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Competition, behaviour and seed size

Abstract: There is enormous variation in the size of seeds on vascular plants. The wide range of seed sizes in the natural world can be explained by recognizing seed size as the center of a nexus of strong adaptive forces at different parts of a plants reproductive cycle. Adaptation at the production stage tends to evolve smaller seeds in greater quantity. Adaptation in dispersal is dependent on the mechanisms of dispersal that are available and will sometimes adapt for smaller more easily dispersed seeds and sometimes larger, seeds that are more attractive to vertebrates. Adaptation in establishment, on balance, pressures towards increased seed size for greater survivability. Overall different adaptive forces at different stages in a plant reproductive cycle act to reduce the effective amount of competition between seeds by creating ‘niche’ plant reproduction pathways.

Keywords: Seed size; reserve effect; seed germination; seed dispersal; plant reproductive allocation.

Introduction

The seed is a complex structure in which the young plant embryo is contained within a protective outer layer called a seed coat. The earliest known seeds were fossilized in late Devonian deposits some 360 million years ago. The seed is perhaps the most important element in the spectacular success of the vascular plants on land since that point.

There is an enormous variation in seed size throughout the range of vascular plants. Even within a single genus of plants, seeds may vary greatly in size. Plants in different families, representing millions of years of evolutionary separation, may have very similar seed sizes. A single plant, such as a corn or sorghum, may produce seeds with significant variation in size (Venable 1992). Traditionally, the standard view of seed size has been as a trade-off with seed number. In this model reproductive, resources are apportioned between seed size and seed number (Smith and Fretwell (1974) in Venable 1992).

In this paper I examine the evolutionary forces that effect seed size at each stage from seed production, to seed dispersal, to seed establishment. The wide range of seed sizes in the natural world can be explained by recognizing seed size as the center of a nexus of strong adaptive forces at different parts of a plants reproductive cycle. By producing multiple reproduction pathways, different evolutionary forces and different adaptive mechanisms reduce effective competition between seeds and create multiple seed size 'niches'. My objectives are to:

1) Dissect the individual evolutionary forces and adaptive mechanisms that can operate in different ways and at different points in a seeds lifecycle.
2) Analyze how these adaptations accumulate to determine a seed's size.
3) Discuss the scope for variation in seed size within an individual plant in response to changing environmental conditions.

Germination, establishment and seed size

When a seed has reached a micro-site it must germinate and establish. Larger seeds are frequently found to be more competitive at a specific micro-site than smaller seeds. This trend is found both within a species and between species. There are several strategies seeds have evolved that explain this observation.

Generally, the larger a seed is, the greater the metabolic reserve it will have available to make up for lack of resources in the environment. This is known as the *reserve effect*. The *reserve effect* is believed to be the underlying mechanism for overcoming hazards to seedling survival and winning competition with other seedlings (Westoby, Leishman et al. 1997).

The *reserve effect* may help a seed to establish and survive in a shaded environment. Examination of the mortality of seeds in dense shade often shows correlations between larger seed mass and greater longevity (Saverimuttu & Westoby 1996). However, this relationship is not found in studies by (Grubb & Metcalfe 1996; Metcalfe & Grubb 1997) who report that there is no correlation between seed size and shade tolerance. It is likely that this shade tolerance to seed size correlation exists in some species but may be masked by other factors.

The *reserve effect* may also help a seed overcome a host of other hazards. A larger seed size confers enhanced ability to penetrate ground cover (Reader 1993), survive burial by litter (Metcalfe & Grubb 1997), avoid desiccation during dry spells (Metcalfe & Grubb 1997), grow in resource poor soils (Rees 1997), and increases a seed's probability of surviving until environmental conditions improve such as, the appearance of a canopy gap or a rainfall. The *reserve effect*, by conferring the advantage of faster growth (Venable 1992; Rees 1997) on a seed, also gives it the competitive advantage over smaller seeds.

Because the *reserve effect* is applicable to enhanced survival ability from several hazards it may have evolved in response to different hazards than those maintaining it (Westoby, Leishman et al. 1997).

Some seeds have evolved to have thicker seed coat as protection, a *defense* strategy, until they germinate. In hot climates a thicker coat helps avoid desiccation. In cold climates a thicker coat helps insulate a seed from frost.

A more complex effect applies to optimal seed size with respect to post-dispersal seed predation. This may depend on the composition of the seed predator guild (Janzen 1969). Where predators are small, such as ants, then larger seeds may face less predation. If predators are larger such as birds and rodents then larger seeds may be targeted because they are easier to find. An experiment in pasture in Canada showed that seeds between .06mg and .14mg suffered little predation while seeds between .29mg and 12.2mg were increasingly strongly predated (Reader 1993). By looking at a seeds physiology it may be possible to establish whether seed has evolved under threat of predation in which it will have a thick coat and proportionally smaller metabolic reserves, or may just be smaller in general, or under stressed or competitive environments in which it will have proportionally larger metabolic reserves.

