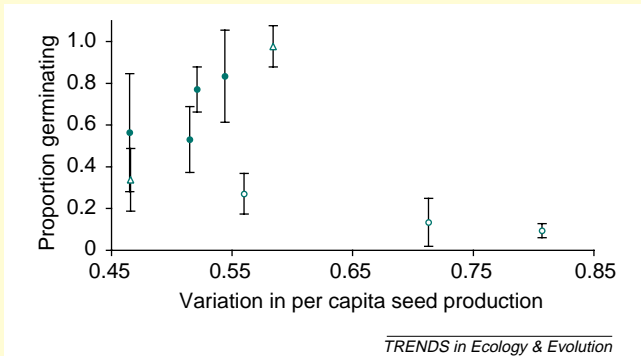


Fig. III. Small-seeded species of annual plants have greater between-year variation in reproductive success, and a lower proportion of the seed bank germinating each year (filled circles, large-seeded species; open triangles, medium-seeded; open circles, small-seeded); Data from [32,33].

Seedling survival under established plants that deplete resources to low levels

For species that become established in continuous grassland swards or in forest understories, tolerance of resource depletion by adult plants is vital. Tilman [15] argued that species that can tolerate the effects of competition as seedlings go on to exert strong competitive effects. Tilman's spatially explicit colonization–competition (CC) model [16] predicts a succession in which such 'superior competitors' rise to dominance (when disturbance rates are low and affect all species similarly), but constant disturbance means they never occupy all patches, and therefore superior colonizers persist indefinitely. Models based on competition with established vegetation makes quite different predictions than do those based on competition among seedlings in gaps (Box 2).

Much empirical work has focused on comparing the traits of early- and late-successional species [17]. The general view is that early-successional species have traits associated with the fast growth of individuals and populations, whereas late-successional species have traits associated with slower growth and depletion of resources to lower levels [17]. Among the traits considered in empirical studies is seed size. Salisbury [1] concluded that shade-tolerant species tend to be larger-seeded than are light-demanding species. Although the comparisons that he made were inappropriate [18], more recent studies have confirmed his conclusion for forest plants [7,14,19,20]. However, the association is loose. Many tiny-seeded

rainforest species can establish and persist in deep shade [14]. Ultimately what matters in shade tolerance is the balance of gas exchange and an ability to maintain defences against microorganisms and herbivores when starved of light. Seed reserves can supply a seedling for only weeks or months, at most a year [21], but, in forests, seedlings might have to survive deep shade for decades. As to the effect of depletion of soil nutrients through root competition, laboratory experiments with young seedlings have shown that smaller-seeded species can be more responsive to nutrient supply [22], but, in the field, they are more quickly dependent on mycorrhiza [23] and might not be more sensitive to nutrient supply. The chief benefit of larger-seededness to later-successional species seems to be in the tolerance of hazards.

Seedlings competing with neighbouring seedlings

Ecological and evolutionary models produce stable mixtures of seed-size strategies, even in homogeneous environments, when larger-seeded species are better competitors and smaller-seeded species are better colonizers, but only when competition is highly asymmetric (i.e. the advantage of larger-seeded species is very strong) (Box 3). The functional groups that are most likely to show competition among seedlings are annual plants that routinely become established on open ground, and the species with varying life spans that routinely become established in large gaps in grassland, scrub or forest. The outcome of competition among seedlings depends on the local pool of species competing for resources, which in turn depends on the relative frequency of species in the community (Box 3). Several different traits can be important in determining success in competition among seedlings (e.g. time of germination and plant morphology), but seed size has been shown to be pre-eminent in several glasshouse experiments.

