

## Review Paper

**Cite this article:** Baskin JM, Baskin CC (2019). How much influence does the paternal parent have on seed germination? *Seed Science Research* **29**, 1–11. <https://doi.org/10.1017/S0960258518000417>

Received: 6 July 2018

Revised: 19 November 2018

Accepted: 25 November 2018

First published online: 10 January 2019

**Keywords:**

epigenetic modification; genomic imprinting; multiple paternity; non-Mendelian genetic effects; parental conflict theory; quality of pollen donor; seed germination; seed provisioning; transgenerational plasticity

**Author for correspondence:**

Carol C. Baskin, Email: [cbask0@uky.edu](mailto:cbask0@uky.edu)

# How much influence does the paternal parent have on seed germination?

Jerry M. Baskin<sup>1</sup> and Carol C. Baskin<sup>1,2</sup>

<sup>1</sup>Department of Biology, University of Kentucky, Lexington, KY 40506-0225, USA and <sup>2</sup>Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY 40546-0312, USA

**Abstract**

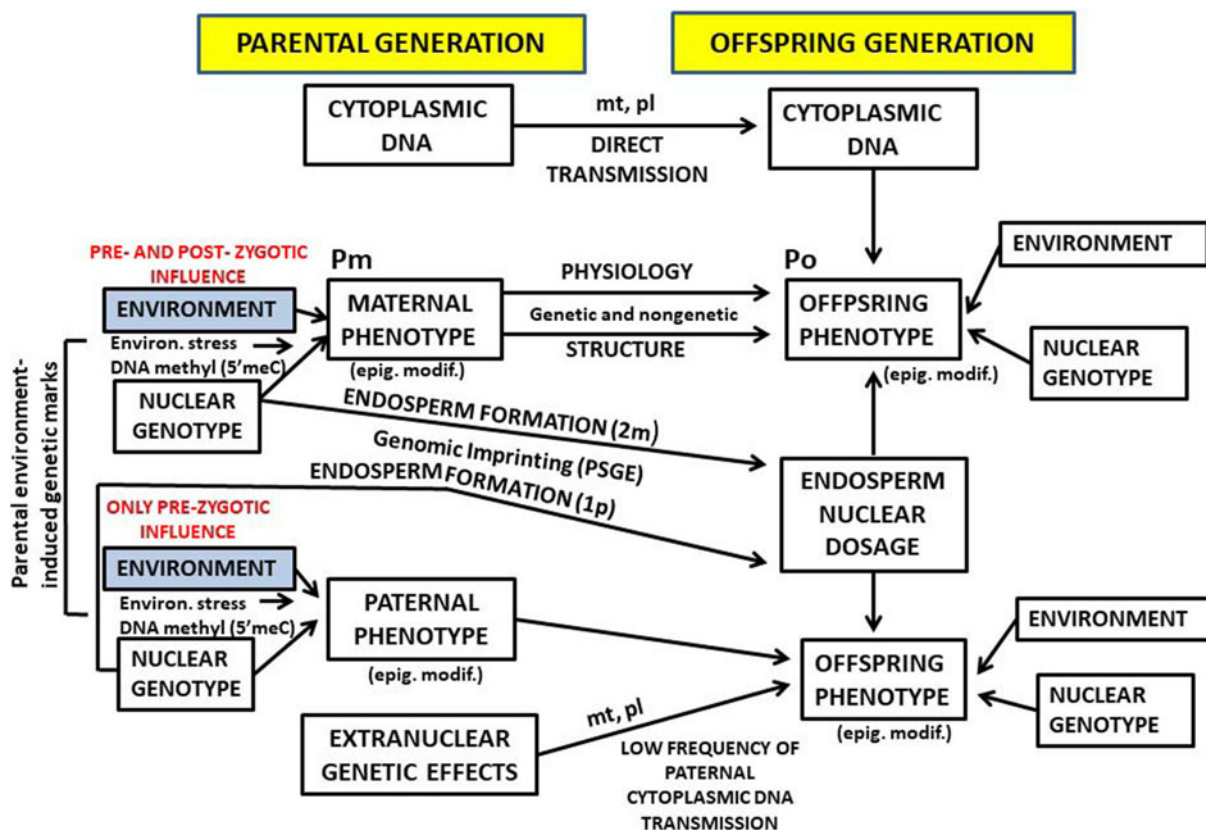
It is well documented that the mother plant has much more influence than the father on seed dormancy/germination, especially of the F<sub>1</sub> offspring, primarily by providing all material (maternally derived tissue) to the diaspore coat(s); by maternal environmental effects and provisioning of nutrient resources, mRNA transcripts, protein, the hormone abscisic acid and nitrate to the seed during its development; and by determining progeny environment via dispersal and phenology. There is some evidence that the paternal influence on seed dormancy/germination of the offspring (seeds) can be mediated through multiple paternity (including mate number and diversity), non-nuclear (cytoplasmic) and nuclear (genotypic) inheritance and paternal environmental effects. Our primary aim was to determine via a literature review the influence (or not) of the paternal parent on seed germination. Altogether, 37 of 59 studies (62.7%) indicated a positive influence of the father on seed germination, although not all of them were statistically significant. In general, however, results of studies reported in the literature do not offer strong support for the paternal parent having a major role in seed germination (or seed size) of his F<sub>1</sub> offspring.

**Introduction**

Offspring traits in plants come from the mother and father, but the mother has more influence on these traits, especially seed dormancy/germination, than the father. Thus, the mother contributes to the traits of her offspring via nuclear and cytoplasmic genetic effects; maternal environmental (including epigenetic) effects; provisioning seeds with nutrient resources, mRNA transcripts, protein, abscisic acid (ABA), which has a positive influence on seed development and can inhibit viviparous germination, and nitrate, which can lower the level of ABA in the seed and act as a signalling molecule in decreasing/overcoming seed dormancy; regulating transfer and distribution of nutrient resources from endosperm to embryo; controlling nutrient storage in and growth of the perisperm, a maternal sporophytic (2n) tissue for embryo growth in seeds of some angiosperms; providing two-thirds of the genetic contribution to the triploid endosperm; and supplying 100% of materials for development of seed coat and diaspore structures external to the seed (Fig. 1). In short, then, the mother plant plays the major role in determining, via diaspore dormancy and dispersal characteristics, maternal architecture (including growth form and height) and seasonal effects (phenology), when and where the seed germinates (Roach and Wulff, 1987; Donohue, 1999, 2009; Raz *et al.*, 2001; Finkelstein *et al.*, 2002; Frey *et al.*, 2004; Alboresi *et al.*, 2005; Kucera *et al.*, 2005; Kanno *et al.*, 2010; Matakias *et al.*, 2009; Herman and Sultan, 2011; Thomson *et al.*, 2011; Costa *et al.*, 2012; Jacobs and Lesmeister, 2012; Rubio de Casas *et al.*, 2012; Tamme *et al.*, 2014; Vu *et al.*, 2015; Piskurewicz *et al.*, 2016; Yan and Chen, 2017; Augspurger *et al.*, 2017; Povilus *et al.*, 2018).

Furthermore, evidence is accumulating that the store of active hydrolytic enzymes, antimicrobial substances and nutrient elements in the dry, dead cells of the maternally derived seed coat, pericarp and floral bracts, which can be released upon rehydration, play a role in seed persistence in the seed bank, seed germination and seedling establishment and vigour (Godwin *et al.*, 2017; Raviv *et al.*, 2017a,b). Finally, in seeds of weedy holoparasitic species of *Orobanch* the perisperm is involved in reception of the simulant from the host plant that is required for the parasite to germinate (Plakhine *et al.*, 2012).

Influence of the father on the traits of his offspring may occur via nuclear (genotype) and non-nuclear genetic material [i.e. mostly plastids transmitted to the progeny by pollen at a low frequency (Corriveau and Coleman, 1988; Azhagiri and Maliga, 2007)] and paternal environmental (including epigenetic) effects (Schmid and Dolt, 1994; Lacey, 1996; Galloway, 2001a,b; Herman and Sultan, 2011) (Fig. 1). In the gynodioecious species [coexistence of male-sterile (female) and hermaphrodite plants in the same natural interbreeding population] *Silene vulgaris* and *S. acaulis*, parental leakage of mitochondrial DNA can result in biparental or strictly paternal inheritance of the mitochondrial genome (Welch *et al.*, 2006; McCauley and Olson,



**Fig. 1.** Conceptual model of the various ways in which maternal and paternal plants can contribute to the phenotype of their progeny. The maternal phenotype portion of the diagram is modified from Roach and Wulff (1987), and paternal phenotype portion is based on information from various sources. Not shown are the various interactions among the maternal environment (Em), maternal nuclear genotype (Gm), offspring environment (Eo) and offspring nuclear genotype (Go), such as  $Gm \times Em$  in determining maternal phenotype (Pm) and  $Gm \times Eo$ ,  $Em \times Eo$  and  $Gm \times Em \times Eo$  in determining offspring phenotype (Po) (e.g. see Rossiter, 1996). DNA methyl (5'meC), DNA methylation; epig. modif., epigenetic modification; mt, mitochondrion; pl, plastid; PSGE, parent (maternal or paternal) specific gene expression; 2m, 2x (where x = base chromosome number), contribution of maternal parent to endosperm; 1p, 1x, contribution of paternal parent to endosperm. The contributions of P<sub>m</sub> to P<sub>o</sub> via physiology and structure can be found in the Introduction.

