Inbreeding depression and the cost of inbreeding on seed germination

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Abstract

We review the literature on effects of inbreeding depression (ID) on seed germination for 743 case studies of 233 species in 64 families. For 216 case studies, we also review the relationship between mass and germination in inbred vs. outbred seeds. Inbred seeds germinated equally well as outbred seeds in 51.1% of 743 case studies, but better than outbred seeds in only 8.1%. In *c.* 50.5% of 216 cases, mass of inbred seeds was equal to (38.0%) or larger than (12.5%) that of outbred seeds. The magnitude of ID spans most of the −1 to +1 range for relative performance for germination of inbred vs. outbred seeds; in contrast to what might be expected, seed germinability often is not negatively correlated with the coefficient of inbreeding (F) or positively corrected with population genetic diversity; neither heterosis nor outbreeding depression for germination is common in crosses between populations; and ID in most endemics is low and does not differ from that of widespread congeners. Our results on the effects of ID on seed mass and germination do not agree with the limited number of comparisons Darwin (1876) made on the effects of selfing vs. outcrossing on these two life-history traits. Recommendations are made on how to improve dormancy breaking and germination procedures in order to make the results of studies on ID more relevant to the natural world.

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Introduction

During an 11-year period, Darwin made numerous comparisons on the effects of self- and cross-pollination on 54 species in 52 genera and 30 families of herbaceous plants, all eudicots except three monocots, i.e. two grasses and a *Canna* species. In *The effects of cross and self fertilisation in the vegetable kingdom*, Darwin (1876) reported on the effects of self- vs. cross-pollination on plant height and shoot mass; relative time to and productiveness of flowering; number and mass of fruits per plant; number and mass of seeds per fruit and per plant; seed size (mass); and relative time to germination. His general conclusion was that, 'The first and most important of the conclusions which may be drawn from observations given in this volume, is that cross-fertilisation is generally beneficial, and self-fertilisation injurious' (Darwin, 1876, p. 436).

However, his limited results on seed mass and germination do not offer strong support for this general conclusion. Thus, in 10 of the 16 comparisons of seed size, selfed seeds were larger than outcrossed seeds. In the other six comparisons, outcrossed seeds were larger than selfed seeds. Interestingly, 'The lighter seeds, whether produced from crossed or self fertilised flowers, generally germinated before the heavier seeds' (Darwin, 1876, p. 58). Furthermore, in 10 of 21 comparisons of relative time to germination, crossed seeds germinated faster than selfed seeds; in ten, selfed seeds germinated faster than crossed seeds; and in one there was no difference in timing. Darwin considered earlier germination to be superior to late germination.

The first extensive literature survey on the effects of inbreeding depression (ID) on seed germination was contained in a review paper by Husband and Schemske (1996) on the magnitude and timing of ID in plants. Their survey included information on 79 populations: 2 families and 13 species of

gymnosperms, and 23 families and 41 species of angiosperms (*sensu* Mabberley, 2008; APG-III, 2009). All species of angiosperms in their survey were herbaceous, except one tree (*Eucalyptus regnans*, Myrtaceae) and one shrub (*Decodon verticillatus*, Lythraceae). A paper by Winn *et al.* (2011) contains information on 59 species (49 angiosperms, 10 gymnosperms; *sensu* Mabberley, 2008; APG-III, 2009). Forty-four of the 68 entries (populations) in this paper are included in the one by Husband and Schemske (1996). *D. verticillatus* and *E. regnans* are also the only woody angiosperms on the species list of Winn *et al.* (2011). Relative fitness values for germination are given for all entries in these two surveys. Our primary purpose was to make an updated and extensive survey of the literature on the effects of ID on seed germination. In addition, dormancy breaking and germination procedures used in studies on ID in plants are reviewed, and recommendations are made on how to improve such studies to make the results more relevant to the real world.

