On wheat and salmon: the trade-off between seed size and number

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Abstract

The concept that availability of resources drives seed production is sound but incomplete as plants can use the same amount of resources to produce many small seeds or few larger seeds. This paper examines evolutionary aspects of the trade-off between number and size of seed in annual grain crops. The analysis is centred on two hypotheses; for a given species and environment, allocation of resources to reproduction involves (H1) high plasticity in seed number, which allows for variable resource availability, and (H2) a relatively narrow range of seed size that results from evolutionary and agronomic constraints. Selected comparisons between crops and fish are used to highlight common evolutionary elements in taxa where parents provide little or no care to their offspring, and early survival of offspring, hence fitness of parents, is partially related to embryo size and reserves.

Key Words

barley, wheat, maize, sunflower, soybean, heritability, modelling

Hypothesis 1: high plasticity in seed number allows for variable resource availability

In both plants and fish, offspring number is related to the growth rate of the mother (Fig. 1). This relationship is consistent with the proposal that high plasticity in number of offspring allows for variable resource availability. Many studies where availability of resources has been manipulated through irrigation, nutrient supply and light regime, conform to a general relationship between plant growth rate and seed number comparable to those in Fig. 1.
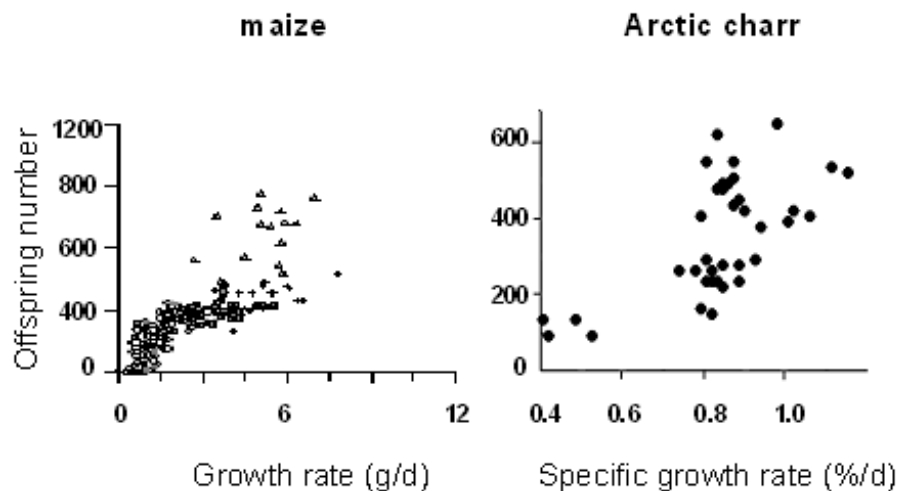

Fig. 1. Relationship between maternal growth rate and offspring production in maize and Arctic charr. Sources: [1, 2]

Important features of this relationship are: a minimum rate threshold for seed set (positive x-intercept in Fig. 1), linearity in species where fruiting sites develop unconstrained as availability of resources increase (e.g. indeterminate soybean), and non-linearity associated with morphological constraints in species with

one or few inflorescences of limited size (e.g. sunflower and maize). A weak point implicit in this hypothesis is that annual plants have to commit a certain number of viable flowers around anthesis on the basis of unknown mechanisms for "projections" of both end-of-season conditions (for grain filling) and prevalent conditions for the next generation. Theoretically, however, the decision on the number of seed to be set could be thought of as a bet-hedging strategy, similar to the problem of allocating axillary buds to the alternative functions of growth, reproduction and re-growth after herbivory. The basic algorithm of allocation of reproductive resources (R) that plants need to solve is

seed number = R / seed mass

if seed number is plastic and highly responsive to resource availability (hypothesis 1) and seed mass is conservative (hypothesis 2), then