2008; Pearl *et al.*, 2009). In most angiosperms, the contribution of the father to the embryo of sexually produced offspring via non-nuclear genetic material is generally minimal compared with that of the mother. In gymnosperms, plastid inheritance is paternal in the conifers, whereas mitochondrial inheritance is paternal in some (taxonomic) families and maternal in others, including the largest family Pinaceae (Mogensen, 1996).

In their highly-cited review of 'Maternal effects in plants', Roach and Wulff (1987) included a very short section on paternal effects. However, although the authors refer to several studies on paternal cytoplasmic inheritance, other non-nuclear *per se* paternal environmental effects on offspring performance are not mentioned. The primary purpose of this paper is to review the literature on the influence of the paternal parent on germination of F<sub>1</sub> seeds. We also briefly discuss the influence of the pollen parent on seed size and development.

### Influence of paternal parent on seed germination

Multiple paternity in plants, which encompasses the number of pollen donors and the non-random ability of the donors to sire offspring (Snow and Spira, 1991a,b), is thought to be common and to be caused by (1) sequential visits by several pollinators, each carrying pollen from a different single male; (2) deposition on the stigma of a mixed pollen load by a single pollinator; and

(3) deposition on the stigma of a mixed pollen load by several pollinators; and to have fitness consequences (Ellstrand, 1984; Marshall and Ellstrand, 1985, 1986; Brown *et al.*, 1986; Ellstrand and Marshall, 1986; Marshall, 1988, 1990, 1991; Marshall and Whittaker, 1989; Karron and Marshall, 1990; Dudash and Ritland, 1991; Ibarra-Perez *et al.*, 1996; Campbell, 1998; Bernasconi, 2003; Mitchell *et al.*, 2005; Karron *et al.*, 2006; Teixeira and Bernasconi, 2007; Llaurens *et al.*, 2008). Using microsatellite DNA markers, Reusch (2000) also demonstrated multiple paternity in *Zostera marina*, a marine angiosperm with hydrophilous (subaqueous) pollination.

The rank order of one, two, three and five pollen parents for seed germination of the F<sub>1</sub> offspring of the tropical herb *Costus allenii* was three (76.6%) > two (72.9%) > one (67.0%) > five (63.0%) and not statistically significant; standard deviations ranged from 11.5 to 16.9% (Schemske and Paulter, 1984). Mean germination percentage across pollen donors was higher (but not significantly so) for seeds of *Vaccinium corymbosum* flowers pollinated by three pollen donors than for those of flowers pollinated by a single donor (Vander Kloet and Tosh, 1984). In a study of single *vs* mixed donor crosses in *Chamaecrista fasciculata*, an annual legume with physical dormancy, germination (ca 38–47% for single-donor progeny and ca 34–37% for three-donor progeny) did not differ significantly among selfed, near-crossed and far-crossed seeds (not scarified, overwintered outside) from

single-donor and three-donor pollen loads. For all crosses (single- and three-donor pollen donors), the range of relative performance (RP) for inbreeding depression (see Appendix) was narrow, i.e. – 0.04 to 0.09 (Sork and Schemske, 1992). In general, multiple pollinations did not increase germination percentage in seeds of *Vaccinium elliotii* (Wenslaff and Lyrene, 2001).

Seed germination percentage of the rare endemic *Cochlearia bavarica* did not increase with number of pollen donors, i.e. one, three and nine from the same population and nine from a neighbouring population. However, pollen recipient (maternal parent) had a significant effect on germination percentages (Paschke *et al.*, 2002). In another study, *C. bavarica* germination percentage did not differ statistically between seeds of one pollen donor hand-cross pollinated plants (47.4%) and those of open-pollinated plants (40.8%), ‘...which likely involves less similar or even several pollen donors’ (Fischer *et al.*, 2003). However, assuming several pollen donors for open-pollinated plants, RP was –0.14 (see Appendix). In which case, seeds from a single-pollen donor outperformed those from multiple-pollen donors (see Appendix).

The results of comparisons by Himes and Wyatt (2005) of self-sterile and self-fertile multiple and (a) single pollen donor(s) on seed germination percentage of *Asclepias exaltata* were as follows: (1) self-sterile single donor > self-sterile multiple donors; (2) self-sterile single donor = self-fertile single donor; (3) self-sterile single donor = self-fertile multiple donors; (4) self-fertile single donor > self-sterile multiple donors; and (5) self-fertile single donor = self-fertile multiple donors. Thus, germination percentages of seeds sired (fathered) by single donors were equal to or greater than those of seeds sired by multiple donors. In weedy *Raphanus sativus*, pattern of seed germination (days to emergence of each seedling) differed ( $P < 0.0001$ ) among maternal plants but not among the three pollen donors; altogether 97.1% of 450 seeds planted germinated (Marshall *et al.*, 2007). However, pollen donor did have a significant effect on some aspects of fitness, i.e. growth and reproduction (Marshall *et al.*, 2007; see also Marshall and Whittaker, 1989; Karron and Marshall, 1990). Maternal, but not paternal, parent had a significant effect on germination percentage of the wind-pollinated tree *Betula pendula* (Pasonen *et al.*, 2001).

In a study of the effect of pollen load size and donor diversity on *Mirabilis jalapa*, days to seedling emergence did not differ significantly among five pollination treatments: (1) large load/multiple donors; (2) large load/single donor; (3) small load/multiple donors; (4) small load/single donor; and (5) single outcross pollen grain. Neither was there a maternal effect on days to emergence (Niesenbaum, 1999). Thus, there was no effect of donor diversity on days to seedling emergence. Also, there was no effect of donor diversity on seed mass. The number of donors did not have a significant effect on proportion of seeds of *Collinsia heterophylla* that germinated. However, proportion of seeds that germinated was significantly affected by pollen recipient  $\times$  paternity diversity, showing that seeds of some maternal plants germinated better when sired by multiple donors (Lankinen and Madjidian, 2011). Neither germination percentage of seeds of the weedy annual mustard *Raphanus raphanistrum* (Snow, 1990) nor those of the bignoniaceous woody vine *Campsis radicans* (Bertin, 1986) differed significantly between progeny of single- and multiple-donor pollinations. Furthermore, neither germination nor number or mass of seeds from fruits sired by one, three and five pollen donors differed significantly in *C. radicans* (Bertin, 1986). However, the best pollen donors of this species

gave rise to statistically more and heavier seeds than the donor mixtures, and although percentage germination was higher for seeds sired by the best donors (46 vs 41%) the difference was not significant.

Seeds of *Swertia perennis* from open-pollinated (i.e. natural, not supplemented by hand pollination, multiple-pollen donors assumed) flowers germinated to 40.83%, whereas those from flowers whose stigmas were saturated with hand-crossed pollen from one donor germinated to 32.24% ( $P < 0.05$ ) (Lienert and Fischer, 2004). Thus, the RP was 0.21, showing that seeds from multiple-pollen donors outperformed those from a single-donor (see Appendix). The authors suggested that the difference might be due to pollen quality, i.e. lower pollen quality representing the single donor than that of open pollen, which they suggested was ‘... most likely from several donors’. In a pollen competition experiment with *Dalechampia scandens*, there was no evidence for paternal (or maternal) effects on seed germination. Furthermore, paternal effects on seed maturation time, seed mass and seedling vigour at 1 month were limited and not statistically significant (Pélabon *et al.*, 2016).

Emergence (germination) of all seedlings of *Asclepias speciosa* from crosses by three donors in a pollen competition experiment (84.8%) was significantly higher than that of seedlings in the single donor experiment (74.8%) (Bookman, 1984). The author stated that, ‘Donors which are superior competitors, therefore, father more seedlings with a higher percentage of emergence than seedlings fathered by all donors’. However, when other results of her study also were considered, Bookman suggested that the differences in seedling emergence were not due to higher pollen vigour of the competitors that fathered the seedlings with the highest emergence percentages but to sperm quality or fertilizing ability.

In *Crepis tectorum* subsp. *pumila*, an alvar species on the Baltic island of Öland (SE Sweden), pollen donor had a significant ( $P < 0.05$ ) effect on seed mass and width and a marginally significant ( $P = 0.053$ ) effect on seed length, and seeds that germinated had a significantly greater mass, length and width than those that did not germinate (Andersson, 1990). Thus, the author concluded that genetic variance among the pollen donors was responsible for these differences. However, Mazer and Gorchoff (1996) questioned this claim. They suggested that maternal effects, extranuclear genes, environmentally induced gene expression acting differently among the pollen donors or gametophytic selection within different pollen donors before pollen maturation could rule out additive genetic variation as being responsible for these differences. Recently, Marshall and Evans (2016) presented strong evidence that the ability of pollen donor families of *Raphanus sativus* to sire seeds in mixed pollinations under competition (i.e. with other pollen donors) is heritable and can respond to selection.

