

Hamilton's rule, imprinting and parent-offspring conflict over seed mass in partially selfing plants

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Abstract

When genes in the offspring control the provisioning of the seed, the optimal seed size can be calculated exactly by applying Hamilton's rule. When seed size is a compromise between mother and offspring, we predict that outcrossing plant species produce larger seeds than selfers. This trend was found in the British flora and in a number of well-studied plant families. The analysis was extended to imprinting, a conditional strategy in which a gene in the offspring takes more resources when derived from the father than from the mother. The conditions for imprinting to be selected were rather restrictive. The analysis is relevant for the current debate about the evolution of imprinting in *Arabidopsis thaliana*.

Introduction

How many resources should a mother give to each of her offspring? Suppose in the mother plant there is a single gene for seed size with many different alleles. For each maternal genotype all seeds are the same size, but seed size differs between mother plants, depending on their genotype. The problem is then to calculate the number of allele copies passed on to the next generation; the allele for which most copies are transmitted wins and goes to fixation (Smith & Fretwell, 1974; see below).

However, it may be that the genotype of the mother is not the sole factor determining the size of all seeds on the plant. If the genotype of the developing seed determines its own size, the calculation of the number of allele copies transmitted becomes different (Charnov, 1982). An allele expressed in the developing embryo or endosperm may increase its transmission by taking more resource from its mother (Hamilton, 1964; Trivers, 1974; Haig & Westoby, 1988; Shaanker *et al.*, 1988; Lloyd, 1992). However, a seed taking more resources does so at the expense of other developing seeds. Some of these other seeds may contain the same allele and for this reason selection does not favour taking ever increasing amounts of resource

from the mother. The optimal seed sizes for genes expressed in parent and embryo are different. Hamilton (1964, p. 48) remarked: 'Thus for one seed to expand at the expense of its neighbours may or may not be advantageous to the inclusive fitness of its genotype but it is certainly not in the interest of that of the parent'.

Haig (1997) further modified this idea by separately examining the allele that the offspring received from its mother and the allele it received from its father. The probability that another seed on the same plant contains the same allele by identical descent is different for the maternally and paternally derived allele in the offspring. For instance, for an outcrossing plant that is fertilized by many males, the probability that two seeds share an allele identical by descent is 50% for the maternally derived allele, but may be close to 0% for the paternally derived allele. Therefore, a conditional strategy – take as much as you can as the paternal allele, but use restraint as the maternal allele – can be selected for (Mochizuki *et al.*, 1996; Haig, 1997, 2000; Wilkins & Haig, 2003). This is known as Haig's kinship theory of genetic imprinting. The conditional strategy can be achieved epigenetically by imprinting; genes with positive effects on embryo or endosperm growth are expressed, switched on, when inherited through the pollen, but silenced when inherited through the seed (Haig, 1997).

While the general ideas above are now firmly established, they still need to be quantified for partly selfing

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organisms, which include the majority of all plant species. In this paper, we show that optimal seed size under offspring control can be calculated exactly using Hamilton's rule. This allows predictions about seed size in outcrossing vs selfing plants. We compare these predictions with literature data. We then ask under which conditions imprinting can evolve and if these conditions are likely to be met in the model species *Arabidopsis thaliana*.

Model and results

Optimal seed mass under maternal control

Smith & Fretwell (1974) plotted the fitness contribution per seed f_x as an increasing, but decelerating, function of seed mass (x). It is simplest to think of f_x as survival per seed. Heavy seeds are more costly to produce and with a limited budget T only T/x seeds can be filled. The absolute fitness (W_x) of a mother with seed mass x is (Smith & Fretwell, 1974):

$$\text{Mother : } W_x = f_x T/x. \tag{1}$$

Optimal seed size for the mother follows from differentiation of fitness W_x with respect to the evolutionary variable x and setting this derivative equal to zero. If we denote the derivative of survival per seed with respect to seed size (df_x/dx) as f'_x , we obtain $f'_x T/x - f_x T/x^2 = 0$ or:

$$f'_x = f_x/x. \tag{2}$$

Optimal seed size for the mother (the Smith-Fretwell or SF seed size) can easily be gleaned from Fig. 1. It is point 1 where the tangent of the f_x curve is a straight line through the origin with slope f_x/x . Without further information about whether an individual seed is selfed or outcrossed, the mother is selected to provision each seed with exactly the same amount of resource.