Inbreeding depression

Formulae and symbols used in this section follow those of many authors, including Ågren and Schemske (1993), Husband and Schemske (1996) and Barringer and Geber (2008). Inbreeding depression (δ) is the reduction in mean fitness of a trait, e.g. number of seeds produced, germination percentage/rate, of selfed progeny (W_s) compared to that of outcrossed progeny (W_o). It is typically estimated using the following equation:

$$\delta = 1 - (W_s/W_o) \text{ or } 1 - \text{(relative fitness)}$$

Thus, when $W_s \leq W_o$ the value of δ is bound between 0 ($W_s = W_o$) and +1 ($W_s = 0$). Inbreeding depression (ID) also applies to the reduction in mean fitness of offspring that results from crosses between close relatives (i.e. biparental ID). In which case, W_s is the reduction in mean fitness of offspring due to crossing with close relatives. Some general conclusions related to ID are given in Table 1.

ID may be caused by increased homozygosity of deleterious recessive or partially recessive alleles (mutations) – the *partial dominance hypothesis* – or by '. . . increased homozygosity for alleles at loci with heterozygote advantage' – the *overdominance hypothesis* (Charlesworth and Willis, 2009). Thus, according to the partial dominance hypothesis, inbreeding increases the chance that two diploid individuals carrying recessive detrimental mutations will mate with each other, and only in the homozygous state will the negative effects of deleterious alleles be expressed in the offspring. In the overdominance hypothesis, heterozygosity is superior to homozygosity,

i.e. individuals carrying two different copies of an allele are more fit than those carrying two identical copies of the same allele. It appears that most ID is caused by mildly deleterious alleles (partial dominance hypothesis), which may be purged by inbreeding (Lande and Schemske, 1985; Charlesworth and Charlesworth, 1987; Charlesworth and Willis, 2009), but see comments under 'Population size and history' in Table 1 with regard to purging.

However, fitness of a trait is not always enhanced by outcrossing, i.e. W_o is not always greater than W_s. Thus, one could also get a higher mean fitness of inbred than of outbred progeny. In which case, $W_s > W_o$, and the value of δ is negative (to $-\infty$), when the fitness value of outcrossed progeny approaches 0. Thus, using the formula $\delta = 1 - (W_s/W_o)$ to calculate ID does not yield a symmetrical value around zero (-1 to $+1$), i.e. it does not give equal weight to $W_s > W_o$ (to $-\infty$) vs. $W_s < W_o$ (to $+1.0$).

A more meaningful way to compare the fitness of inbred and outcrossed individuals and families is to use a measure of relative performance (RP), for which the phenotypic values will be equidistant from zero, when $W_s > W_o$ (to -1) and when $W_s < W_o$ (to $+1$). Thus, a positive value indicates that outbred plants outperformed inbred plants, and the closer the value to 1.0 the greater the ID. A negative value indicates that inbred plants outperformed outbred plants, and the more negative the value the greater the inbreeding benefit. The equation for relative performance is:

$$\text{RP} = (W_o - W_s)/W_{max}$$

where W_{max} is the larger of the two values, i.e. W_o or W_s. RP is the same as $\delta = 1 - (W_s/W_o)$ when $W_s < W_o$ and the same as $\delta = (W_o/W_s) - 1$ when $W_s > W_o$.

For most traits measured in ID studies, higher numbers represent better performance. However, in calculating rate (speed), e.g. days to 50% germination of selfed vs. outcrossed seeds, the higher value represents reduced performance. Thus, if W_o has a faster rate (speed, i.e. fewer days to germinate) than W_s the equation to use in calculating performance is $1 - (W_o/W_s)$, i.e. relative fitness $= 1/(W_s/W_o) = W_o/W_s$, whereas when W_s has a faster rate the equation to use is $(W_s/W_o) - 1$.