Pollen donor had a significant effect on seed germination rate (speed) but not on germination success (%) in *Iris hexagona*. The variation in germination rate of seeds of this species among pollen donors indicated ‘... a potential for a paternal contribution to seed quality’. Pollen donor  $\times$  parental population was significant for both germination rate and germination success (Van Zandt and Mopper, 2004). In a study of cryptic self-fertility in *Campsis radicans* by Bertin *et al.* (1989), days to germination of seeds sired by (1) pollen recipient/pollen donor 12 (maternal and paternal parent selfed) and pollen donor 1 (outcross paternal parent), and (2) pollen recipient/pollen donor 12 and pollen donor 3A were: self – 24.2, cross – 25.3; and self – 36.6, cross – 33.7, respectively. Self and cross seeds sired by 12/1 did not differ

significantly in days to germination, whereas self seeds sired by 12/3A germinated in significantly fewer days than outcrossed seeds. Bertin (1990) tested the effect of different pollen ratios of two donors (paternal parents) on germination percentage of seeds produced on two pollen recipients (maternal parents) of *C. radicans*. For pollen recipient 8, germination percentage of seeds from four pollen combination ratios (amount) of two pollen donors were [(2:3A) = (2:1)] < [(1:10) = (10:3)]. For pollen recipient 10, germination percentage of seeds from two pollen combination ratios were (2:3) < (2:1). Thus, not only pollen donor identity *per se* but also the ratio of the amount of pollen from different donors in a multiple-donor pollen load may affect seed germination.

In nature, plants can be limited in the number of seeds produced due to low pollinator activity. Experimentally, pollen limitation is shown to occur when plants that are open-pollinated plus hand-cross pollen supplemented ( $P_s$ , treatment) produce more seeds than those that are open-pollinated only ( $P_o$ , control), i.e. no pollen supplementation (Burd, 1994; Larson and Barrett, 2000; Ashman *et al.*, 2004; Knight *et al.*, 2005). Only a small percentage of the numerous studies on pollen limitation have measured the germination responses of seeds from treatment vs control, and some of them showed that pollen supplementation increased seed germination percentage. Of 30 cases (18 species) reviewed by Baskin and Baskin (2018) that compared germination of seeds produced by  $P_s$  and  $P_o$  plants,  $P_s > P_o$  in 12,  $P_s = P_o$  in 11 and  $P_s < P_o$  in 7. Thus, based on relative performance (see Appendix), in 40% of the cases pollen supplementation enhanced germination percentages/rate (speed). In these 12 cases, pollen supplementation may have been equivalent to an increase in number/quality of pollen donors.

For seeds of *Eschscholzia californica*, dormancy in interpopulation crosses ‘... seems to have been maternally inherited, although in a few cases (828-4, 873-2) the pollen parent may have had some effect’ (Cook, 1962). In a study of the quantitative genetics of life history and fitness components of *Raphanus raphanistrum*, Mazer (1987a) found no effect of pollen parent on seed germination date or on seed mass. Twelve of 15 paternal genotypes of *Raphanus sativus* exhibited higher rates of germination (1/days to germinate) at high than at low or medium planting densities (Mazer and Schick, 1991a). In another study by these authors on *R. sativus* (Mazer and Schick, 1991b), paternal genotype had a significant effect on germination rate in medium planting density plots, but not in low and high planting density plots.

A study of the dark germination of reciprocal hybrid 6-mo afterripened seeds from light-requiring (R) and indifferent (I) tobacco (*Nicotiana glauca*) selections (Kasperbauer, 1968) showed that both parents contributed to light sensitivity of the seeds, but the contribution of the seed parent was greater [or slightly greater *sensu* Karssen *et al.* (1983)] than that of the pollen parent, i.e. germination percentage of R [seed (maternal) parent] × I [pollen (paternal) parent] in darkness was < (I × R). Overall, (R × R) < (R × I) < (I × R) < (I × I) (uninterrupted darkness) and (R × R) = (R × I) = (I × R) = (I × I) (illuminated). Interestingly, in a much earlier study than that of Kasperbauer, Honing (1930) reported that the light requirement for germination of tobacco seeds was influenced by both parents, with the maternal parent predominating. The results of a diallel cross between five sugar beet (*Beta vulgaris*) plants showed that genotype of the maternal parent controlled germination to a large extent (Battle and Whittington, 1971). Reciprocal hybrid seeds of lettuce (*Lactuca sativa*) showed paternal control over seed

dormancy. Genotype MQS was more dormant than 466, and 466 (seed parent) × MQS (pollen parent) was more dormant than MQS × 466 (Rideau *et al.*, 1976). Seed dormancy in the annual weedy mustard *Sinapis arvensis* had both a maternal and an embryo component, but there was an ‘... overriding importance of the maternal genotype in seed dormancy ...’ (Garbutt and Witcombe, 1986). Reciprocal crosses of the most dormant (Th<sub>7</sub>) and least dormant (M<sub>30</sub>) lines of *Petunia hybrida* showed paternal control over seed dormancy (Girard, 1990). The order of seed dormancy of parents and reciprocal hybrids was Th<sub>7</sub> > (M<sub>30</sub> × Th<sub>7</sub>) > (Th<sub>7</sub> × M<sub>30</sub>) > M<sub>30</sub> for primary dormancy and for the ability of the seeds to enter secondary dormancy. Thus, dormancy is predominantly under paternal control.

In a diallel cross using five parental plants (A→E) of *Lupinus texensis*, maternal and paternal effects on germination percentage were similar in A, C, D and E. For parental plant B, however, seeds of the paternal outcross germinated to a considerably higher percentage than those of the maternal outcross and self, which were similar. Both maternal and paternal parents and their interaction significantly affected seed mass, and seeds that germinated had significantly more mass than those that did not germinate (Helenurm and Schaal, 1996). The paternal parent had significant effects on germination time of the progeny in two of three sets of reciprocal diallel crosses in the monocarpic perennial species *Aster kantoensis*, whose seeds are non-dormant at maturity (Kagawa *et al.*, 2011).

For the grass *Anthoxanthum odoratum*, paternal genotype did not have an overall effect on germination percentage, but in two of six randomized blocks in the experimental design it did have a significant effect on germination percentage. Also, germination percentage differed significantly for seeds sired by different fathers in four of the six blocks for maternal genotype D2 (Schmitt and Antonovics, 1986). For *Lychnis flos-cuculi*, Biere (1991a,b) found significant differences for germination among paternal offspring within families of female progeny and significant variation in time to emergence of progeny of maternal and of paternal parents with different genotypes. Male parents had a significant influence on seed germination in within-population crosses of *Lobelia cardinalis* (Schlichting and Devlin, 1992). Germination of seeds from crosses between the weedy *Silene vulgaris* and the narrow Swedish alvar endemic *S. uniflora* var. *petraea* was strictly determined by the pollen parent. Thus, hybrid seeds germinated to the same percentage and rate as outcrossed (non-hybrid) seeds of the paternal species rather than to a percentage and rate intermediate between those of the parental species (Andersson *et al.*, 2008). The authors hypothesized ‘... that the germination behavior of *Silene* seeds is affected by nonnuclear (cytoplasmic) factors inherited from the male parent or that nuclear genes from the maternal parent are “silenced” during germination’.

Days to emergence in seeds of *Campanula americana* did not differ between high and low pollen loads, but there were significant maternal and paternal effects on this trait. Seed mass had no effect on days to emerge (Richardson and Stephenson, 1992). Pollen parent had a significant effect on germination percentage in *Purshia tridentata* seed progeny in response to 2 weeks of chilling (cold stratification). Among-year variation in maturation environment was not significant, indicating no paternal environmental effect (Meyer and Pendleton, 2000). Paternal genotype of *Eucalyptus globulus* had a significant effect on six measures of proportion and rate (speed) of seed germination (Rix *et al.*, 2012). In red (R, *Morus rubra*) and white (W, *M. alba*) mulberry, progeny of W mothers had the highest

cumulative fitness (Burgess and Husband, 2004). Offspring (seeds) of W mothers germinated to a significantly higher percentage than those of R and hybrid (R × W) mothers, which did not differ. However, the paternal parent did not have an effect on cumulative fitness or germination, and paternal × maternal interactions were not significant. Thus, the authors attributed the strong influence of the mother and lack of influence of the father on fitness to non-nuclear (maternal) effects.

Sire (paternal parent) had a significant effect on percentage and time to germinate and on dormancy in seeds of *Nemophila menziesii* (Platenkamp and Shaw, 1993). However, in a follow-up study on this species, Byers *et al.* (1997) found that the paternal effect on time to germinate (and on seed mass) was weak and inconsistent. In both studies, the dam (maternal parent) had a greater effect on time to germinate than the sire. In *Brassica campestris*, percentage germination of F<sub>1</sub> (high pollen load HF<sub>1</sub>) was greater than that of F<sub>1</sub> (low pollen, LF<sub>1</sub>), but there were no second generation effects, i.e. no difference in percentage germination of HF<sub>1</sub> and LF<sub>1</sub> progeny using the same amount of pollen. However, there was a paternal influence on plant fitness, including germination (Palmer and Zimmerman, 1994). Lassere *et al.* (1996) found no effect of pollen competition on seedling emergence time in *Silene latifolia*. However, paternal parents had a significant effect on days required for seedling emergence.