Calculating relatedness between offspring in inbreeding diploids

Because selfing causes asymmetry in relatedness, we have to be careful in our definitions. The coefficient of relatedness r between two seeds (embryos) J and K is, in the context of our model, best viewed as the probability that K will pass on an allele that J and K have by identical descent, divided by the probability that J itself passes on this allele. Bulmer (1994) formalized this as $r_{JK} = F_{JK}/F_{JJ}$. Here F_{JK} denotes the coefficient of consanguinity between J and K , which is the chance that randomly drawn alleles from J and K are identical by descent. F_{JJ} is the chance that, with replacement, an allele drawn twice from the same individual J is identical by descent. If an individual has two different alleles it is called allozygous and $F_{JJ} = 0.5$. If the individual has two identical alleles, it is autozygous and $F_{JJ} = 1$. For instance, if we consider

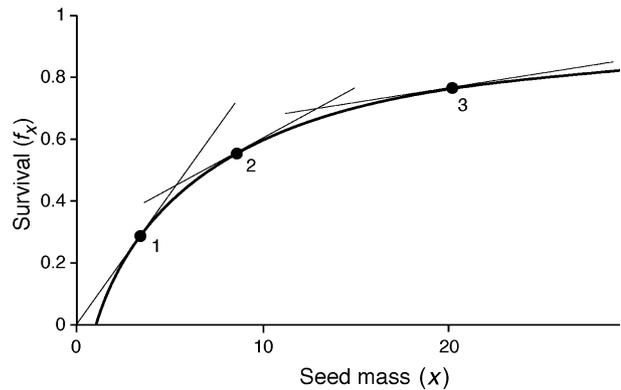


Fig. 1 Relation between mass per seed (x) and the survival per seed (f_x). Under maternal control the optimal seed size (SF seed size) is at point 1 where a line through the origin touches the f_x graph. Here the slope of the line equals f_x/x . When seeds have relatedness = 1, as in full selfing, the optimal seed size for the offspring equals that for the mother. If relatedness among seeds is less, the optimal seed size for the offspring shifts to the right and can be found as the point where the derivative equals rf_x/x . For $r = 0.5$ this means that the optimal seed size for the offspring is found in point 2. For $r = 0.25$ (full outcrossing) this is point 3. For calculations $f_x = \frac{x-1}{x+5}$ was used, with $f_x = 0$ when seeds are too small to be viable ($x \leq 1$).

the relatedness of the allozygous individual J (AB) to the autozygous individual K (AA), $r_{JK} = 0.5/0.5 = 1$ and $r_{KJ} = 0.5/1 = 0.5$. These details do not matter in a large outbreeding population in which all individuals are allozygous and relatedness is simply twice the coefficient of consanguinity.

The average relatedness r_{JK} of a focal seed J , selfed or outcrossed, to another selfed or outcrossed seed K is then specified in Table 1. Next to calculate average relatedness between two random seeds, we averaged over the probabilities that both seeds are selfed (S^2), that the focal seed is outcrossed and the other seed is selfed $[(1-S)S]$,

Table 1 Components of relatedness between focal seeds that are either selfed and outcrossed, and other selfed or outcross seeds on the same plant. Calculation of coefficient of relatedness r is based on a random allele from each seed, this value can be split up in a value for the maternally (m) and paternally derived allele (p). The condition $r = (m + p)/2$ holds for each trio of r , m and p values. The number of competing fathers is n and F denotes the inbreeding coefficient of the population.