'Colonizing ability' and 'local dispersal'

When considering 'colonizing ability', it is important to distinguish between the number of seeds a plant produces and how far those seeds are dispersed, as both traits may contribute towards the chances of a seed reaching an establishment sites (Box 4). Several models in the past decade have explored the implications for coexistence of 'local dispersal' (i.e. dispersal of seeds for only short distances from the parent) [24]. These models have utilized advances in computer simulations and mathematical techniques that provide summaries of complex systems (Box 4). Spatially explicit models agree broadly on the consequence of local dispersal for competition between species. Because it leads to spatial aggregation of each species, the extent of interspecific competition is reduced, and the requirement that inferior competitors be superior colonizers to persist can be relaxed.

The biological significance of weak correlations

Theoretical models are often based on deterministic relationships, involving tradeoffs that produce consistent hierarchies of species. In the case of the CC mechanism, the number of species that are enabled to coexist diminishes severely when the tradeoffs are not consistent. That is

Box 2. Tolerance of established vegetation

In most natural and semi-natural communities, seedlings have to contend with the competition imposed on them by established plants. Yet theoretical models rarely distinguish the competitive effects of one seedling on another from the effects of established vegetation. For example, Tilman's colonization–competition (CC) model [16] assumes that the competitive ability of species is hierarchical, and that superior competitors instantly win all patches in which their seeds land, irrespective of whether the patches are already occupied by an inferior competitor. They are prevented from conquering all patches because they produce too few seeds to reach all sites, enabling superior colonizers to remain in the system, and even flourish when mortality rates are high. Unlimited numbers of species can coexist by the mechanism originally described, but fewer species may coexist when the competitive hierarchy is imperfect, or when the habitat is limited in size [63]. The assumption of instantaneous replacement is hardly realistic. Theoretical studies show that if the displacement of inferior competitors is delayed, they have time to produce and disperse seeds into surrounding patches (a temporal refuge) [24,64]. The need for inferior competitors to have superior colonizing abilities diminishes as the time taken to displace them increases, because they produce enough seeds to ensure they reach a large number of suitable patches.

In gap-phase models, seedlings compete with one another to win gaps that are being created continuously by the death of adult plants. The most basic gap models, with complete mixing of propagules and homogeneous environmental conditions, have much in common with the CC models described in Box 3, except that only some of the sites are available for colonization. Larger- and smaller-seeded species can coexist when competition is entirely asymmetric, but not when the advantages of larger-seeded species are less strongly asymmetric. Otherwise, species can coexist in heterogeneous environments if they have the attributes set out in Box 1.

Box 3. The importance of seed size for competition among seedlings

The $f(m)$ term in the Smith and Fretwell (SF) model in Box 1 is an amalgamation of the many influences on an offspring performance, starting from the moment of germination and continuing until sexual maturity. One such influence is competition with neighbouring seedlings, the outcome of which depends upon their local density and identity. Consider a seedling that germinated from a seed of mass m_i competing for resources against N_j seedlings that germinated from seeds of mass m_j , and so forth for all competitors present. The effect of competition is given by (Eqn I):

$$C(m_i, m) = \left(1 + \sum_j N_j (m_j/m_i)^s \right)^{-1} \quad \text{[I]}$$

which is introduced into the SF model to give (Eqn II):

$$W(m) = f(m) C(m_i, m) R/m \quad \text{[II]}$$

The competitive advantage of having large seeds is defined by the $(m_j/m_i)^s$ term. Large-seeded species have no advantage when $s = 0$ (symmetric competition), but have a huge advantage when s is large (i.e. competition is strongly asymmetric). Using different approaches, both Geritz and colleagues [5,9] and Rees and Westoby [8] found that introducing seedling–seedling competition into the SF models leads to the evolution of a stable mixture of seed size lineages when competition is highly asymmetric (Fig. 1). Larger-seeded lineages consistently win sites by outcompeting smaller-seeded lineages, whereas the smaller-seeded produce more seeds and thereby get to some vacant sites that the larger-seeded fail to reach. However, a single seed size evolves when seedling–seedling competition is symmetric, because the model becomes equivalent to the SF model [8]. A few discrete seed size clusters evolve at intermediate symmetry levels [9].