A seed may have evolved a *dormancy* strategy in which it receives feedback from the environment as to when conditions are right for germination(Rees 1997). This strategy may allow a seed to remain small even when it is evolved to operate in stressed environments. Firstly, because relying on greater resource availability requires smaller metabolic reserves and secondly, because a dormancy strategy increases risk of predation which selects for smaller seeds. A dormancy strategy may also have evolved from parent-offspring competition, which the parent wins by giving its seeds a thicker coat to delay germination (Rees 1997).

Dispersal and seed size

It is a well-documented observation that seed mortality increases with proximity to the parent plant. This mortality is caused by density-dependent factors such as high predation, pathogens, and competition near the parent (Venable 1992). In Panama, predation by weevils causes overwhelming mortality of *Virola surinamensis* seeds and seedlings near the parent tree (Howe 1990). As with establishment at a micro-site, a seed may use one of several strategies to ensure successful dispersal, and its choice of strategy may effect seed size.

A seed may be large and attractive to animals. Animal dispersals selects for seeds that are matched in size to the animal guild they target. If the seed is too large then it will be ignored or eaten in pieces. If the seed is too small it will inefficient in terms of energy-use for an animal to gather them. Seed size in this situation may be complicated by the various fruiting strategies plants may use to package seeds.

A seed that is wind dispersed is limited in its dispersal range by the size of its seed and the height above the ground that the seed is released. This leads to the prediction that smaller plants with wind dispersed seeds will have smaller seeds (Venable 1992).

The coconut demonstrates elegantly the effect dispersal has on seed size. In this rare instance increasing size has a positive correlation, rather than the usual negative correlation, with dispersal range. The result is seeds that have been recorded at 27kg! The only limitation on the size of the coconut is the resources available to the parent to produce the seed.

The species *Camelina sativa* shows evolution of seed size, due to dispersal strategy, in a striking way. This species is a common weed in flax in Europe. The subspecies growing in association with cultivated flax is taller and has heavier seeds that are matched in size to those of the host flax. This allows *Camelina sativa* to disperse by wind over the same distances as its flax protectors (Britannica.com 2001).

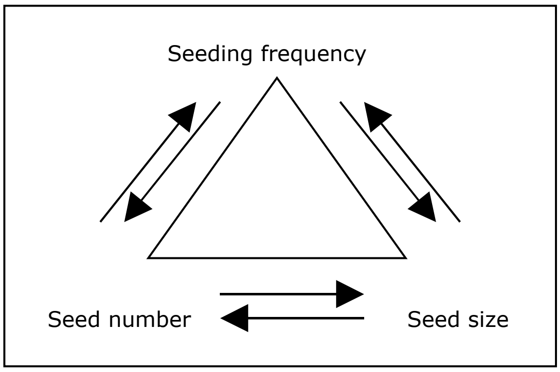
The theory of patches and patch dynamics explains how plants may be less fit than competing species and still survive by adapting to heterogeneous patches and surviving in disturbed patches (Pickett & White 1985). In a heterogeneous environment a plant may adapt to colonizing patches that cannot be reached by larger seeds with weaker dispersal strategies, such as rock outcrops. In a frequently disturbed environment seeds with good dispersal mechanism will be able to colonize and establish in disturbance patches more quickly than poorly dispersed seeds. These early successional species can survive in a “shifting mosaic” of disturbance patches (Pickett & White 1985). Additionally a smaller, wind dispersed seed may be able to penetrate further into a disturbed patch than larger, wind dispersed seeds. Animal dispersal is subject to the preference of the dispersers. Some animal species are adapted to forest edge environments and will cross between patches. Other species will never venture from deep forest cover.

Patch dynamics mean that some patches will be good for small seeds because they are hard to colonize but have plenty of resource. Other patches may be better for larger seeds because they are easily colonized and smaller seeds will be out-competed. The large amount of variation of dispersal mechanisms is a type of niche differentiation. Pair-wise comparison of the seeds of two species may find they are not in competition with each other if one species can reach a colonization micro-site more easily and the other can win competition when both reach the micro-site. In this way, differing dispersal mechanisms and capabilities can be seen to ensure that no single seed size will be optimal.

Reproduction and seed size

Currently, the considerable number of factors operating on seed size and seed number at the plant reproduction stage has confounded analyses aimed at developing general models capable of making predictions about seed size. The general model produced by (Venable 1992) is wider than the models it is based on by Smith and Fretwell (1974), Parker and Begon (1986) and McGinley (1989) but is still only able to account for a subset of the factors effecting seed size.