| | K: Other seed selfed | | | K: Other seed outcross | | |
|----------------------------|----------------------|------|------|-------------------------|-------|------------------|
| | r_{JK} | m | p | r_{JK} | m | p |
| Maternal parent allozygous | | | | | | |
| J: Focal seed selfed | 0.75 | 0.75 | 0.75 | 0.375 | 0.375 | 0.375 |
| J: Focal seed outcross | 0.50 | 1 | 0 | $0.25 + \frac{1+F}{4n}$ | 0.5 | $\frac{1+F}{2n}$ |
| Maternal parent autozygous | | | | | | |
| J: Focal seed selfed | 1 | 1 | 1 | 0.5 | 0.5 | 0.5 |
| J: Focal seed outcross | 1 | 2 | 0 | $0.5 + \frac{1+F}{4n}$ | 1 | $\frac{1+F}{2n}$ |

that the focal seed is selfed and the other outcrossed [again $(1-S)S$] and that both seeds are outcrossed $(1-S)^2$. Finally, we averaged over the probability F that the mother is autozygous and $1-F$ that she is allozygous. The parameter F denotes the inbreeding coefficient of the population. This yields the average relatedness between two randomly chosen seeds on the same plant:

$$r = F \left[-0.5S^2 + 1.5S + (1-S)^2 \left(0.5 + \frac{1+F}{4n} \right) \right] + (1-F) \left[-0.125S^2 + 0.875S + (1-S)^2 \left(0.25 + \frac{1+F}{4n} \right) \right] \quad (3)$$

In an infinitely large population at equilibrium $F = S/(2-S)$ (Hartl & Clark, 1989).

With some algebra eqn 3 can then be rewritten as

$$r = 0.25(1+S)^2 + \frac{0.5(1-S)^2}{n(2-S)} \quad (4)$$

If all fathers contribute equally to the pollen pool, n is the number of plants that sire seeds on one maternal parent and then compete for resources. If all competition occurs within a single fruit and not between fruits, n is the number of sires per fruit. More generally $1/n$ represents the probability that another competing pollen grain came from the same plant, averaged across all (nonselfed) pollen grains, in which case n may take on noninteger values. Relatedness between seeds increases with the selfing rate and declines with the number of fathers n (eqn 4).

Instead of picking a random allele from the focal individual, we can also select the maternally derived or paternally derived allele and go through the same procedure to estimate the chance that the identical allele is passed on by another seed on the plant (Haig, 1997). The relatedness coefficients differ markedly for the maternally derived (m) and paternally derived allele (p) and $m \geq p$ (Table 1). Using the values in Table 1 and applying the above procedure, gives the relatedness between the maternally derived allele in the focal seed and alleles in other seeds on the same plant:

$$m = F(-0.5S^2 + 0.5S + 1) + (1-F)(-0.125S^2 + 0.375S + 0.5), \quad (5)$$

which, in a large population at equilibrium, reduces to:

$$m = \frac{0.25(1+S)(4-S-S^2)}{(2-S)}. \quad (6)$$

For the paternally derived allele in the focal seed the relatedness coefficient equals:

$$p = F(0.375S^2 + 0.375S + (1-S)^2 \frac{1+F}{2n}) + (1-F) \left[0.5S^2 + 0.5S + (1-S)^2 \frac{1+F}{2n} \right], \quad (7)$$

which, in a large population at equilibrium, reduces to:

$$p = \frac{0.25(1+S)(3S-S^2)}{(2-S)} + \frac{(1-S)^2}{n(2-S)}. \quad (8)$$

When we average over p and m , we obtain again r (eqn 4).

Finally, we need in later calculations the probability q that if seed J has a rare selfish allele the other seeds on the plant also contain this allele by identical descent. This probability is $q_{JK} = F_{JK}/F_{KK}$, i.e. it is twice as high when the other seed is allozygous instead of autozygous. For two seeds of given genotype, r_{JK} and q_{JK} may well be different. However, when we compare two random seeds we have to average over all possibilities as outlined above. From symmetry considerations it then follows that $q = r$.