Ecologists have worked on models that make predictions similar to those from the evolutionary models, and can be unified into a common theory. For example, the ecological model of Levine and Rees [13] shows that large-seeded species of annual plants can coexist with smaller-seeded species only when competition is extremely asymmetric. Two recent experiments cast doubt on whether larger-seeded species have enough of a competitive advantage to promote

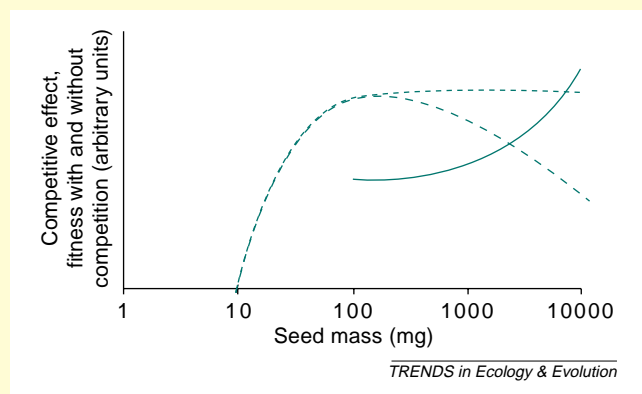


Fig. 1. Strong asymmetric competition leads to seed-size polymorphism, when seed size is correlated with competitive ability. The competition function shown (continuous line) is that occurring at evolutionary equilibrium. Fitness in the absence of competition is shown by the dotted line, and fitness with competition in the presence of competition by the dashed line.

coexistence by this mechanism. Freckleton and Watkinson [65] quantified competitive asymmetry by reanalyzing data from a previous experiment [66] (Fig. 1(a)). Competition was asymmetric ($s = 0.62$), but the degree of asymmetry would not be sufficient to allow annual plants to coexist in simulations [65]. Leishman [10] sowed mixtures of chalk grassland species into trays. Increasing the proportion of medium- or large-seeded species in the sowing mixtures caused significant reductions in the survival of small-seeded species, providing some evidence of asymmetric competition [Fig. 1(b)]. However, the degree of asymmetry was weak.