Relation of inbreeding effect to inbreeding coefficient (*F*)

Theoretical aspects

The material in this section is based primarily on that in Sorensen (1969), Anderson *et al.* (1992), Keller and Waller (2002) and Charlesworth and Willis (2009). If deleterious mutations at different loci affecting fitness have independent (multiplicative) effects

Table 1. A general summary of the results obtained in studies on inbreeding depression (δ) in plants

- **Inbred vs. outbred plants**. In general, outbred plants (W_o) have higher fitness than inbred plants (W_s), indicating inbreeding depression ($W_s/W_o < 1.0$) (Darwin, 1876; Husband and Schemske, 1996; Angeloni *et al.*, 2011). However, in many cases inbred seeds germinate equally well as, and sometimes better than, outbred seeds (Darwin, 1876; this review).
- **Competition** may or may not increase δ, i.e. density-dependent δ; also frequency-dependent δ, i.e. frequency of inbred versus outbred neighbours (Belaoussoff and Shore, 1995; Cheptou *et al.*, 2000b, 2001; Goodwillie, 2000; Cheptou and Schoen, 2003; Koelewijn, 2004; Lhamo *et al.*, 2006; Pujol and McKey, 2006; Willi *et al.*, 2007; Kennedy & Elle, 2008).
- **Herbivory** may or may not increase δ, which may vary between populations and fitness traits (Carr and Eubanks, 2002).
- **Physical environment**. δ may or may not increase with stress; thus, e.g. [$(\delta_{field}/\delta_{greenhouse}) \geq 1.0$ (or even < 1.0)] (Schemske, 1983; Dudash, 1990; Ashman, 1992; Heywood, 1993; Willis, 1993b; Eckert and Barrett, 1994; Norman *et al.*, 1995; Durel *et al.*, 1996; Del Castillo, 1998; Koelewijn, 1998; Cheptou *et al.*, 2000a; Groom and Preuninger, 2000; Armbruster and Reed, 2005; Hayes *et al.*, 2005b; Heschel *et al.*, 2005; Mena-Ali *et al.*, 2008; Waller *et al.*, 2008; Hirao, 2010; Prill *et al.*, 2014). Cheptou and Donohue (2011) found '... compelling evidence that inbreeding depression is environment-dependent'. However, in a meta-analysis, Angeloni *et al.* (2011) found that the magnitude of δ did not differ significantly among greenhouse, field and common garden environments.
- **Breeding system.** Outbreeders may or may not show greater δ than inbreeders (Husband and Schemske, 1996; Vogler *et al.*, 1999; Fishman, 2001; Busch, 2005). Husband and Schemske (1996) found a significant negative correlation between cumulative δ and primary selfing rate. These authors also found a negative relationship between $\delta_{germination}$ and primary selfing rate, but it was not significant. In the meta-analysis by Angeloni *et al.* (2011), δ was significant for both self-compatible and self-incompatible species, but the magnitude did not vary between mating systems. In a study by Winn *et al.* (2011), three-stage and four-stage cumulative δ was significantly lower in highly selfing [primary selfing rate (r) > 0.8] species than in those with mixed ($0.2 \leq r \leq 0.8$) and highly outcrossing (r > 0.8) mating systems, which did not differ from each other. The high δ and its lack of difference in mixed-mating and outcrossing species indicate that selfing in mixed-mating species is not sufficient to purge deleterious alleles (and thus does not reduce δ). Winn *et al.* (2011) also found that δ for germination did not differ in the analysis that included all angiosperms and gymnosperms. However, δ for germination and of other life-history stages of selfing angiosperm taxa was significantly lower than that of those with mixed and outcrossing taxa, which did not differ from each other. Thus, the prediction that species with a mixed mating system are in a transition from highly outcrossing species to highly selfing species was not supported.