Applying Hamilton's rule

As noted we need to calculate how many copies of an allele are transmitted through the focal seed and through other seeds on the same plant. Inclusive fitness is the sum of these two fitness components and the coefficient of relatedness estimates the probability that the other seeds transmit an allele present in the focal seed (Hamilton, 1964; Reeve & Keller, 1999). When all seeds are of size x , the fitness contribution of the focal seed is f_x . After the focal seed has taken its share of the resource, $T-x$ resources remain for the others. The inclusive fitness when each seed takes x resources, is then given by:

$$\text{Offspring} : W_x = f_x + \frac{rf_x(T-x)}{x} \quad (9)$$

Next calculate inclusive fitness of a selfish mutant that claims $x + \Delta x$ resource instead of x . The selfish mutant is rare within the population but there is a high probability that the other seeds on the plant share the selfish allele by identical descent. After the focal seed has made its claim, $T-x-\Delta x$ remains for the other seeds. From the other seeds a fraction r will be of size $x + \Delta x$ and a fraction $1-r$ will be of size x , so that the mean seed weight on the plant is $r(x + \Delta x) + (1-r)x$. The number of other seeds can then be calculated as the resource available $(T-x-\Delta x)$ divided by mean seed weight. The inclusive fitness of the selfish mutant is then:

$$\text{Offspring} : W_{x+\Delta x} = f_{x+\Delta x} + \frac{rf_{x+\Delta x}(T-x-\Delta x)}{r(x+\Delta x) + (1-r)x} \quad (10)$$

We can now compare the absolute inclusive fitness of the two types, the type with the highest inclusive fitness wins. This procedure is equivalent to applying Hamilton's rule (Reeve & Keller, 1999). The selfish type (allele) wins when its inclusive fitness is higher than that of the other type. With some rewriting, this implies that $(f_{x+\Delta x} - f_x)/\Delta x > rf_x/x$. For small Δx the left hand side equals the derivative of f_x with respect to seed size x . We thus obtain the Evolutionarily Stable Strategy (ESS) for seed size under offspring control at the point where:

$$f'_x = rf_x/x. \tag{11}$$

Clutton-Brock & Godfray (1991) first derived eqn 11, using a more implicit approach, and several earlier papers (MacNair & Parker, 1978; Parker & MacNair, 1978; Queller, 1984) found it to apply to more restricted cases.

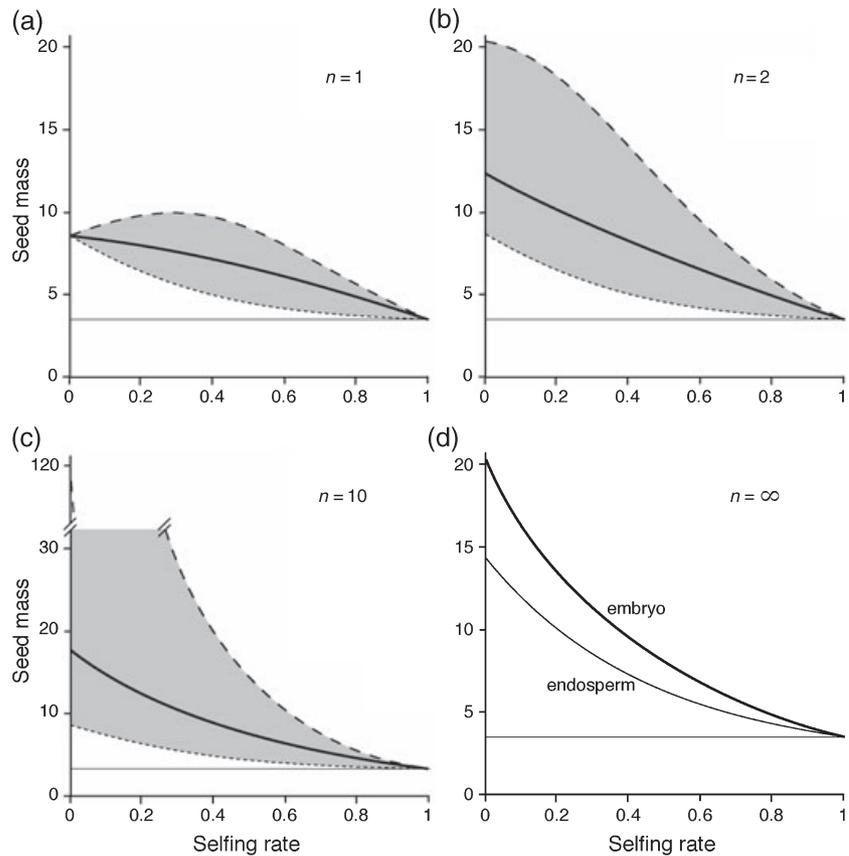
For any shape of the f_x function, optimal seed size can be calculated using eqn 11 and the appropriate value for the coefficient of relatedness. With 100% selfing ($r = 1$), optimal seed size under offspring control equals the SF seed size (eqn 4). With lower relatedness between seeds (low selfing, high number of fathers) the optimal seed size under offspring control is higher than the SF seed size (Figs 1 and 2).