In *Campanula rapunculoides*, strength of self-incompatibility (weak, intermediate, strong) of neither the father nor the mother had a significant effect on seed germination (Good-Avila and Stephenson, 2003). Germination percentage of seeds of *Silene latifolia* was strongly influenced by the population of origin of the female parent but not by that of the male parent (Jolivet and Bernasconi, 2007). For *S. latifolia*, number of pollen donors (one vs two) had no effect on percentage or rate (speed) of germination, whereas paternal family had a significant effect on both measures of germination (Teixeira *et al.*, 2009). Many studies have shown the effects of the environment of the maternal plant during seed formation/maturation on germination, but very little attention has been given to paternal environmental effects, which can be prezygotic only (Fig. 1). However, although paternal environmental effects are considered to be minimal they do occur. *Raphanus raphanistrum* seeds sired by pollen of low- vs high-nutrient stressed plants did not differ in number of days to germination (Young and Stanton, 1990). In a growth chamber experiment on *Plantago lanceolata*, paternal (prezygotic) temperature influenced seed germination more than maternal (prezygotic or postzygotic) temperature (Lacey, 1996). However, in a follow-up combined growth chamber-field experiment on this species there was essentially no prezygotic paternal or maternal temperature effect on germination, whereas postzygotic (maternal) temperature strongly influenced germination (Lacey and Herr, 2000). Seeds of male parents of *Solidago altissima* grown in soil germinated faster than seeds of male parents grown in sand (Schmid and Dolt, 1994). The authors suggested that this positive effect on germination, as well as that on post-germination growth, was probably due to differences in pollen quality than in pollen quantity. In studies by Galloway (2001a,b) and Etterson and Galloway (2002), the (prezygotic) light environment of the pollen parent had significant effects on seed germination in the winter annual/strict biennial *Campanula americana*. However, the expression of paternal effects on germination percentage and rate, and also on seed mass, depended on the maternal light (high, medium, low) environment. In animals, environmentally (level of competition) induced (adaptive) paternal effects

have been unequivocally demonstrated in the broadcast-spawning marine invertebrate the solitary ascidian *Styela plicata* (Crean *et al.*, 2013).

Androdioecy refers to the coexistence of males (female-sterile, thus produce only pollen) and hermaphrodites (produce both pollen and ovules/seeds) in a breeding population (Pannell, 2000). We have found only three cases in which germination percentages of male-sired seeds (MS) were compared with those of (outcross) hermaphrodite-sired seeds (HS). In *Datisca glomerata* MS = HS (Riesberg *et al.*, 1993), *Fraxinus ornus* MS = HS (Verdu *et al.*, 2004) and *Laguncularia racemosa* Ms > HS (Landry and Rathcke, 2007). In the trioecious (population consisting of males, females and hermaphrodites) cactus *Pachycereus pringlei*, germination percentage of seeds of females pollinated by males was higher than that of seeds in the other pollination treatments, i.e. seeds of females × males germinated to higher percentages, but not significantly (Sosa and Fleming, 1999).

To summarize, in 37 of the 59 studies (62.7%) discussed above on the influence of the paternal parent on seed germination, we conclude that the father had a positive influence on germination, whereas in the other 22 studies it did not (Table 1, see footnote to table).

### Influence of paternal parent on seed size and development

As with seed dormancy/germination, most studies on the parental effects on seed size have shown that the paternal influence on seed development and seed mass is small or non-existent, and when there is a paternal effect on seed size it is usually considerably smaller than that of the maternal parent (e.g. Antonovics and Schmitt, 1986; Marshall and Ellstrand, 1986; Mazer *et al.*, 1986; Mazer, 1987b; Marshall, 1988, 1991; Nakamura and Stanton, 1989; Pittman and Levin, 1989; Fenster, 1991; Richardson and Stephenson, 1991; Lyons, 1996; Lacey *et al.*, 1997; Shaw and Byers, 1998; de Jong and Scott, 2007; Holland *et al.*, 2009; Diggle *et al.*, 2010; de Jong *et al.*, 2011; Li *et al.*, 2015; Pélabon *et al.*, 2016). However, although maternal genotype explained 29.3% of the variation in seed size in reciprocal crosses among four accessions of *Arabidopsis thaliana*, the paternal genotype explained ‘... a substantial proportion of the variation (10.4%)’ (House *et al.*, 2010). A recent study by Pires *et al.* (2016) showed that paternal effects on the control of seed development in *Arabidopsis thaliana* exists but are buffered by the maternal genome, i.e. genomic imprinting, an epigenetic mechanism for the parent-of-origin-specific [female or male (monoallelic)] expression of alleles that, in plants, occurs mostly in the endosperm of the developing seed (Vinkenoog *et al.*, 2003; Köhler *et al.*, 2012; Gehring, 2013; Pires, 2014; Rodrigues and Zilberman, 2015; Pires *et al.*, 2016).

More specifically, *MEDEA* (*MEA*) is an imprinted maternally expressed gene essential for normal seed development. Thus, seeds of *Arabidopsis thaliana* that maternally inherit a loss-of-function *mea* allele exhibit excessive cell proliferation and abort when the pollen parent is accession *Ler* (Grossniklaus *et al.*, 1998; Pires *et al.*, 2016). Pires *et al.* (2016) have shown that when *mea* ovules are pollinated by some other accessions of *A. thaliana* the paternal effect is released and the seeds develop normally, i.e. *mea* seed abortion can be paternally suppressed. They suggest that *MEA* acts as a maternal buffer against the paternal genome on seed development and conclude that this provides support of the (intra-genomic) parental conflict theory in angiosperms whose seeds are sired by multiple donors.

**Table 1.** Positive (+) or no positive (0) influence of the paternal parent on seed germination [percentage and/or rate (speed)] of F<sub>1</sub> offspring (seeds) in 59 studies on 45 species of angiosperms [3 monocots (M) and 42 eudicots] in 38 genera and 27 families

Species	Family	Influence on seed germination*	References
<i>Anthoxanthum odoratum</i>	Poaceae (M)	+	Schmitt and Antonovics, 1986
<i>Asclepias exaltata</i>	Apocynaceae	0	Himes and Wyatt, 2005
<i>Asclepias speciosa</i>	Apocynaceae	+	Bookman, 1984
<i>Aster kantoensis</i>	Asteraceae	+	Kagawa <i>et al.</i> , 2011
<i>Beta vulgaris</i>	Amaranthaceae	0	Battle and Whittington, 1971
<i>Betula pendula</i>	Betulaceae	0	Pasonen <i>et al.</i> , 2001
<i>Brassica campestris</i>	Brassicaceae	+	Palmer and Zimmerman, 1994
<i>Campanula americana</i>	Campanulaceae	+	Richardson and Stephenson, 1992
<i>Campanula americana</i>	Campanulaceae	+	Galloway, 2001a
<i>Campanula americana</i>	Campanulaceae	+	Galloway, 2001b
<i>Campanula americana</i>	Campanulaceae	+	Etterson and Galloway, 2002
<i>Campanula rapunculoides</i>	Campanulaceae	0	Good-Avila and Stephenson, 2003
<i>Campsis radicans</i>	Bignoniaceae	+	Bertin, 1986
<i>Campsis radicans</i>	Bignoniaceae	+	Bertin <i>et al.</i> , 1989
<i>Campsis radicans</i>	Bignoniaceae	+	Bertin, 1990
<i>Chamaecrista fasciculata</i>	Fabaceae	0	Sork and Schemske, 1992
<i>Cochlearia bavarica</i>	Brassicaceae	0	Paschke <i>et al.</i> , 2002
<i>Cochlearia bavarica</i>	Brassicaceae	0	Fischer <i>et al.</i> , 2003
<i>Collinsia heterophylla</i>	Plantaginaceae	+	Lankinen and Madjidian, 2011
<i>Costus allenii</i>	Costaceae (M)	0	Schemske and Pautler, 1984
<i>Crepis tectorum</i> subsp. <i>pumila</i>	Asteraceae	+	Andersson, 1990
<i>Dalechampia scandens</i>	Euphorbiaceae	0	Pélabon <i>et al.</i> , 2016
<i>Datisca glomerata</i>	Datisceae	0	Riesberg <i>et al.</i> , 1993
<i>Eschscholzia californica</i>	Papaveraceae	+	Cook, 1962
<i>Eucalyptus globulus</i>	Myrtaceae	+	Rix <i>et al.</i> , 2012
<i>Fraxinus ornus</i>	Oleaceae	0	Verdu <i>et al.</i> , 2004
<i>Iris hexagona</i>	Iridaceae (M)	+	Van Zandt and Mopper, 2004
<i>Lactuca sativa</i>	Asteraceae	+	Rideau <i>et al.</i> , 1976
<i>Laguncularia racemosa</i>	Combretaceae	+	Landry and Rathcke, 2007
<i>Lobelia cardinalis</i>	Campanulaceae	+	Schlichting and Devlin, 1992
<i>Lupinus texensis</i>	Fabaceae	+	Helenurm and Schaal, 1996
<i>Lychnis flos-cuculi</i>	Caryophyllaceae	+	Biere, 1991a
<i>Lychnis flos-cuculi</i>	Caryophyllaceae	+	Biere, 1991b
<i>Mirabilis jalapa</i>	Nyctaginaceae	0	Niesenbaum, 1999
<i>Morus alba</i> and <i>M. rubra</i>	Moraceae	0	Burgess and Husband, 2004
<i>Nemophila menziesii</i>	Boraginaceae	+	Platenkamp and Shaw, 1993
<i>Nemophila menziesii</i>	Boraginaceae	0	Byers <i>et al.</i> , 1997
<i>Nicotiana tobacum</i>	Solanaceae	+	Honing, 1930
<i>Nicotiana tobacum</i>	Solanaceae	+	Kasperbauer, 1968
<i>Pachycereus pringlei</i>	Cactaceae	+	Sosa and Fleming, 1999
<i>Petunia hybrida</i>	Solanaceae	+	Girard, 1990
<i>Plantago lanceolata</i>	Plantaginaceae	+	Lacey, 1996
<i>Plantago lanceolata</i>	Plantaginaceae	0	Lacey and Herr, 2000

(Continued)

Table 1. (Continued.)