- **Level of inbreeding**. There may or may not be a significant negative relationship between fitness and the coefficient of inbreeding (F). Effect of inbreeding may vary among individual traits, growth conditions, families, populations, genotypes and even gender (male vs. female) (Hellman and Moore, 1983; Molina-Freaner and Jain, 1993; Willis, 1993a; Seavey and Carter, 1994; Hauser and Loeschcke, 1995, 1996; Nason and Ellstrand, 1995; Durel *at al.*, 1996; Mayer *et al.*, 1996; Del Castillo, 1998; Koelewijn, 1998; Wang *et al.*, 1999; Buza *et al.*, 2000; Cheptou *et al.*, 2000b; Ouborg *et al.*, 2000; Richards, 2000a; Galeuchet *et al.*, 2005; Hayes *et al.*, 2005a; Hensen and Wesche, 2006; Aegisdóttir *et al.*, 2007; Kochánková and Mandák, 2009; Hirao, 2010).
- **Population genetic diversity**. There may or may not be a significant positive correlation between fitness and population genetic diversity (Oostermeijer *et al.*, 1994, 1995; Fischer and Matthies, 1998; Lammi *et al.*, 1999; Greimler and Dobeš, 2000; Kahman and Poschold, 2000; Luijten *et al.*, 2000; Schmidt and Jensen, 2000; Pluess and Stöcklin, 2004; Hensen and Oberprieler, 2005; Leimu and Mutikainen, 2005; Bachmann and Hensen, 2007; de Vere *et al.*, 2009).
- **Timing of δ.** δ may occur in any and all stages of the life cycle. It can vary in magnitude among stages of the life cycle, but the majority of δ is expressed in the late life stages of selfing species and in both early and late stages of outcrossing species (Husband and Schemske, 1996; Brennan *et al.*, 2005; Galloway and Etterson, 2007; Angeloni *et al.*, 2011). Furthermore, in long-lived perennials the magnitude of δ for a life-history trait such as survival may increase with time and thus plant age, i.e. from early in the life cycle to late in the life cycle (Koelewijn *et al.*, 1999; Wagenius *et al.*, 2009). In *Pinus leucodermis*, selection did not act against progenies in the seed maturation or germination stages of the life cycle. However, inbreds had been eliminated by the time they were 5 years old (Morgante *et al.*, 1993). In their review of the magnitude and time of δ in plants, Husband and Schemske (1996) stated that 'The greatest inbreeding depression within a population generally was found early, during seed maturation (mean δ = 0.24), or late, during growth/reproduction (δ = 0.25), but rarely during germination (δ = 0.12), or juvenile survival (δ = 0.15).'
- **Taxonomic group, life form and life span**. In general, δ in gymnosperms > angiosperms; trees > shrubs > herbs; and perennials > annuals (Husband and Schemske, 1996; Angeloni *et al.*, 2011).
- **Ploidy level**. δ may or may not be higher in diploids than in tetraploids, and the magnitude of δ can vary between families and fitness traits (Johnston and Schoen, 1996; Husband and Schemske, 1997; Rosquist, 2001; Barringer and Geber, 2008).
- **Maternal families**. δ can vary considerably among maternal families (= offspring of a female and includes both selfed and outcrossed progeny, i.e. half-sibs and full-sibs) within populations and with population of origin. Differences in δ among maternal families may be lower in selfing than in outcrossing populations. δ, especially in the early stages of the life cycle, may be modified by maternal environmental effects (Dudash, 1990; Biere, 1991a; Platenkamp and Shaw, 1993; Carr and Dudash, 1995; Norman *et al.*, 1995; Parker *et al.*, 1995; Ruckelshaus, 1995; Durel *et al.*, 1996; Hauser and Loeschcke, 1996; Holtsford, 1996; Ramsey and Vaughton, 1998; Kärkkäinen *et al.*, 1999; Kephart *et al.*, 1999; Koelewijn *et al.*, 1999; Richards, 2000a; Picó *et al.*, 2004b; Stephenson *et al.*, 2004; Galeuchet *et al.*, 2005; Hayes *et al.*, 2005a; Bailey and McCauley, 2006; Goodwillie and Knight, 2006; Jolivet & Bernasconi, 2007; Raabová *et al.*, 2009). Paternal family also may have a significant effect on offspring fitness (Teixeira *et al.*, 2009).