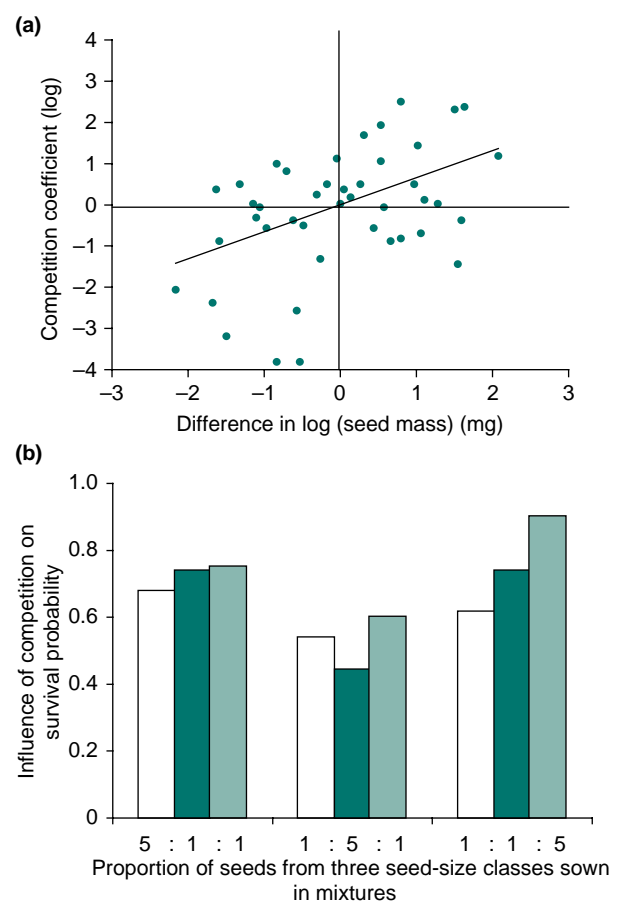


Fig. 2. Quantification of competitive asymmetry: (a) species with differing seed mass were pitted against each other, and competitive coefficients calculated by the reduction in harvested biomass caused by competition (from [65], based on results from [66]), (b) survival of small-seeded species (white bars), medium-seeded (dark-green bars), and large-seeded (light-green bars) grown for nine weeks in mixtures containing different proportions of the three seed sizes (results of Leishman [10]; the survival probabilities are indexed against those observed in a low-density 1:1:1 mixture, in which it is assumed that competition was weak).

important because empirical studies show that associations between seed size and other life-history traits are often rather weak. The allocation of dry mass to reproduction can vary appreciably within a functional group, per-capita seed production does not decline with seed mass as much as expected in the simplest tradeoff, and species can vary appreciably in the proportion of seed dry mass in

embryo-cum-endosperm so that initial seedling size is uncoupled from seed mass (Table 1).

Also, rates of predation on seeds vary hugely between species, so that the number of seeds available for germination can be strongly uncoupled from the number produced [41]. There are sound theoretical reasons to expect larger-seeded species to be more predated upon [42], but

Box 4. Seed size and the colonization of establishment sites

There are two key issues here. First, do smaller-seeded species reach a greater number of sites? Second, if the answer is yes, do they do so simply because they are more numerous or because they are more widely dispersed in space or time?

For dispersal in space, the evidence for wind-dispersed plants is that smaller seeds are dispersed greater distances on average than are larger-seeds [67], but the situation is much more complex where most seeds are dispersed by animals (as in tropical rainforests), because large-seeded species can be carried large distances by the animals that disperse them. For species needing gaps for establishment, the movement of birds from one gap to another can provide directed dispersal [68] for at least a small proportion of the seeds, and in theory a larger-seeded species might compensate for lower numbers of seeds by being more directionally dispersed [67–69].

As for dispersal in time, we have to separate seed-banks in the soil from those in protective organs (woody capsules or cones) on plants in fire-prone vegetation. The evidence for temperate species in soil seed-banks is that generally smaller seeded species last longer in the soil, although this is not always the case [70]. Also, the deeper the seed is in the soil at germination, the larger the seed needed to ensure emergence [71]. There seems to be no good evidence that among species with aerial seed-banks the seeds last longer in the capsules or cones in species with smaller seeds. In Australia, the Myrtaceae, which have notably small seeds, have either short-lived capsules (2–3 years as in *Eucalyptus*) or long-lived (5–10 years as in *Callistemon*; D.H. Ashton, pers. commun.), whereas the Proteaceae, which have larger seeds, have the same range of longevity of capsules [72].

'Recruitment limitation' means that species fail to reach sites that are otherwise suitable for their establishment [73]. The phenomenon is believed to be widespread, and is now well documented for tropical rainforest plants [54]. Clark *et al.* [67] analyzed the phenomenon in temperate deciduous forest using maps of adult trees and seedlings, along with seeds captured in 100 traps, to calculate how many seeds each species of tree produced (per unit basal area to accommodate differences in size), and how far those seeds are dispersed (Fig. 1a). Some smaller-seeded species produced more seeds, which were further carried further from the parent tree (Fig. 1a). The cause and extent of recruitment limitation differed among species and replicates, some being limited more by seed production, and others more by seed dispersal (Fig. 1b).

Ecologists often fail to consider adequately the scale on which dispersibility should be measured [24]. For example, in a forest, larger and smaller seeded gap-demanding species might both be found to reach every tree-fall gap, whereas the smaller-seeded species reaches, on average, a much greater number of microsites capable of supporting a one-year-old plant. The scale that is relevant to a competition-colonization tradeoff model depends on the number of individuals that can, on average, reach maturity in a gap. If that number is one, then reaching just one microsite in the gap is all-important, but if it is (say) ten, then the number of microsites reached is more important.