$$seed\ number = R\ /\ k \qquad\qquad (1b)$$

where k is a constant "target" allocation which, in theory, maximises parental fitness. For prolific maize, barley and wheat, this model of equitable resource allocation (eq. 1b) provided sound estimates of actual seed number production (Fig. 2). The model diverged from actual seed production in maize plants morphologically restricted to a single ear (Fig. 2a inset). A corollary from this analysis, supported by empirical comparisons reported in the literature, is that seed size plasticity may increase with reduced plasticity in seed number, eg. from multi-eared teosinte, to prolific cultivated maize, to single-eared maize and from branched to single-headed sunflower.
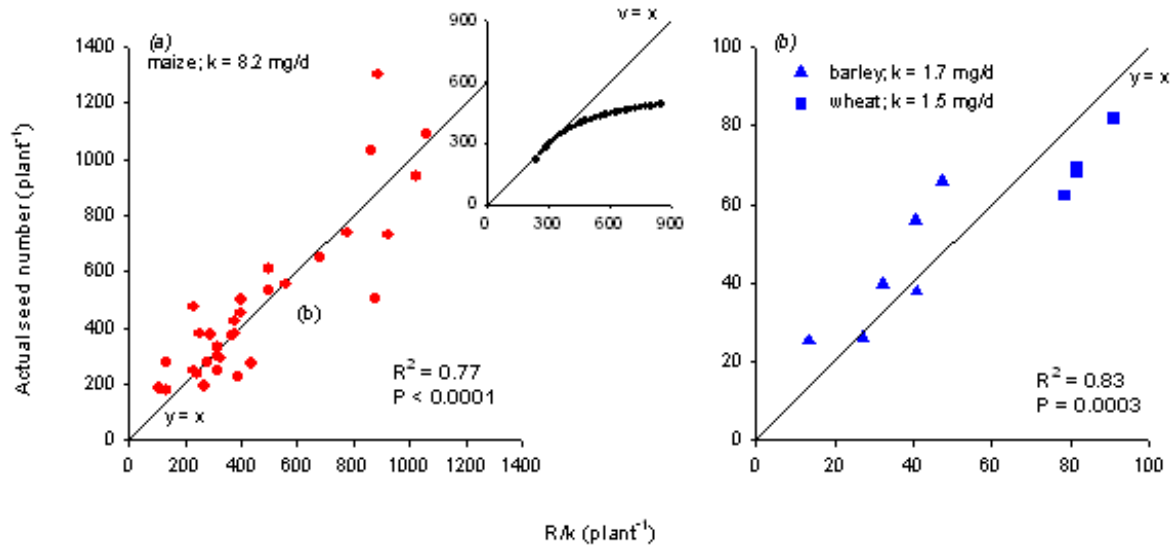

Fig. 2. A model of equitable resource allocation (eq. 1b) describes well seed production for *(a)* prolific maize, *(b)* barley and wheat, but not for *(inset)* single-eared maize. Sources: [3, 4, 5].

Hypothesis 2: A narrow range of seed size resulting from evolutionary and agronomic constraints?

The idea that seed size is under stabilising selection depends on four conditions: (1) mean seed size is conservative for a given species and environment, (2) seed size affects fitness, (3) seed size is heritable, and (4) there is a trade-off between seed size and number. The trade-off between size and number is well established, and seed size heritability is generally large in crop species (Fig. 3).
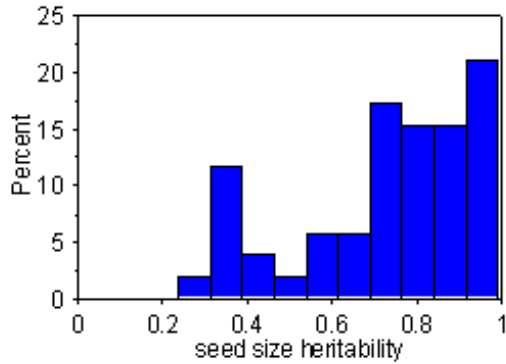
Fig. 3. Frequency distribution of seed size heritability derived from reports for cereals, grain legumes and oilseed crops.

Mean seed size is conservative

Figure 4 illustrates the interannual variation in yield components of soybean crops in the experiment of Kelley et al. [6]: the range of variation in seed size of 46% compared with a range of 291% for seed number. Elliot and Hurley [7] showed interannual variation in reproductive output of trout fry was related to a range of variation in egg size of 24%, compared with a range of 1600% for number. Thus, whereas offspring size varied, the magnitude of this variation was small in relation to the variation in number (hypothesis 2). The generality of the supposedly narrow range of variation in offspring size in relation to number was verified using data sets for plants (n = 166) and fish (n = 54). Maize and sunflower departed from the general pattern, with many cases where variation in seed size was large and comparable to the variation in number. In these crops, where domestication and breeding for one or few viable inflorescences has possibly reduced plasticity in seed number, variation in seed size is large in comparison both to their wild ancestors with multiple inflorescences, and to crops like wheat or soybean where tillers and branches allow for greater responsiveness of seed number to resource availability.
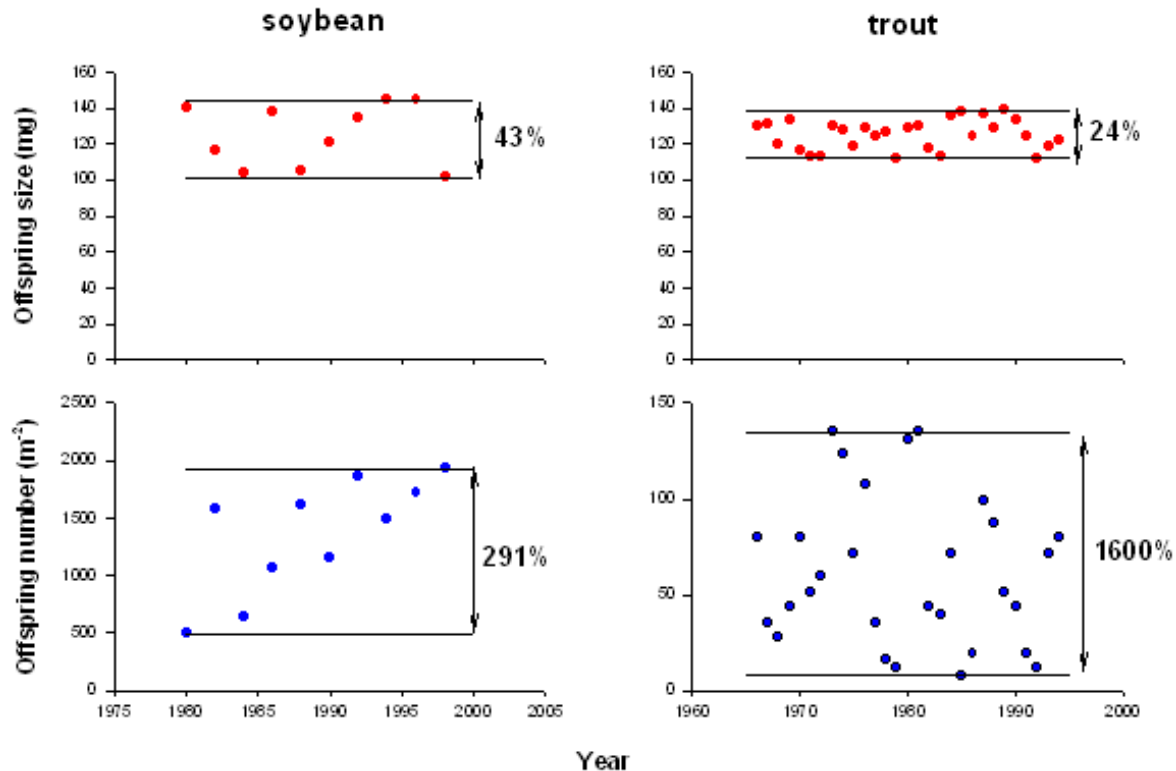
Figure 4. Interannual variation in offspring size and number in soybean and sea-trout fry. Sources: [6, 7].

