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The Paradox of Seed Size and Adaptation

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Correlations between habitat and seed size suggest that this character is adaptive. Mean seed size is a relatively invariant species characteristic and seed size has marked effects upon fitness. These observations have previously led to the conclusion that seed size is under stabilizing selection. This conclusion, originally based mainly on evidence from crop plants grown in controlled environments, is questioned here on the grounds that recent studies of wild plants show marked phenotypic plasticity and low heritability of seed size. If seed size is not readily altered by natural selection in the wild, then its effects on fitness are evidence that this character is a constraint on habitat distribution. Constancy of mean seed size may be due to developmental canalization to a size set by previous selection, rather than a continuing process of stabilizing selection.

Clear correlations have been established between seed size (measured as weight) and habitat. In Britain, woodland herbs have larger seeds than comparable species of open habitats[1]; in California, seed size is positively related to the aridity of habitats[2]; and in the neotropics, forest trees that regenerate in small canopy gaps have larger seeds than species that regenerate in large canopy gaps[3]. One interpretation of these correlations is that large seed size is an adaptation to shaded or dry habitat conditions, because seedlings with large seed reserves perform better than those with small reserves when light or moisture limit growth[4]. But are large seeds an adaptation, or are small seeds a constraint preventing the species that produce them from invading shaded or dry habitats? Of course both can be true, but framing the question this way emphasizes that we need to know how easily natural selection may change seed size. If it is to be subject to selection, seed size should show heritable variation and should have significant effects upon fitness.

In their 1970 review of seed size, Harper, Lovell and Moore[5] commented that, within species, this character was remarkably constant over a wide range of planting densities. Although Harper *et al.* gave examples of seed size variation within individual plants, they concluded that 'seed sizes which are found under natural conditions are likely to represent selective optima or selective compromises'. This view was based upon studies of crop plants, for many of which there was evidence of heritable variation for seed size, and of trade-offs between seed size and number. Stabilizing selection for a particular size of seed would therefore limit the number of seeds a plant produced.

The view that seed size is a relatively invariant character subject to stabilizing selection remained influential for over a decade and was reinforced by plentiful evidence that seed size has major effects upon fitness. Black's study[6] of the consequences of seed size variation in *Trifolium subterraneum* is a frequently cited example; he showed that seedlings emerging from small seeds were totally overgrown by seedlings from large seeds when they were sown together. The most convincing evidence of seed size evolution occurring in the short term is in weeds whose seeds mimic those of the crops they infest, and with which they are harvested and re-sown[7].

The importance of stabilizing selection in wild populations must now be re-evaluated in the light of recent studies which have shown that seed size in many wild plants is phenotypically plastic and has low heritability. This evidence implies the paradox that although seed size shows marked phenotypic variation and has significant effects upon plant fitness, it might not always be subject to natural selection. If this is correct, then we should regard seed size primarily as a character that constrains the distribution of species. This view is supported by Baker's discovery[2] that species introduced into California show the same correlations between seed size and habitat as native species do. The adaptiveness of seed size is not a unique evolutionary problem, but on the contrary is one of the clearest examples of the general difficulties inherent in the evolutionary interpretation of a character considered in isolation from the rest of the phenotype, particularly when it is phenotypically plastic.

Variation and its sources

The evidence that seed size is constant is based to a large extent upon mean seed weights per plant, which obscures within-plant variation. As further evidence of stabilizing selection, the supposed invariability of seed size has been contrasted with the extreme variability of seed number between large and small plants[5]. This contrast is misleading, because it ignores the modular construction of plants. Differences in plant size within a population tend to reflect differences in module numbers between large and small individuals, rather than differences in the size of modules. If module size is constant, so too will be the size of seeds that they bear. Hence, when plants vary in size it is *module* size, not *seed* size *per se*, that is conserved at the expense of module (and therefore seed) number. If we take the conservation of module size as a fundamental feature of plant construction and growth, then we should really measure seed size variability between modules rather than between plants. There is within- and between-plant variation in both module size and seed size, but we do not yet know sufficient about how closely these are correlated.

As long ago as 1921 Sinnott[8] suggested that the size of plant organs, including seeds, was related to the size of meristems from which they originate. Since the modules that develop from meristems are physiologically quasi-independent units, we may expect a level of phenotypic variation between them. Studies that have measured within-plant (i.e. between-module) variation in seed size usually show this variation to be considerable. A recent survey of seed size variation within populations of 39 North American species found significant variation in seed mass between plants in 37 species. Most of the total variance originated from differences between seeds within plants[9]. In another study that looked at variance between populations as well as within populations, Waller[10] found that mean seed size varied very little between four populations of *Impatiens capensis*, but that there were highly significant differences between plants and within plants. Seed weight increased linearly with height on the stem. Cavers and Steel[11] found that there was significant variation in seed size between individuals within populations and within individuals during a growing season in eight herbaceous species. In one species, *Verbascum blattaria*, seed weight changed by [illegible]5% during the season.

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Variation in seed size frequently occurs within an individual fruit, with the position of the fruit on a branch or of the branch on a stem, and between plants within a population[12]. The seed yield of an entire plant can be broken down into a series of hierarchical components: the size of seeds, the number of seeds per fruit, fruit per branch and branches per plant. Negative correlations (trade-offs) between these components of yield, particularly between seed size and seed number, are commonly found in studies of crop plants, but *positive* correlations between components of yield have been reported for plants growing in the wild[13] where environmental heterogeneity has a significant influence upon individual plant growth. How variation in seed size is partitioned within and between plants will determine how heritable it is likely to be.