Endosperm control

One could argue that the endosperm also has a major effect on seed size. Calculation of the coefficient of relatedness between two triploid endosperms is problematic because the two maternally derived alleles in the endosperm are identical. Nevertheless, it is interesting to examine by simulation how alleles expressed in the endosperm are selected. We did this by comparing two

alleles in each simulation and carrying on with the winner until we had reached an ESS that could not be invaded by other alleles. Presentation of simulations in Fig. 2d was limited to the case of an infinite number of fathers. With additive gene effects and a $2n$ endosperm (*Oenothera*-type), genetically identical to the embryo, the simulation results matched eqn 11 exactly. With dominance there was a slight (less than 1%) deviation, depending on whether the allele for heavier seeds was dominant or recessive. With a $3n$ (*Polygonum*-type) endosperm and dominance, the same result was obtained. However, with additive gene effects and a $3n$ endosperm there was a systematic bias; optimal seed size was smaller than predicted by eqn 11 (Fig. 2d). The result arises because, with two alleles with additive effects on seed size (b_1 and b_2), there are four endosperm genotypes ($b_1b_1b_1$, $b_2b_2b_2$, $b_1b_1b_2$, $b_2b_2b_1$), corresponding to four seed sizes. The maternal allele now has a double influence, increasing the effects of maternal parent on seed size (Hårdling & Nilsson, 2001). While it is good to acknowledge that this effect exists, it does not qualitatively affect our conclusion about parent offspring conflict and how it depends on the model parameters.

Fig. 2 (a–c) The relation between optimal seed size and selfing rate for $n = 1, 2, 10$ and an infinite number of competing fathers. The SF seed size denotes the maternal optimum at 3.449, which does not depend on the selfing rate. The optimum for the offspring (thick line) lies between the optimum for the maternally derived allele in the offspring (dotted lines) and the paternally derived allele (broken line). If the realized seed size lies in the shaded area imprinting is expected to evolve, as the paternally derived allele in the offspring is selected to take more resource and the maternally derived allele in the offspring is selected to take less. In Fig. 2d the thick line for the offspring (embryo) is compared with the optimal seed size that is reached when a triploid endosperm is in control and the maternal and paternal alleles have additive effects on seed size. For calculations $f_x = \frac{x-1}{x+5}$ was used, so that $\frac{df_x}{dx} = 6/(x+5)^2$. Substitution in eqn 11 yields the ESS seed mass, $x^* = -2 + 3/r + 0.5\sqrt{(4-6/r)^2 + 20}$. r is average relatedness between seeds (eqn 4) and, to calculate seed size for the maternal and paternal allele separately, this parameter can be replaced by its maternal (eqn 6) or paternal (eqn 8) component.



Imprinting

The optimal seed sizes for the maternal and paternal allele in the embryo are shown separately in Fig. 2. Because generally $p > m$, the optimal seed size for the paternally derived allele in the offspring is larger than for the maternally derived allele, the more so if many different fathers compete for resources. For high selfing rates the optimal seed mass for the maternally derived allele in the offspring was close to that for the mother, whereas the two optima diverged at low selfing rates. In general, selfing increases relatedness, which selects for smaller seeds. However, with only one father ($n = 1$) p first decreased with higher selfing and then increased; the minimum was at $S = 0.28$. This resulted in an optimum curve for the relation between the selfing rate and the optimal seed size for the paternally derived allele in the offspring (Fig. 2a).