Stabilising selection for seed size?

There is evidence supporting the concept that natural selection acts directly on the size component of the size-number trade-off. Smith and Fretwell [8] proposed a model relating parental fitness and partitioning of fixed resources among offspring. Variations on this theme led to more complex models accounting for environmental variability, maintenance respiration, parent-offspring conflict and degree of selfing, trade-off between size and number of flowers within a plant, and density-dependent mechanisms. The essence of the original model, however, remains valid particularly for semelparous species that produce numerous offspring that are given little or no parental care; it assumes that (i) there is a minimum size for offspring to be viable, (ii) the relationship between offspring size and its fitness is described by the law of diminishing returns, and (iii) there is a trade-off between size and number. The rationale of the Smith-Fretwell model for stabilising selection of offspring size is simple. Increasing seed size could increase fitness of plants, particularly annuals, as larger seed with larger embryos and more reserves would imply faster emergence and increased competitive ability, greater probability of seedling establishment, access to resources in deeper soil layers, and greater probability of recovery after drought, damage caused by herbivores and other environmental hazards. Beyond a certain size, the parental fitness benefit from larger offspring is offset by the benefit from creating and provisioning additional offspring – hence the optimum size. Some empirical studies are consistent with the Smith-Fretwell model, and further support that both threshold and optimum offspring sizes are higher in less favourable environments [9-16]. The agreement between actual seed production and estimates assuming an equitable partitioning of reproductive resources among offspring in this paper (Fig. 2) is primarily consistent with the Smith-Fretwell model.

Donald [17] provided an insightful account of the process of seed size selection in wheat. The increase in seed size from the earliest wheats to modern varieties involved a "modest doubling" from 20 to 40-45 mg. In analysing an experiment were large seeds (45 mg) were sown alternatively with small seeds (27 mg) of the same wheat variety, he highlighted that the large seeds produced larger seedlings, leading to plants

which outyielded their small-seed counterparts by 57%. As seeds of the two sizes were of the same genotype, they produced grain of the same size. But if the difference in seed size had had a genetic basis, i.e. plants from 45 mg seed producing seed of 45 mg, and plants from 27 mg seed producing seed of 27 mg, a 57% difference in yield in favour of the heavier-seeded plant would have corresponded to 6% fewer seed. Thus, he concluded "two factors, the greater competitive advantage of plants with large seed and the greater prolificacy of plants with small seed would eventually lead to stabilising selection for seed size within wheat crops of mixed genotypes".

Conclusion

Although adaptive interpretations are often speculative, C.M. Donald and others demonstrated the insight gained from consideration of evolutionary aspects of individual plant traits. Comparison of variation in offspring size and number against a normalised scale reinforced the established notion that offspring size is generally more conservative than number. Consistent with Bradshaw's [18] proposal that stability of a given trait can be considered to be at least partially the outcome of the plasticity of other characters, this paper showed that seed size is relatively more variable in plant types where morphological restrictions constraint the plasticity of seed number. An adaptive, narrow range of offspring size maybe a critical element in the number-size equation.

Simulation models can achieve significant accuracy in estimating grain yield through convenient shortcuts to deal with reproductive allocation, e.g. using a stress-responsive harvest index. However, when the purpose of modelling is the understanding of plant biology, and where the interest is to scale up from gene to phenotype, the trade-off between seed number and size is of great significance. Further work along this line may benefit from consideration of the equitable model of resource allocation including a hypothetical "target" seed size, in addition to the "potential" rate of grain filling and grain filling duration currently used in CERES-type models.

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