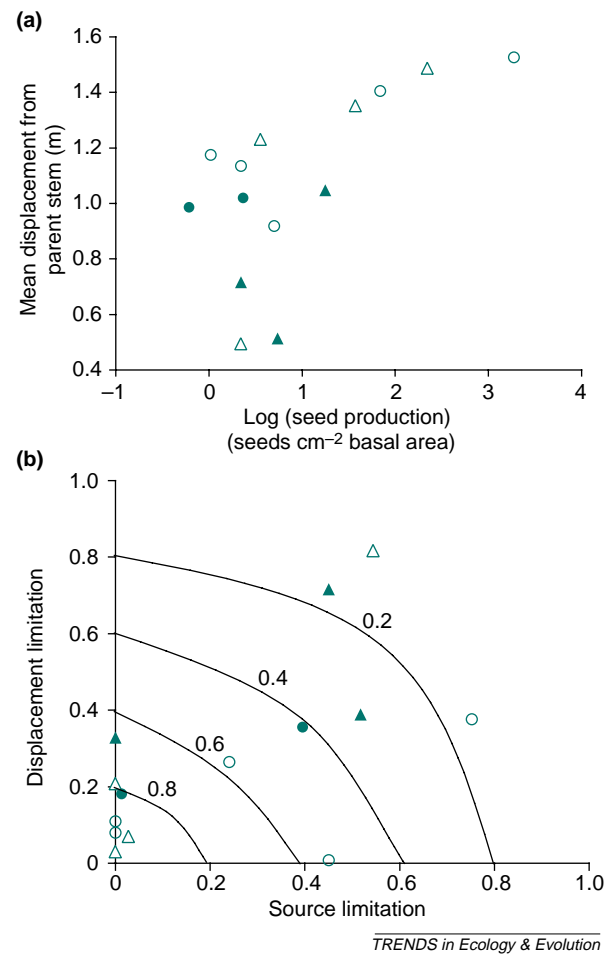


Fig. 1. (a) Relationship between the number of seeds produced and mean dispersal distance of 14 North American trees with seed masses 0–10 mg (open circle; *Amelanchier*, *Betula*, *Oxydendrum*, *Pinus*, *Tsuga*), 10–100 mg (open triangle; *Acer*, *Fraxinus*, *Liriodendron*, *Robinia*), 100–1000 mg (closed triangle; *Cornus*, *Nyssa*, *Tilia*), and > 1000 mg (closed circle; *Carya*, *Quercus*); (b) the extents of source limitation (the probability of a seed arriving in a given patch if seeds were globally dispersed) and dispersal limitation (degree to which the probability of a seed reaching a patch is reduced by limited dispersal) for these trees, with contours representing the fraction of patches expected to receive some seeds.

the evidence is that predation is often uncorrelated with seed size [43,44].

The mechanistic basis of seed-size variation in selected functional groups

Annuals

We consider two functional groups: winter annuals of sand dunes and shallow rocky soils, and annuals in semi-deserts (some winter, some summer).

For diminutive winter annuals (mostly 2–5-cm tall at maturity) growing in an extremely sparse and short matrix of perennials on coastal dunes in northern Europe, Rees [6] suggested that the range of seed sizes is maintained by a CC tradeoff. More recent work by Rees and collaborators has shown that this cannot be the case

because there is a lack of strongly asymmetric competition between the species (*cf.* Box 3); the effects among most species in most years are weak and nonhierarchical [12,45,46]. A different way of maintaining the mixture of seed sizes now seems important [12,13]. It involves differences among species in their ability to expand their numbers, and in their ability to tolerate particular microsites. The populations of at least some smaller-seeded species crash in 'bad' years, but recover quickly in subsequent years because each plant has the potential to produce many seeds [12,45]. The populations of larger-seeded species are steadier among years, but generally smaller. Consequently, the seed size–abundance relationship for species, considered across years and sites, is 'triangular', with smaller-seeded species having a higher