Species	Family	Influence on seed germination*	References
<i>Purshia tridentata</i>	Rosaceae	+	Meyer and Pendleton, 2000
<i>Raphanus raphanistrum</i>	Brassicaceae	0	Mazer, 1987a
<i>Raphanus raphanistrum</i>	Brassicaceae	0	Snow, 1990
<i>Raphanus raphanistrum</i>	Brassicaceae	0	Young and Stanton, 1990
<i>Raphanus sativus</i>	Brassicaceae	+	Mazer and Schick, 1991a
<i>Raphanus sativus</i>	Brassicaceae	+	Mazer and Schick, 1991b
<i>Raphanus sativus</i>	Brassicaceae	0	Marshall <i>et al.</i> , 2007
<i>Silene latifolia</i>	Caryophyllaceae	+	Lassere <i>et al.</i> , 1996
<i>Silene latifolia</i>	Caryophyllaceae	0	Jolivet and Bernasconi, 2007
<i>Silene latifolia</i>	Caryophyllaceae	+	Teixeira <i>et al.</i> , 2009
<i>Silene uniflora</i> var. <i>petraea</i> and <i>S. vulgaris</i>	Caryophyllaceae	+	Andersson <i>et al.</i> , 2008
<i>Sinapis arvensis</i>	Brassicaceae	0	Garbutt and Witcombe, 1986
<i>Solidago altissima</i>	Asteraceae	+	Schmid and Dolt, 1994
<i>Swertia perennis</i>	Gentianaceae	+	Lienert and Fischer, 2004
<i>Vaccinium corymbosum</i>	Ericaceae	+	Vander Kloet and Tosh, 1984
<i>Vaccinium elliotii</i>	Ericaceae	0	Wenslaff and Lyrene, 2001

\*Several of the studies (e.g. Schmitt and Antonovics, 1986; Bertin *et al.*, 1989; Helernum and Schaal, 1996) had more than one outcome for a taxon, i.e. positive influence versus no positive influence of paternal parent on seed germination. In those cases, even if only one of the outcomes was positive we show a positive influence for the paternal parent.

According to the parental conflict theory (Haig and Westoby, 1989, 1991; Moore and Haig, 1991) [the predominant theory of several (theories) on genomic imprinting, for example see Rodrigues and Zilberman, 2015], the maternal parent has equal interest in all of her sib and half-sib progeny, and thus it would be to her best interest to devote equal resources to all of them (maternal family). On the other hand, for plants that receive pollen from more than one father, it would be in the best interest of each of the multiple paternal parents, who do not father all sibs and half-sibs of the maternal family, to get preferential treatment (i.e. relatively more resources) for the progeny he sires, i.e. to have more than an equal share of the resources devoted to his offspring. Thus, there is conflict between maternal and paternal genes within offspring over how the resources from maternal tissue via the endosperm are devoted to the developing embryos. The results of a study on seeds of *Arabidopsis thaliana* by Scott *et al.* (1998) provide support for the parental conflict theory. Thus, seeds with a double dose of paternal genes [ $2x \times 4x$  (1m : 2p endosperm)] produce large endosperms and embryos, while maternal plants with a double dose of genes [ $4x \times 2x$  (2m : 1p endosperm)] produce small endosperms and embryos. According to Pires *et al.* (2016), MEA activity buffers the paternal effects from maximizing growth ‘... suggesting that they were likely shaped by parental conflict’. In sum, then, the study by Pires *et al.* (2016) shows that paternal effects on seed development do exist but are buffered by the maternal genome.

### General conclusion

Although undoubtedly the mother has much more influence than the father on dormancy and germination (and development and size-mass) of offspring seeds produced, the pollen parent

sometimes can have an effect on variation in these life history traits. However, in general, the influence of the father on these stages of the plant life cycle is minimal compared with that of the mother.

Author ORCIDs.  Carol C. Baskin 0000-0001-7680-154X

### References

- Alboresi A, Gestin C, Leydecker M-T, Bedu M, Meyer C and Truong H-N (2005) Nitrate, a signal relieving seed dormancy in *Arabidopsis*. *Plant, Cell and Environment* **28**, 500–512.
- Andersson S (1990) Paternal effects on seed size in a population of *Crepis tectorum* (Asteraceae). *Oikos* **59**, 3–8.
- Andersson S, Månsby E and Prentice HC (2008) Paternal effects on seed germination: a barrier to the genetic assimilation of an endemic plant taxon? *Journal of Evolutionary Biology* **21**, 1408–1417.
- Antonovics J and Schmitt J (1986) Paternal and maternal effects on propagule size in *Anthoxanthum odoratum*. *Oecologia* **69**, 277–282.
- Ashman T-L, Knight TM, Steets JA, Amarasekare P, Burd M, Campbell DR, Dudash MR, Johnston MO, Mazer SJ, Mitchell RJ, Morgan MT and Wilson WG (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* **85**, 2408–2421.
- Augsburger CK, Franson SE and Cushman KC (2017) Wind dispersal is predicted by tree, not diaspore, traits in comparisons of neotropical species. *Functional Ecology* **31**, 808–820.
- Azhagiri AE and Maliga P (2007) Exceptional paternal inheritance of plastids in *Arabidopsis* suggests that low frequency leakage of plastids via pollen may be universal in plants. *The Plant Journal* **52**, 817–823.
- Baskin JM and Baskin CC (2018) Pollen limitation and its effect on seed germination. *Seed Science Research*. <https://doi.org/10.1017/S0960258518000272>
- Battle JP and Whittington WJ (1971) Genetic variability in time to germination of sugar-beet clusters. *Journal of Agriculture Science, Cambridge* **76**, 27–32.