Imprinting may evolve as a conditional strategy when the embryo can exert sufficient control over seed size to pull it away from the SF seed size towards a value higher than the optimum for the maternally derived allele in the embryo, i.e. into the shaded area in Fig. 2. Two factors make this more difficult. First, imprinting cannot evolve if the surface of the shaded area is zero, which is at $p = m$. This is only the case when either $S = 1$ or when $S = 0$ and $n = 1$. Imprinting is most likely to evolve if the shaded area is large, which will be the case when p and m differ most. By comparing eqns 6 and 8 one can see that the absolute difference between p and m is largest when $S = 2 - \sqrt{3 - \frac{2}{n+1}}$. With a single father $p - m$ is maximal at $S = 2 - \sqrt{2} = 0.586$; with many fathers $p - m$ is maximal at $S = 2 - \sqrt{3} = 0.268$. Selection for imprinting may be strongest at intermediate selfing rates.

Second, imprinting cannot evolve when the embryo is unable to pull seed size past the optimum for the maternal allele in the embryo, into the shaded area. This becomes more difficult if the distance that needs to be bridged is larger, i.e. when the distance between the SF seed size and the optimal seed size for the maternal allele in the embryo is greater. If the embryo cannot exert sufficient control, both alleles in the offspring will be selected to take more and there is no selective advantage to imprinting. The distance between the SF seed size and the lower border of the shaded area is largest with full outcrossing (Fig. 2).

These conditions for imprinting to evolve are most easily met in a species with intermediate selfing and not necessarily in an outcrosser. For instance, with one father and full outcrossing (Fig. 2a), there is no selective advantage to imprinting.

Discussion

Do selfers produce smaller seeds?

If seed size were a compromise between parent and offspring, one would expect seed size to increase with the

outcrossing rate. To test this idea, we first considered trends among common British grassland plants (Grime *et al.*, 1988). The database of Grime *et al.* (1988) combined accurate data on seed mass with qualitative data on the selfing rate for a fairly large (265) number of species. We pooled 58 plant species that were classified as mainly selfing, 120 species with partial selfing and 87 outcrossing species that were either self-incompatible or dioecious. Seed mass was log-normally distributed in this data set (Rees, 1997). The $^{10}\log$ of mean seed mass in the selfing group (-1.437 ; 95% confidence limit = 0.399) was smaller than in the intermediate group (-0.253 ; CL = 0.313) and outcrossing group (-0.202 ; CL = 0.374), in which seeds were of similar size. While it is encouraging that selfers do indeed have smaller seeds in the British grassland flora, there are many confounding effects. Factors like plant size, life history and phylogeny are interrelated with breeding system (Westoby *et al.*, 1997) and it will be difficult, if not impossible, to separate their effects in this data set. The best way to test our hypothesis would be to compare closely related species, which are as similar as possible but differ with respect to their outcrossing rate.

Few data were available in this respect, but they pointed in the predicted direction. *Arabidopsis thaliana* (seed length 0.3–0.5 mm) and *A. suecica* (a hybrid between *A. thaliana* and *A. arenosa*, seed length 0.5–0.8 mm) are selfers. The outcrossing sister species all had larger seeds; *A. arenosa* (0.8–1.2 mm), *A. halleri* (0.8–1.2 mm) and *A. lyrata* (0.8–1.2 mm) (Mitchell-Olds, 2001; Al-Shehbaz & O’Kane, 2002). We also compared *Plantago* species for which accurate information on seed size, breeding system and phylogeny was available (Kuiper & Bos, 1992; Sharma *et al.*, 1999; Ronsted *et al.*, 2002). When we compared species pairs that were closest together in the branches of the phylogenetic tree, all comparisons were consistent with the model prediction. The outcrosser *P. lanceolata* had heavier seeds (1.35 mg) than the intermediate selfer *P. lagopus* (0.34 mg), the outcrosser *P. maritima* had heavier seeds (1.05 mg) than the intermediate selfer *P. coronopus* (0.06 mg) and finally the outcrosser *P. media* (0.57 mg) had heavier seeds than the predominantly selfing *P. major* (0.20 mg). Positive correlations between outcrossing rate and seed size were also reported for 20 species in the tribe Delphinieae (Bosch *et al.*, 2001) and for crucifers (Boaz *et al.*, 1994). Inconsistent with our results is a study on between-population variation in *Leavenworthia crassa* (Lyons, 1996); plants originating from a more selfing population produced heavier seeds in the greenhouse.