Allocation of reproductive resource is a three-way trade-off between larger seeds, more seeds or seeding more often. Though it is very difficult to develop a general theory of where a species will be within this trade-off we can examine the forces that effect a species position.



It useful to consider whether a plant can vary its position in this trade-off in response to environment conditions or if seed size is solely a genetic trait. Some plants produce seeds that are remarkably similar in mass to their siblings. *Ceratonia siliqua* seeds were originally used as the basis for the unit of weight, the carat (Britannica.com 2001). This suggests that seed size for *Ceratonia siliqua* is specified by genetics. It is possible that it has evolved in response to a highly targeted dispersal mechanism.

Hakea sericea produces smaller seeds when grown in nutrient-enriched soils suggesting the parent plant can control it seed number, seed size fitness ratio is response to changing environmental conditions (Venable 1992). In nutrient-enriched soils seed reserves may be less important for establishment so seeds are smaller.

The opposite effect is also possible. In some species, more resources available to a plant are predictive of an offspring environment subject to fiercer competition (Venable 1992). An increase in seed size would give offspring a competitive edge against interspecies competition and at the same time, decrease intra-species competition due to lower seed quantities.

Sibling competition can play an important part in determining seed fitness. There are both density-dependent reduction in fitness and accelerating fitness returns. Reduction in fitness is due to increased competition between seeds and tends to force larger seeds to evolve. An increase in fitness is based on local predator satiation (Venable 1992). Beech masting, when environmental factors trigger beech trees to produce well above average quantities of seed in a single season, is one such example.

Most variation in seed size occurs among different seeds on an individual plant showing that seed size is largely due to the development process and is not heritable (Westoby, Leishman et al. 1997). However this variation is development process may itself enhance fitness. In much the same way that genetic variation in a population makes the population more able to adapt to change, variation in seed size on an individual plant may make that plant more able to adapt to a changing environment.

Plant strategy and seed size

It is clear that seed traits are embedded in the lifecycle of plants so a seed’s strategy must match the strategy of the established plant (Rees 1997). It is unlikely a seed will be able to adapt to establish under a forest canopy if the established plant is not adapted to survive and reproduce under the same conditions.

In terms of Grime’s plant strategies, we may make prediction about plant and seed strategy (Grime 1977). A stress-tolerant plant must have seeds that are adapted to germinate and establish in stressed environments. A disturbance focused (ruderal) plant must have seeds that can quickly and easily take advantage of disturbance. A highly competitive plant must have seeds that can give it the advantage in competition.

This correlation between the strategy of an established plant and the strategy of its seed is a result of co-evolution of different parts of a plants life history. It will generally dampen the adaptive forces acting to alter a seed’s size if those forces will make a seed successful in an environment where the established plant cannot survive and reproduce itself.

Conclusion

Plant strategy is strongly related to seed strategy. A plant that has evolved to live in a particular habitat must have seeds that can disperse to, germinate and establish in those habitats. A range of seed size and strategy ‘niches’ may have the same probability of success at a single micro-site because of trade-offs between risk of predation and lack of resources to complete germination. Therefore, a single, optimal seed size cannot be specified at a specific micro-site. Dedicating a large proportion of mass to a seed reserve helps seeds to survive stressed environments that are low in light or nutrients and grow more quickly to out compete smaller seeds. Alternately, adopting a dormancy strategy may allow a seed to survive until resources become available. Dedicating a large proportion of mass to a protective seed coat helps protect a seed from predators. Alternately, seeds may adapt to be to small to be noticed by local seed predators or too big to be predated.

Optimal seed size for dispersal is dependent on dispersal mechanism. Relying on a specific animal guild for dispersal puts a seed in competition with other seeds using that animal guild for dispersal but allows a seed to provide a larger seed reserve. A wind dispersal mechanism is not subject to competition but this mechanism forces a plant to trade-off between seed size and dispersal range. The patch nature of the environment allows smaller, less competitive seeds to pursue an opportunistic strategy by taking advantage of disturbances or niche habitats.

Some plants will use variable reproduction resources to produce more seeds, others will produce seeds more frequently and some will make larger seeds. The amount of genetic control a plant exercises over seed size in the presence of excess resources can be a good indicator of how a seed strategy has evolved. A plant that uses additional resources to produce more seeds of precisely controlled size may be pursuing an opportunistic strategy dependent on colonizing as many micro-sites as possible. A plant that uses additional resources to produce larger seeds may have evolved a strategy to out-compete other seeds at small numbers of micro-sites.

Overall different adaptive forces at different stages in a plant reproductive cycle act multiplicatively on seed form resulting in the wide variation of seed sizes we see in vascular plants today. Competition between seeds is less than it may appear to be at first because of different reproductive pathways form ‘niches’ that may give seeds of differing sizes the same fitness.

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