- Bernasconi G** (2003) Seed paternity in flowering plants: an evolutionary perspective. *Perspectives in Plant Ecology, Evolution and Systematics* **6**, 149–158.
- Bertin RI** (1986) Consequences of mixed pollinations in *Campsis radicans*. *Oecologia* **70**, 1–5.
- Bertin RI** (1990) Parental success following mixed pollinations of *Campsis radicans*. *The American Midland Naturalist* **124**, 153–163.
- Bertin RI, Barnes C and Guttman SI** (1989) Self sterility and cryptic self-fertility in *Campsis radicans* (Bignoniaceae). *Botanical Gazette* **150**, 397–403.
- Biere A** (1991a) Parental effects in *Lychnis flos-cuculi*. I: Seed size, germination and seedling performance in a controlled environment. *Journal of Evolutionary Biology* **3**, 447–465.
- Biere A** (1991b) Parental effects on *Lychnis flos-cuculi*. II: Selection on time of emergence and seedling performance in the field. *Journal of Evolutionary Biology* **3**, 467–486.
- Bookman SS** (1984) Evidence for selective fruit abortion in *Asclepias*. *Evolution* **38**, 72–86.
- Brown AHD, Grant JE and Pullen R** (1986) Outcrossing and paternity in *Glycine argyrea* by paired fruit analysis. *Biological Journal of the Linnean Society* **29**, 283–294.
- Burd M** (1994) Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *The Botanical Review* **60**, 83–139.
- Burgess KS and Husband BC** (2004) Maternal and paternal contributions to the fitness of hybrids between red and white mulberry (*Morus*, Moraceae). *American Journal of Botany* **91**, 1802–1808.
- Byers DL, Platenkamp GA and Shaw RG** (1997) Variation in seed characters in *Nemophila menziesii*: evidence of a genetic bases for maternal effect. *Evolution* **51**, 1445–1456.
- Campbell DR** (1998) Multiple paternity in fruits of *Ipomopsis aggregata* (Polemoniaceae). *American Journal of Botany* **85**, 1022–1027.
- Cook SA** (1962) Genetic system, variation, and adaptation in *Eschscholzia californica*. *Evolution* **16**, 278–299.
- Corriveau JL and Coleman AW** (1988) Rapid screening method to detect potential biparental inheritance of plastid DNA and results for over 200 angiosperm species. *American Journal of Botany* **75**, 1443–1458.
- Costa LM, Yuan J, Rouster J, Wyatt P, Dickinson H and Gutierrez-Marcos JF** (2012) Maternal control of nutrient allocation in plant seeds by genomic imprinting. *Current Biology* **22**, 160–165.
- Crean AJ, Dwyer JM and Marshall DJ** (2013) Adaptive paternal effects? Experimental evidence that the paternal environment affects offspring fitness. *Ecology* **94**, 2575–2582.
- de Jong TJ, Hermans CM and van der Veen-van Wijk K(C)AM** (2011) Paternal effects on seed mass in *Arabidopsis thaliana*. *Plant Biology* **13** (suppl. 1), 71–77.
- de Jong TJ and Scott RJ** (2007) Parental conflict does not necessarily lead to the evolution of imprinting. *Trends in Plant Science* **12**, 439–443.
- Diggle PK, Abrahamson NJ, Baker RL, Barnes MG, Koontz TL, Lay CR, Medeiros JS, Murgel JL, Shaner MGM, Simpson HL, Wu CC and Marshall DL** (2010) Dynamics of maternal and paternal effects on embryo and seed development in wild radish (*Raphanus sativus*). *Annals of Botany* **106**, 309–319.
- Donohue K** (1999) Seed dispersal as a maternally influenced character: mechanistic basis of maternal effects and selection on maternal characters in an annual plant. *The American Naturalist* **154**, 674–689.
- Donohue K** (2009) Completing the cycle: maternal effects as missing links in plant life histories. *Philosophical Transactions of the Royal Society B* **364**, 1059–1074.
- Dudash MR and Ritland K** (1991) Multiple paternity and self-fertilization in relation to floral age in *Mimulus guttatus* (Scrophulariaceae). *American Journal of Botany* **78**, 1746–1753.
- Ellstrand NC** (1984) Multiple paternity within the fruits of the wild radish, *Raphanus sativus*. *The American Naturalist* **123**, 819–828.
- Ellstrand NC and Marshall DL** (1986) Patterns of multiple paternity in populations of *Raphanus sativus*. *Evolution* **40**, 837–842.
- Etterson JR and Galloway LF** (2002) The influence of light on paternal plants in *Campanula americana* (Campanulaceae): pollen characteristics and offspring traits. *American Journal of Botany* **89**, 1899–1906.
- Fenster CB** (1991) Effect of male pollen donor and female seed parent on allocation of resources to developing seeds and fruit in *Chamaecrista fasciculata* (Leguminosae). *American Journal of Botany* **78**, 13–23.
- Finkelstein RR, Gampala SSL and Rock CD** (2002) Abscisic acid signaling in seeds and seedlings. *The Plant Cell* **14** (suppl.), S15–S45.
- Fischer M, Hock M and Paschke M** (2003) Low genetic variation reduces cross-compatibility and offspring fitness in populations of a narrow endemic plant with a self-incompatibility system. *Conservation Genetics* **4**, 325–336.
- Frey A, Godin B, Bonnet M, Sotta B and Marion-Poll A** (2004) Maternal synthesis of abscisic acid controls seed development and yield in *Nicotiana plumbaginifolia*. *Planta* **218**, 958–964.
- Galloway LF** (2001a). The effect of maternal and paternal environments on seed characters of the herbaceous plant *Campanula americana* (Campanulaceae). *American Journal of Botany* **88**, 832–840.
- Galloway LF** (2001b) Parental environmental effects on life history in the herbaceous plant *Campanula americana*. *Ecology* **82**, 2781–2789.
- Garbutt K and Witcombe JR** (1986) The inheritance of seed dormancy in *Sinapis arvensis* L. *Heredity* **56**, 25–31.
- Gehring M** (2013) Genomic imprinting: insights from plants. *Annual Review of Genetics* **47**, 187–208.
- Girard J** (1990) Study of the inheritance of seed primary dormancy and the ability to enter secondary dormancy in *Petunia*: influence of temperature, light and gibberellic acid on dormancy. *Plant, Cell and Environment* **13**, 827–832.
- Godwin J, Raviv B and Grafi G** (2017) Dead pericarps and dry fruits function as long-term storage for active hydrolytic enzymes and other substances that affect germination and microbial growth. *Plants* **6**, 64. doi: 10.3390/plants6040064
- Good-Avila SV and Stephenson AG** (2003) Parental effects in a partially self-incompatible herb *Campanula rapunculoides* L. (Campanulaceae): influence of variation in the strength of self-incompatibility on seed set and progeny performance. *The American Naturalist* **161**, 615–630.
- Grossniklaus U, Vielle-Calzada J-P, Hoepfner MA and Gagliano WB** (1998) Maternal control of embryogenesis by *MEDEA*, a polycomb group gene in *Arabidopsis*. *Science* **280**, 446–450.
- Haig D and Westoby M** (1989) Parent-specific gene expression and the triploid endosperm. *The American Naturalist* **134**, 147–155.
- Haig D and Westoby M** (1991) Genomic imprinting in endosperm: its effect on seed development in crosses between species, and between different ploidy levels of the same species, and its implications for the evolution of apomixis. *Philosophical Transactions of the Royal Society of London B* **222**, 1–13.
- Helenurm K and Schaal B** (1996) Genetics and maternal effects on offspring fitness in *Lupinus texensis*. *American Journal of Botany* **83**, 1596–1608.
- Herman JJ and Sultan SE** (2011) Adaptive transgenerational plasticity in plants: case studies, mechanisms, and implications for natural populations. *Frontiers in Plant Science* **2** (article 102), 1–10.
- Himes SL and Wyatt R** (2005) Costs and benefits of self-sterility in *Asclepias exaltata* (Apocynaceae). *Journal of the Torrey Botanical Society* **132**, 24–32.
- Holland JN, Chamberlain SA, Waguespack AM and Kinoy AS** (2009) Effects of pollen load and donor diversity on seed and fruit mass in the columnar cactus *Pachycereus schottii* (Cactaceae). *International Journal of Plant Sciences* **170**, 467–475.
- Honing JA** (1930) Nuclear and plasma in the heredity of the need of light for germination in *Nicotiana* seeds. *Genetics* **12**, 441–468.
- House C, Roth C, Hunt J and Kover PX** (2010) Paternal effects in *Arabidopsis thaliana* indicate that offspring can influence their own size. *Proceedings of the Royal Society B* **277**, 2885–2893.
- Ibarra-Perez FJ, Ellstrand NC and Waines JG** (1996) Multiple paternity in common bean (*Phaseolus vulgaris* L., Fabaceae). *American Journal of Botany* **83**, 749–758.
- Jacobs BS and Lesmeister SA** (2012) Maternal environment effects on fitness, fruit morphology and ballistic seed dispersal distance in an annual forb. *Functional Ecology* **26**, 588–597.
- Jolivet C and Bernasconi G** (2007) Within/between population crosses reveal genetic basis for siring success in *Silene latifolia* (Caryophyllaceae). *Journal of Evolutionary Biology* **20**, 1361–1374.
- Kagawa M, Tani T and Kachi N** (2011) Maternal and paternal effects on the germination time of non-dormant seeds of a monocarpic perennial species, *Aster kantoensis* (Compositae). *Plant Species Biology* **26**, 66–72.