Imprinting in *Arabidopsis thaliana* and control over seed size

Some genes are maternally imprinted and paternally expressed in the endosperm of *A. thaliana* (Grossniklaus *et al.*, 2001). It is currently debated whether imprinting

in *A. thaliana* can be expected in the context of Haig's kinship theory of genetic imprinting (Mochizuki *et al.*, 1996; Hurst & McVean, 1998; Wilkins & Haig, 2003) or that it serves another function. Does *A. thaliana* fit our model? In order for there to be selection for imprinting, the embryo must exert sufficient control over seed size that the seed size becomes greater than the optimum for a maternally derived gene in the offspring. Marshall & Ellstrand (1989) estimated $n = 2$ sires per fruit for *Brassica napus*. Estimates of selfing rate of *A. thaliana* ranged between 99.7 and 73.8% (references in Hoffman *et al.*, 2003). A recent study (Hoffman *et al.*, 2003) estimated that only 1% of the flowers were visited in natural populations of this species in Halle, Germany. Nevertheless flowers are protogynous, so that more flower visitation in warmer habitats with abundant insect activity could well result in higher outcrossing rates. With $n = 2$ and 90% selfing the shaded area in Fig. 2b was relatively large (69.1% of the seed size range). Under these conditions the embryo should increase seed size from 3.449 to more than 3.497 before imprinting becomes selectively advantageous. With 1% selfing the shaded area was smaller (16.7% of the seed size range), but the embryo should only increase seed size from 3.449 to more than 3.450 for conditions to favour imprinting. If the species were fully outcrossing seed size under embryo control would need to be greater than 8.582 for imprinting to evolve.

Can the embryo exert enough control over its resource supply to pull the seed size into the shaded area in Fig. 2? The seed consists of three parts with different genetic structure: the embryo, the endosperm and the seed coat. These structures interact in a complex way during seed filling. While each aspect has been extensively studied, their relative importance for seed size is still being discussed. A large role for the endosperm gains support from so-called parent-of-origin studies: if the endosperm receives a double dosage of paternal genomes it develops much more vigorously than if it receives a double dose of maternal genomes (Scott *et al.*, 1998; Alleman & Doctor, 2000). However, this is a rather crude approach and crossing studies have typically shown that the genotype of the paternal parent explains only a small percentage of the variance in seed size. The majority of the variation is explained by genotype and nutrition of the maternal parent (Montalvo & Shaw, 1994; Byers *et al.*, 1997). The crosstalk between embryo, endosperm and maternal tissues is currently of interest to plant physiologists (Ray, 1998), but it would seem to us that, despite the extensive work in this field, we do not know the relative degree of control over seed mass that is exerted by the three tissues.

There are two ways to address the control problem. First, most directly, one could map genes for seed size, examine if these genes are expressed in mother plant, endosperm or embryo and study mutants in which specific genes are silenced. Seed sizes varied considerably

in *A. thaliana* and crosses between lines differing in seed weight showed interesting results, which depended on the direction of the cross (Alonso-Blanco *et al.*, 1999). This would make *A. thaliana* a suitable species for addressing questions about the control of seed size.

Second, if we know the precise shape of the survival curve as a function of seed weight (Fig. 1), we could graphically determine if the observed seed size matches the SF seed size. If the observed seed size in the field were much larger than the SF seed size, this would suggest offspring control over seed size. Many studies, including one on *A. thaliana* (Krannitz *et al.*, 1991), showed that large seeds can survive longer during stressful conditions, can successfully emerge from a greater depth and so on. There are, however, few data that accurately estimated the shape of the survival curve under natural conditions. Winn (1988) carried out an extensive study on the self-compatible *Prunella vulgaris*, using seeds that differed 10-fold in mass. Her results indicated that seed sizes roughly matched, or were smaller than, the SF seed size. It would be interesting to have more such detailed studies, both on plants species with small and large seeds.

Physiologists and ecologists need to combine efforts to solve these questions about relative control by parent and offspring over seed size and *A. thaliana* could well be an ideal species for these studies.

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