Table 1. Associations between seed size and other life-history attributes in selected types of plant

Life-history attribute	Annuals	Biennials and perennials in temperate mesic grasslands	Trees in tropical lowland rainforests
Allocation to reproduction	0.31–0.54 of adult dry mass depending on species [25]	Varies greatly year to year in mature plants, often 0; in non-gap-demanders 0.10–0.36 of dry mass depending on species [26]	Very little information
Slope of allometric relationship between per-capita seed production and seed mass ^a	Slope of –1 reported in one study [27] but species with larger adults generally have larger seeds [28]	One large-scale study gives a slope of –0.6 [29], the species that make larger seeds having larger individuals	For fleshy-fruited species, which make up most species, the slope < –1. The proportion of fruit dry mass in seed increases with seed size (0.2–0.3 versus 0.4–0.6) [14]
Proportion of seed dry mass in embryo-plus-endosperm	Relatively low variability (e.g. 0.45–0.85 [30])	Relatively low variability (e.g. 0.39–0.80 [30] and 0.28–0.56, [P.J. Grubb, unpublished])	Hugely variable (0.01 to nearly 1.0 in one study [31])
Relationship between seed size and tolerance of hazards	Larger-seeded species are less variable in fitness than smaller-seeded in temporally variable conditions [32–34]	Higher rate of establishment of larger-seeded species in some tests [29] probably a result of greater tolerance of dry spells, frost-heaving and cover by litter	For shade-tolerators, greater seed size valuable in tolerance of dry spells, litter cover, scratching by animals, and partial destruction by herbivores or falling branches [14]. For gap-demanders, survival of dry spells greater in larger-seeded species [35]
Relationship between seed size and tolerance of competition with adult plants	Fitness hierarchies of semi-desert annuals were not affected by presence or absence of shrubs [33]	Sensitivity to shade in non-gap species not tightly related to seed size [30]. Sensitivity to root competition in these species is dependent on mycorrhiza, not seed size [36]	Shade-tolerators do tend to have larger seeds than do light-demanders [7,14,19], but strongly shade-tolerant species with tiny seeds (<1 mg) are found in >16 families in Old World Tropics [14] so the association of greater shade-tolerance of seedlings/saplings with larger seeds is correlative, not causal. Survival of 'tolerant species' in shade is not related to seed mass after one year [21,37]
Relationship between seed size and competitive ability	Species with larger seedlings are superior [4], but those with smaller seedlings have higher relative growth rates [28], and can become superior competitors if seeds are far enough apart [38]	In one study, the ability to occupy a gap competitively was not related to seed size [39,40]	There is no published test of the expected advantage of larger seed size among gap-demanding species.

^aA slope of –1 indicates that all species put the same amount of resources into seed production.

mean abundance [12,13]. If larger- and smaller-seeded species are to coexist indefinitely, there must be some refuge for the smaller-seeded species in the years most favourable to the larger-seeded. With few exceptions, this is not in the form of a seed bank in the soil [47]. A plausible explanation is as follows. The larger-seeded species are most abundant on older surfaces with soils richer in humus, and these patches move over the dunes with time as new sand is accreted [12]. Possibly, the smaller-seeded species are protected on the patches with the most infertile topsoils [13]. Of course, the smaller-seeded species also need refuges in the years that are unfavourable to them, and these seem to be localized patches where the unfavourable weather conditions are somehow mitigated [12].

In northern Europe, the suite of annual species found in thin grassland on rocky soils overlaps with that found on dunes, and it might be that coexistence of larger- and smaller-seeded species has much the same basis as on dunes. Turnbull *et al.* [27] sowed seeds of seven species of differing seed size into grassland on limestone at a range of

densities; the three with the largest seeds comprised 49% of individuals at low density but 83% at high density, suggesting that the larger-seeded species were more competitive at the microsites that they reached. However, all species showed spatial aggregation, and the authors suggested that the smaller-seeded species are perhaps protected by their ability to persist at microsites that were not tolerated by the larger-seeded species, which tend to mature later in the season. Such sites might have particularly shallow soil that is prone to drying out early in the year.