- Kanno Y, Jikumaru Y, Hanada A, Nambara E, Abrams SR, Kimiya Y and Seo M (2010). Comprehensive hormone profiling in developing *Arabidopsis* seeds: examination of the site of ABA biosynthesis, ABA transport and hormone interactions. *Plant and Cell Physiology* **51**, 1988–2001.
- Karszen CM, Brinkhorst-van der Swan DLC, Breckland AE and Koornneef M (1983) Induction of dormancy during seed development by endogenous abscisic acid: studies on abscisic acid deficient genotypes of *Arabidopsis thaliana* (L.) Heynh. *Planta* **157**, 158–165.
- Karron JD and Marshall DL (1990) Fitness consequences of multiple paternity in wild radish *Raphanus sativus*. *Evolution* **44**, 260–268.
- Karron JD, Mitchell RJ and Bell JM (2006) Multiple pollinator visits to *Mimulus ringens* (Phrymaceae) flowers increase mate number and seed set within fruits. *American Journal of Botany* **93**, 1306–1312.
- Kasperbauer MJ (1968) Dark-germination of reciprocal hybrid seed from light-requiring and -indifferent *Nicotiana tobacum*. *Physiologia Plantarum* **21**, 1308–1311.
- Knight TM, Steets JA, Vamosi JC, Mazer SJ, Burd M, Campbell DR, Dudash MR, Johnston MO, Mitchell RJ and Ashman T-L (2005) Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology, Evolution and Systematics* **36**, 467–497.
- Köhler C, Wolff P and Spillane C (2012) Epigenetic mechanisms underlying genomic imprinting in plants. *Annual Review of Plant Biology* **63**, 331–352.
- Kucera B, Cohn MA and Leubner-Metzger G (2005) Plant hormone interactions during seed dormancy release and germination. *Seed Science Research* **15**, 281–307.
- Lacey EP (1996) Parental effects in *Plantago lanceolata* L. I: a growth chamber experiment to examine pre- and postzygotic temperature effects. *Evolution* **50**, 865–878.
- Lacey EP and Herr D (2000) Parental effects in *Plantago lanceolata* L. III. Measuring parental temperature effects in the field. *Evolution* **54**, 1207–1217.
- Lacey EP, Smith S and Case AL (1997) Parental effects on seed mass: seed coat but not embryo/endosperm effects. *American Journal of Botany* **84**, 1617–1620.
- Landry CL and Rathcke BJ (2007) Do inbreeding depression and relative male fitness explain the maintenance of androdioecy in white mangrove, *Laguncularia racemosa* (Combretaceae)? *New Phytologist* **176**, 891–901.
- Lankinen Á and Madjidian JA (2011) Enhancing pollen competition by delaying stigma receptivity: pollen deposition schedules affect siring ability, paternal diversity, and seed production in *Collinsia heterophylla* (Plantaginaceae). *American Journal of Botany* **98**, 1191–1200.
- Larson BMH and Barrett SCH (2000) A comparative analysis of pollen limitation in flowering plants. *Biological Journal of the Linnean Society* **69**, 503–520.
- Lassere T.B, Carroll SB and Mulcahy DL (1996) Effect of pollen competition on offspring quality at varying stages of the life cycle of *Silene latifolia* Poirlet (Caryophyllaceae). *Bulletin of the Torrey Botanical Club* **123**, 175–179.
- Li N, Peng W, Shi J, Wang X, Liu G and Wang H (2015) The natural variation in seed weight is mainly controlled by maternal genotype in rapeseed (*Brassica napus* L.). *PLoS ONE* **10**, e0125360.
- Lienert J and Fischer M (2004) Experimental inbreeding reduced seed production and germination independent of fragmentation of populations of *Swertia perennis*. *Basic and Applied Ecology* **5**, 43–52.
- Laurens V, Castric V, Austerlitz F and Vekemans X (2008) High parental diversity in the self-incompatible *Arabidopsis halleri* despite clonal reproduction and spatially restricted pollen dispersal. *Molecular Ecology* **17**, 1577–1588.
- Lyoons EE (1996) Breeding system evolution in *Leavenworthia*. II. Genetic and nongenetic parental effects on reproductive success in selfing and more out-crossing populations of *Leavenworthia crassa*. *The American Naturalist* **147**, 65–85.
- Marshall DL (1988) Postpollination effects on seed paternity: mechanisms in addition to microgametophyte competition operate in wild radish. *Evolution* **42**, 1256–1266.
- Marshall DL (1990) Nonrandom mating in a wild radish, *Raphanus sativus*. *Plant Species Biology* **5**, 143–156.
- Marshall DL (1991) Nonrandom mating in wild radish: variation in pollen donor success and effects of multiple paternity among one- to six-donor pollinations. *American Journal of Botany* **78**, 1404–1418.
- Marshall DL and Ellstrand NC (1985) Proximal causes of multiple paternity in wild radish, *Raphanus sativus*. *The American Naturalist* **126**, 596–605.
- Marshall DL and Ellstrand NC (1986) Sexual selection in *Raphanus sativus*: experimental data on nonrandom fertilization, maternal choice, and consequences of multiple paternity. *The American Naturalist* **127**, 446–461.
- Marshall DL and Evans AS (2016) Can selection on a male mating character result in evolutionary change? A selection experiment on California wild radish, *Raphanus sativus*. *American Journal of Botany* **103**, 553–567.
- Marshall DL, Reynolds J, Abrahamson NJ, Simpson HL, Barnes MG, Medeiros JS, Walsh S, Oliveras DM and Avritt JJ (2007) Do differences in plant and flower age change mating patterns and later offspring fitness in *Raphanus sativus* (Brassicaceae)? *American Journal of Botany* **94**, 409–418.
- Marshall DL and Whittaker KL (1989) Effects of pollen donor identity on offspring quality in wild radish, *Raphanus sativus*. *American Journal of Botany* **76**, 1081–1088.
- Matakiadis T, Alboresi A, Jikumaru Y, Tatematsu K, Pichon O, Renou J-P, Kamiya Y, Nambara E and Truong H-H (2009) The *Arabidopsis* abscisic acid catabolic gene CYP707A2 plays a key role in nitrate control of seed dormancy. *Plant Physiology* **149**, 949–960.
- Mazer SJ (1987a) The quantitative genetics of life history and fitness components of *Raphanus raphanistrum* L. (Brassicaceae): ecological and evolutionary consequences of seed-weight variation. *The American Naturalist* **130**, 891–914.
- Mazer SJ (1987b) Parental effects of seed development and seed yield in *Raphanus raphanistrum*: implications for natural and sexual selection. *Evolution* **41**, 355–371.
- Mazer SJ and Gorchov DL (1996) Parental effects on progeny phenotype in plants: distinguishing genetic and environmental causes. *Evolution* **50**, 44–53.
- Mazer SJ and Schick CT (1991a) Constancy of population parameters for life history and floral traits in *Raphanus sativus* L. I. Norms of reaction and the nature of genotypes by environment interactions. *Heredity* **67**, 143–156.
- Mazer SJ and Schick CT (1991b) Constancy of population parameters for life history and floral traits in *Raphanus sativus* L. II. Effects of planting density on phenotype and heritability estimates. *Evolution* **45**, 1888–1907.
- Mazer SJ, Snow AA and Stanton ML (1986) Fertilization dynamics and parental effects upon fruit development in *Raphanus raphanistrum*: consequences for seed size variation. *American Journal of Botany* **73**, 500–511.
- McCaughey DE and Olson MS (2008) Do recent findings in plant mitochondrial molecular and population genetics have implications for the study of gynodioecy and cytonuclear conflict? *Evolution* **62**, 1013–1025.
- Meyer SE and Pendleton RL (2000) Genetic regulation of seed dormancy in *Purshia tridentata* (Rosaceae). *Annals of Botany* **85**, 521–529.
- Mitchell RJ, Karron JD, Holmquist KG and Bell JM (2005) Patterns of multiple paternity in fruits of *Mimulus ringens* (Phrymaceae). *American Journal of Botany* **92**, 885–890.
- Mogensen HL (1996) The hows and whys of cytoplasmic inheritance in seed plants. *American Journal of Botany* **83**, 383–404.
- Moore T and Haig D (1991) Genomic imprinting in mammalian development: a parental tug-of-war. *Trends in Genetics* **7**, 45–49.
- Nakamura RR and Stanton ML (1989) Embryo growth and seed size in *Raphanus sativus*: maternal and paternal effects in vivo and in vitro. *Evolution* **43**, 1435–1443.
- Niesenbaum RA (1999) The effects of pollen load size and donor diversity on pollen performance, selective abortion, and progeny vigor in *Mirabilis jalapa* (Nyctaginaceae). *American Journal of Botany* **86**, 261–268.
- Palmer TM and Zimmerman M (1994) Pollen competition and sporophyte fitness in *Brassica campestris*: does intense pollen competition result in individuals with better pollen? *Oikos* **69**, 80–86.
- Pannell JR (2000) The evolution and maintenance of androdioecy. *Annual Review of Ecology and Systematics* **33**, 397–425.
- Paschke M, Abs C and Schmid B (2002) Effects of population size and pollen diversity on reproductive success and offspring size in the narrow endemic *Cochlearia bavarica* (Brassicaceae). *American Journal of Botany* **89**, 1250–1259.
- Pasonen H-L, Pulkkinen P and Käpylä M (2001) Do pollen donors with fastest-growing pollen tubes give the best offspring in an anemophilous tree, *Betula pendula* (Betulaceae)? *American Journal of Botany* **88**, 854–860.
- Pearl SA, Welch ME and McCaughey DE (2009) Mitochondrial heteroplasmy and paternal leakage in natural populations of *Silene vulgaris*, a gynodioecious plant. *Molecular Biology and Evolution* **26**, 537–545.