Heritability and phenotypic plasticity

Evidence that there is heritable variation (narrow-sense heritability) for seed size, and thus scope for natural selection to operate on this character in natural populations, can be sought directly by parent/offspring regression with families bred from seeds collected in the wild, or indirectly by transplant experiments that measure the phenotypic plasticity of seed size when the same genotype is grown in different environments. A character that shows high phenotypic plasticity will, by definition, have low heritability. Because of genotype × environment interactions, neither approach can give a definitive answer about how heritable seed size is. Nevertheless, the cumulative results of many studies might lead to some general conclusions.

Hurka and Benneweg[14] measured the heritability of seed weight in families of shepherd's purse (*Capsella bursa-pastoris*) from six populations and found values that varied between 0.05 and 0.79, emphasizing that there are likely to be strong interactions between genotype and environment influencing the inheritance of seed weight. Wild radish (*Raphanus raphanistrum*), which shows a 20-fold variation in seed weight within populations, has become a favourite species for the study of the causes and consequences of seed size variation. Although in one study Stanton[15] found a significant correlation between maternal and offspring seed weight, suggesting that seed weight could be heritable, a study of a different population by Mazer[16] detected no additive genetic variance for seed weight. Primack and Antonovics[17] found no significant heritability of seed size in eight populations of *Plantago lanceolata* collected from the wild. Seed weight in this species was, however, a relatively invariable character both in the field and in experimentally controlled conditions. Two studies of variation in seed weight in the grass *Anthoxanthum odoratum* concluded that environmental effects were predominant[18,19]. Waller[10] estimated the heritability of seed weight in a population of *Impatiens capensis* to be less than 0.26.

Heritability estimates apply to variation *within* populations and tell us little about the scope for selection and genetic differentiation *between* populations. Transplant studies between habitats are more instructive. Winn[20] transplanted *Prunella vulgaris* rosettes between natural populations growing in deciduous woodland and an old-field. She found that seeds produced in the wood were significantly larger and that the difference between sites depended entirely upon environment. This is a particularly interesting observation because such a difference between plants in shaded and open conditions would normally be considered adaptive, and likely to be due to genetic differentiation rather than to phenotypic plasticity. Winn's study highlights the possibility that phenotypic plasticity of seed size may be adaptive.

Developmental constraints

Opposite in effect to phenotypic plasticity, but equally problematic for the view that seed size is easily altered by selection, is the operation of developmental constraints. In a survey of taxonomic trends in seed size in a regional sample of dicot families, Hodgson and Mackey[21] found a 100-fold range of seed weight within families, but nevertheless detected developmental constraints in the flora they examined. Families with one ovule per carpel had significantly larger seeds than families with many ovules per carpel. They also found a correlation between size of seed and the type of embryogenesis, and that species with a well developed endosperm (a taxonomically conservative character) tended to have larger seeds. This trend occurred both within and between families. Although significant, these trends have evidently provided plenty of latitude for seed size evolution within families.

Possible evidence of a tighter developmental constraint comes from the significant allometric relationships that Primack[22] found between length of leaf (which was correlated with plant height) and length of seed within five of the six plant genera he examined. Thompson and Rabinowitz (unpublished) have also found a significant correlation between seed size and plant height among herbaceous species in five of eight families. It is not known whether any of these correlations between plant size and seed size are due to pleiotropy, and therefore place a developmental constraint on the evolution of seed size, or are due to co-adaptation. As an example of the latter explanation, Thompson and Rabinowitz suggest that a positive relationship between seed size and plant height could result from selection against small plants producing large seeds, because large seeds would be more poorly dispersed than small ones when falling from a short parent. For an example of a non-adaptive explanation of allometric variation in seed size we need look no further than the positive correlation between height on the stem and seed size in *Impatiens capensis*[10]. If this relationship holds equally for plants of different size (which it may not), then taller plants would have larger seeds.

Adaptation reconsidered

Of itself, phenotypic plasticity in seed size does not rule out the notion that seed size is adaptive, but it does shift the emphasis of such a theory. Sultan[23] has argued that the importance of phenotypic plasticity as an adaptation in plants has been underrated and this aspect of seed size variation is still relatively unexplored. There are at least two distinct ways in which plasticity of seed size could be adaptive. The first is exemplified by *Prunella vulgaris*, which appears to alter mean seed size as a plastic response to environment. It is assumed that there is a single optimum seed size for a particular plant in each environment, and that this is determined by a trade-off between seed size and number. Variation about this size is a side consequence of the phenotypic plasticity which enables a plant to track the optimum.

The second, suggested by Capinera[12] amongst others, proposes that there is no single optimum seed size for a plant because the environment is heterogeneous: seed size variation is not due to plants tracking the environment, but to plants firing a shotgun at it. McGinley *et al.*[24] model this situation and conclude that parents employing such a strategy are favoured only when seeds of different size can be selectively dispersed to their individually appropriate microhabitats. This is clearly impossible for the majority of cases of seed size variation because all sizes of seed are dispersed by a similar mechanism. Plants that produce seeds that differ in dispersal mechanism (e.g. some with and some without a pappus) generally show a parallel, discontinuous variation in seed size that is quite different from the examples of continuous seed size variation discussed above.

As I have already argued, the evolutionary interpretation of the correlation between seed size and habitat presents no unique problems, but it is perhaps the clearest example of the difficulties to be faced before it is possible to establish that a phenotypically plastic character is adaptive. The original idea that seed size is under stabilizing selection depends upon four main observations: (1) mean seed size is constant, (2) seed size has a major effect upon fitness, (3) seed size is heritable, and (4) there is a trade-off between seed size and seed number. All of these observations have been made repeatedly, but with plants grown under controlled conditions where phenotypic plasticity is limited. Experiments with plants in natural populations tend to show these effects to be weaker than was once thought, suggesting that constancy of mean seed size may be due to developmental canalization, of which selection is the ultimate but not the immediate cause.

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