Communities of annuals in semi-deserts, set in a matrix of widely separated shrubs, vary enormously in density between wet and dry years. Two research teams, led by Venable and Brown respectively, have found in Arizona that, taken over runs of years, smaller-seeded species often, but not always, have the higher mean abundance, and are found in a higher proportion of samples [32–34]. Competition with neighbours reduces the maximum size that an annual can reach, but many individuals do not

reach that limit (another ‘triangular’ relationship, this time between plant size and local crowding) [34]. We can interpret seed-size variation in this community tentatively in a way that is analogous to that suggested for dune annuals. The smaller-seeded species rise in density more quickly in favourable years, but, in this case, they are protected in bad years by persistence in soil seed banks [32,33]. In the years when the weather is most favourable to the larger-seeded species, the smaller-seeded are partially protected by higher rates of seed predation on the larger-seeded [48]. The conditions necessary for coexistence via the ‘storage effect’ (Box 3) are all met. There are shifts in fitness rankings among years, differential germination responses, and covariance between germination fraction and reproductive success [32,33].

Biennials and perennials in temperate grasslands

We consider two functional groups: species establishing only in gaps (typically those made by animals), and species not needing such gaps.

Concerning the gap-demanders, Platt and Weis [39] made a classic study of five wind-dispersed fugitive perennials on badger mounds in tall-grass prairie, and found that coexistence at the local landscape scale was a result of competitive ability being traded off consistently against colonizing ability. The study site involved ridges separated by valleys. The five species have their peaks of abundance ordered downslope according to increasing colonizing ability, which reflects the fact that badger activity also drops off sharply downslope, and mounds become distinctly sparser [39]. In summer, the relevant soil layer contains much more water per unit mass in downhill mounds (25–30% versus 4–8%), and thus niche differentiation might also play a part in the distribution of species [40]. Fascinatingly, this CC tradeoff is not an SNSS tradeoff, because there is no simple relation between either competitive ability or colonizing ability and disseminal dry mass, which changes idiosyncratically among the species in the downhill sequence (15.7, 0.95, 0.52, 8.8 and 1.2 mg) [40].

Concerning species that establish without gap-formation, there is some evidence that less abundant perennial species in calcareous grassland in Britain have superior colonizing ability [49], but there is only a nonsignificant correlation between sparsity and smaller seed dry mass [11]. In two seed-addition experiments, it was found that larger-seeded species had a higher chance of establishment [29,50], but in another that was not the case [51]. For nonfugitive perennials in grasslands, co-existence depends very much on the competitive relations among long-lived adults, and the ‘refuges’ enjoyed by species that are permanently or temporarily less abundant. In particular, species of lower stature might benefit from being eaten less than are taller species [49] or performing relatively better in drier years [52].

The results of Jacobsson and Eriksson (Box 1, Fig. 1) suggest that an SNSS tradeoff might play a part in the maintenance of coexistence of nonfugitive perennials in grassland, but new work is needed to determine its role relative to other forms of niche differentiation.

Trees in tropical lowland rainforests

We consider three arbitrarily separated functional groups: gap-demanding, initially tolerant and persistently tolerant.

For gap-demanders, Dalling and collaborators [35,53,54] have evidence from Panama that smaller-seeded species reach more sampling sites in gaps, but have higher mortality rates as seedlings. Thus, an SNSS tradeoff is in operation. But it is not a CC tradeoff because the smaller-seeded species suffer greater mortality in periodic dry spells, and do not die as a result of competition with neighbouring seedlings [35]. The SNSS tradeoff is only one of the mechanisms maintaining coexistence. Another tradeoff, between growth rate and susceptibility to attack by stem-borers in second-year seedlings, is also important [35]. Moreover, another recent study in the same forest by Pearson *et al.* [55] has shown a further kind of niche differentiation in these species. Those with smaller seeds are favoured in smaller gaps where the change in red:far-red ratio is sufficient to trigger their germination, but diurnal fluctuations in topsoil temperature regime are not sufficient to trigger that of larger-seeded species.