- Pélabon C, Hennet L, Bolstad GH, Albertsen E, Opedal ØH, Ekrem RK and Armbruster WS** (2016) Does stronger pollen competition improve offspring fitness when pollen load does not vary? *American Journal of Botany* **103**, 522–531.
- Pires ND** (2014) Seed evolution: parental conflicts in a multi-generational household. *Biomolecular Concepts* **5**, 71–86.
- Pires ND, Bemer M, Müller LM, Baroux C, Spillane C and Grossniklaus U** (2016) Quantitative genetics identifies cryptic genetic variation involved in the paternal regulation of seed development. *PLoS Genetics* **12**, e1005806.
- Piskurewicz U, Iwasaki M, Susaki D, Megies C, Kinoshita T and Lopez-Molina L** (2016) Dormancy-specific imprinting underlies maternal inheritance of seed dormancy in *Arabidopsis thaliana*. *eLife* **5**, e19573.
- Pittman KE and Levin DA** (1989) Effects of parental identities and environment on components of crossing success in *Phlox drummondii*. *American Journal of Botany* **76**, 409–418.
- Plakhine D, Tadmor Y, Ziadne H and Joel DM** (2012) Maternal tissue is involved in stimulant reception by seeds of the parasitic plant *Orobancha*. *Annals of Botany* **109**, 979–986.
- Platenkamp GAJ and Shaw RG** (1993) Environmental and genetic maternal effects on seed characters in *Nemophila menziesii*. *Evolution* **47**, 540–555.
- Povilus RA, Diggle PK and Friedman WE** (2018) Evidence for parent-of-origin effects and interparental conflict in seeds of an ancient flowering plant lineage. *Proceedings of the Royal Society B* **285**, 20172491.
- Raviv B, Aghajanyan L, Granot G, Makeover V, Frenkel O, Gutterman Y and Grafi G** (2017a) The dead seed coat functions as a long-term storage for active hydrolytic enzymes. *PLoS ONE* **12**, e01811102.
- Raviv B, Granot G, Chilifa-Caspi V and Grafi G** (2017b). The dead, hardened floral bracts of dispersal units of wild wheat function as storage for active hydrolases and in enhancing seedling vigor. *PLoS ONE* **12**, e0177537.
- Raz V, Bergervoet JHW and Koornneef M** (2001) Sequential steps for developmental arrest in *Arabidopsis* seeds. *Development* **128**, 243–252.
- Reusch TBH** (2000) Pollination in the marine realm: microsatellites reveal high outcrossing rates and multiple paternity in eelgrass *Zostera marina*. *Heredity* **85**, 459–464.
- Richardson TE and Stephenson AG** (1991) Effects of parentage, prior fruit set and pollen load on fruit and seed production in *Campanula americana* L. *Oecologia* **87**, 80–85.
- Richardson TE and Stephenson AG** (1992) Effect of parentage and size of the pollen load on progeny performance in *Campanula americana*. *Evolution* **46**, 1731–1739.
- Rideau M, Monin J, Dommergues P and Cornu A** (1976) Etude sur les mécanismes héréditaires de la dormance des akènes de *Lactuca sativa* L. *Comptes rendus hebdomadaires des séances de l'Académie des sciences. Série D, Sciences naturelles* **283**, 769–772.
- Riesberg LH, Philbrick CT, Pack PE, Hanson MA and Fritsch P** (1993) Inbreeding depression in androdioecious populations of *Datisca glomerata* (Datisceae). *American Journal of Botany* **80**, 757–762.
- Rix KD, Gracie AJ, Potts BM, Brown PH, Spurr CJ and Gore PL** (2012) Paternal and maternal effects on the response of seed germination to high temperatures in *Eucalyptus globulus*. *Annals of Forest Science* **69**, 673–679.
- Roach DA and Wulff RD** (1987) Maternal effects in plants. *Annual Review of Ecology and Systematics* **18**, 209–235.
- Rodrigues JA and Zilberman D** (2015) Evolution and function of genomic imprinting in plants. *Genes and Development* **29**, 2517–2531.
- Rossiter MC** (1996) Incidence and consequences of inherited environmental effects. *Annual Review of Ecology, and Systematics* **27**, 451–476.
- Rubio de Casas R, Willis CG and Donohue K** (2012) Plant dispersal phenotypes: a seed perspective of maternal habitat selection, pp. 171–184 in Clobert J, Baguette M, Benton TG and Bullock JM (eds), *Dispersal Ecology and Evolution*. Oxford, Oxford University Press.
- Schemske DW and Pautler LP** (1984) The effects of pollen composition on fitness components in a neotropical herb. *Oecologia* **62**, 31–36.
- Schlichting CD and Devlin B** (1992) Pollen and ovule sources affect seed production of *Lobelia cardinalis* (Lobeliaceae). *American Journal of Botany* **79**, 891–898.
- Schmid B and Dolt C** (1994) Effects of maternal and paternal environment and genotype on offspring phenotype in *Solidago altissima* L. *Evolution* **48**, 1525–1549.
- Schmitt J and Antonovics J** (1986) Experimental studies on the evolutionary significance of sexual reproduction. III. Maternal and paternal effects during seedling establishment. *Evolution* **40**, 817–829.
- Scott RJ, Spielman M, Bailey J and Dickinson HG** (1998) Parent-of-origin effects on seed development in *Arabidopsis thaliana*. *Development* **125**, 3329–3341.
- Shaw RG and Byers DL** (1998) Genetics of maternal and paternal effects, pp. 97–111 in Mousseau TA and Fox CW (eds), *Maternal Effects as Adaptations*. Oxford, Oxford University Press.
- Snow AA** (1990) Effects of pollen-load size and number of donors on sporophyte fitness in wild radish (*Raphanus raphanistrum*). *The American Naturalist* **136**, 742–758.
- Snow AA and Spira TP** (1991a) Pollen vigour and the potential for sexual selection in plants. *Nature* **352**, 796–797.
- Snow AA and Spira TP** (1991b) Differential pollen-tube growth rates and nonrandom fertilization in *Hibiscus moscheutos* (Malvaceae). *American Journal of Botany* **78**, 1419–1426.
- Sork VL and Schemske DW** (1992) Fitness consequences on mixed-donor pollen loads in the annual legume *Chamaecrista fasciculata*. *American Journal of Botany* **79**, 508–515.
- Sosa VJ and Fleming TH** (1999) Seedling performance in a trioecious cactus, *Pachycereus pringlei*: effects of maternity and paternity. *Plant Systematics and Evolution* **218**, 145–151.
- Tamme R, Götzemberger L, Zobel M, Bullock JM, Hooftman DAP, Kaasik A and Pärtel M** (2014) Predicting species' maximum dispersal distances from simple plant traits. *Ecology* **95**, 505–513.
- Teixeira S and Bernasconi G** (2007) High prevalence of multiple paternity within fruits in natural populations of *Silene latifolia*, as revealed by microsatellite DNA analysis. *Molecular Ecology* **16**, 4370–4379.
- Teixeira S, Foerster K and Bernasconi G** (2009) Evidence for inbreeding depression and post-pollination selection against inbreeding in the dioecious plant *Silene latifolia*. *Heredity* **102**, 101–112.
- Thomson FJ, Moles AT, Auld TD and Kingsford RT** (2011) Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology* **99**, 1299–1307.
- Vander Kloet SP and Tosh D** (1984) Effect of pollen donors on seed production, seed weight, germination and seedling vigor of *Vaccinium corymbosum* L. *The American Midland Naturalist* **112**, 392–396.
- Van Zandt PA and Mopper S** (2004) The effects of maternal salinity and seed environment on germination and growth of *Iris hexagona*. *Evolutionary Ecology Research* **6**, 813–832.
- Verdu M, Montilla AI and Pannell JR** (2004) Paternal effects on functional gender account for cryptic dioecy in a perennial plant. *Proceedings of the Royal Society, London B* **271**, 2017–2023.
- Vinkenoog R, Bushell C, Spielman M, Adams S, Dickinson HG and Scott RJ** (2003) Genomic imprinting and endosperm development in flowering plants. *Molecular Biotechnology* **25**, 149–184.
- Vu WT, Chang PL, Moriuchi KS and Friesen ML** (2015) Genetic variation of transgenerational plasticity of offspring germination in response to salinity stress and seed transcriptome of *Medicago truncatula*. *BMC Evolutionary Biology* **15**, 59.
- Welch ME, Darnell MZ and McCauley DE** (2006) Variable populations within variable populations: quantifying mitochondrial heteroplasmy in natural populations of the gynodioecious plant *Silene vulgaris*. *Genetics* **174**, 829–837.
- Wenslaff TF and Lyrene PM** (2001) Results of multiple pollination in blueberry (*Vaccinium elliotii* Chapm.). *Euphytica* **117**, 233–240.
- Yan A and Chen Z** (2017) The pivotal role of abscisic acid signaling during transition from seed maturation to germination. *Plant Cell Reports* **36**, 689–703.
- Young HJ and Stanton ML** (1990) Influence of environmental quality on pollen competition ability in wild radish. *Science* **248**, 1631–1633.

## Appendix. Relative performance

A meaningful way to compare the effect of one-pollen donor versus multiple-pollen donors on seed germination is to use a measure of relative

performance (RP):

$$RP = (W_m - W_s) / W_{\max}[W_m, W_s],$$

where  $W_m$  is mean germination percentage of seeds (progeny) resulting from multiple-donor pollinations, and  $W_s$  is the mean germination percentage of seeds resulting from a single-donor pollination.

Using this equation, values will be equidistant from 0, i.e. they are bound between  $-1.0$  and  $+1.0$ , when  $W_s > W_m$  (to  $-1$ ) and  $W_s \leq W_m$  (to  $+1$ ). Thus, a positive value indicates that seeds from multiple-donor pollinations

germinated better than those from a single-donor pollination, and the closer the value is to  $1.0$  the greater the difference in performance. A negative value indicates that seeds from a single-donor pollination germinated better than those from multiple-donor pollinations, and the more negative the value the greater the single-donor benefit.

Relevant to the study by Sork and Schemske (1992) discussed in the present paper, the above equation can be used to calculate inbreeding depression of seed germination by substituting  $W_o$  (germination of outcrossed seeds) for  $W_m$  and letting  $W_s$  be germination of selfed seeds instead of germination of a single-donor pollination.