Most species in the forest are initially or persistently tolerant. For them, there is no published evidence that, in a single forest, smaller-seeded species reach more sampling sites than do larger-seeded, whilst larger-seeded species have greater survival rates as seedlings, but such evidence was found for a forest in Peru by Miles Silman (PhD thesis, Duke University, 1996), and thus the scene is set for a SNSS model to be appropriate.

It is convenient to recognize three major sub-groups based on seed mass, as set out in Table 1 (<1-mg dry mass, 0.1–1.0 g and >2 g). Within each of these sub-groups, an SNSS tradeoff, in which greater colonizing ability is set against lower mortality in the face of various hazards at the seedling stage, might be important for coexistence. Such a system could be stabilized if larger-seeded species suffer higher rates of predation before germination [14], but only if there is spatio-temporal variation in predation rate. Higher predation rates on larger-seeded species have been reported for some forests [56] but not all [57]. Alternatively, density-dependent mortality could stabilize the system [58]. The operation of SNSS tradeoffs is compatible with the other mechanisms currently accepted as contributing to coexistence in rainforests [59].

Conclusion

There is evidence that, in a few cases, an SNSS tradeoff is partially responsible for maintaining coexistence of larger- and smaller-seeded species in a functional group (Box 5). However, coexistence seems generally to be explained in other ways and, for perennials particularly, depends on differentiation between species at several stages in the life cycle, which are summarized in the regeneration niche, and other niches [60].

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Box 5. Major findings and outstanding questions

Findings

- Recent models have placed serious limits on the potential of seed number–seedling survival (SNSS) tradeoffs to lead to long-term coexistence of larger- and smaller-seeded species. Where larger-seeded species are favoured by greater resistance to hazards during establishment, there must be spatiotemporal variation in the incidence of hazards. Where larger-seeded species are favoured in competition among seedlings, that superiority must be very strong.
- The potential of an SNSS model to explain the coexistence of a large number of species with different-sized seeds in one functional group is severely constrained by the fact that the relationship between seed mass and seedling mass is not sufficiently strong to maintain a consistent tradeoff between greater ability to colonize and greater ability to survive as a seedling. Also, allocation to seed production can vary appreciably among species in one functional group, so that the seed number–seed size tradeoff is not complete.
- For various annuals, the competitive advantage of larger-seeded species in the field is not strong, and the mechanism maintaining coexistence of larger- and smaller-seeded species would seem to involve greater potential for recovery after ‘bad’ years in species producing many small seeds, and refuges for small-seeded species in periods when larger-seeded species are most abundant. For gap-demanding trees in rainforests, the SNSS tradeoff concerns resistance to hazards, rather than competition, and is coupled with at least two other forms of niche differentiation.
- In functional groups that establish in continuous vegetation, greater seedling survival of larger-seeded species has generally been thought to result from superiority in tolerance of resource depletion, but it now appears to result mostly from superiority in tolerance of hazards. For non-gap-demanding trees of tropical rainforests, the SNSS model has promise as a partial explanation of maintenance of coexistence of species within each of three functional sub-groups.

Questions

- Is it true, as we have assumed, that competition can be treated as being of negligible importance among seedlings establishing naturally in continuous vegetation?
- How can we quantify the relative impacts of SNSS tradeoffs and various other forms of niche differentiation in the maintenance of coexistence of larger- and smaller-seeded species within functional groups in a few well-studied kinds of vegetation that include a wide variety of climates and dominant life forms?
- What are the most important benefits enjoyed by larger-seeded species under field conditions in the vegetation-types that have not been well studied so far in this respect?

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