Table 1. *Continued*

- **Population size and history.** δ within populations can be affected by current and past (bottlenecks, founder effects and genetic drift) population size and genetic variation. It is expected to be lower in small than in large populations, and in populations with low than with high genetic variation (Mustajärvi *et al.*, 2005; Hirayama *et al.*, 2007; Thiele *et al.*, 2010; Angeloni *et al.*, 2011). In general, lower levels of δ are expected in small populations with a long history of inbreeding because deleterious genes presumably have been purged from populations of selfers. However, see Byers and Waller (1999), who did not find much evidence for purging; Cheptou and Donohue (2011), who found evidence for purging to be equivocal; and Fox *et al.* (2008), who stated that purging seems to vary among species, populations and families within populations and is, at least in part, environment specific. For an outcrossing population of *Mimulus guttatus*, Willis (1999a) showed that lethal or sterility alleles of large effect are easy to purge, whereas mildly deleterious alleles are not. He concluded that '... mildly deleterious, partially recessive alleles cause most of the inbreeding depression in this population of *Mimulus guttatus*. Major deleterious alleles such as lethals and steriles contribute little to inbreeding load'. These conclusions about the outcrossing population of *M. guttatus* were further substantiated by Willis (1999b).
- **Isolated populations.** Fitness may or may not be affected by isolation of small populations away from the central population, and by plant density and isolation within populations (Menges, 1991; Hauser and Loeschcke, 1994; Groom, 1998; Meier and Holderegger, 1998; Lammi *et al.*, 1999; Taylor *et al.*, 1999; Groom and Preuninger, 2000; Richards, 2000a, b; Hooftman *et al.*, 2003; Watanabe *et al.*, 2003; Davis *et al.*, 2004; Lienert and Fischer, 2004; Galeuchet *et al.*, 2005; Le Cadre *et al.*, 2008).
- **Space and time.** δ can vary considerably over space and time within and among populations and habitats. It can vary geographically and from year to year at a single location for a species (Johnston, 1992; Willis, 1993b; Kärkkäinen *et al.*, 1996; Kephart *et al.*, 1999; Cheptou *et al.*, 2000a; Galloway *et al.*, 2003; Wallace, 2003; Lofflin and Kephart, 2005; Goodwillie & Knight, 2006; Galloway & Etterson, 2007).
- **Within- vs. between-population crosses.** Fitness of progeny from within-population crosses can be greater than, equal to or less than that of those from between-population crosses, and it may vary between populations and fitness traits (Riley, 1956; van Treuren *et al.*, 1993; Hauser and Loeschcke, 1994; Dahlgaard and Warncke, 1995; Trame *et al.*, 1995; Fischer and Matthies, 1997; Byers, 1998; Richter and Weiss, 1998; Affre and Thompson, 1999; Sheridan and Karowe, 2000; Emery and McCauley, 2002; Luijten *et al.*, 2002; Colling *et al.*, 2004; Heliyanto *et al.*, 2005; Becker *et al.*, 2006; Busch, 2006; Ricardo *et al.*, 2006; Billingham *et al.*, 2007; Willi *et al.*, 2007; Caño *et al.*, 2008; Raabová *et al.*, 2009; Forrest *et al.*, 2011). In a meta-analysis, Angeloni *et al.* (2011) found that δ did not vary between intra- and interpopulation crosses, which indicates that neither outbreeding depression nor heterosis commonly occurs as a result of crosses between populations.
- **Optimum outcrossing distance.** The idea here is that progeny fitness at an intermediate crossing distance is higher than that at near- or far-crossing distances. Low fitness at near-crossing distances between parents is the result of (biparental) inbreeding depression, and that at far-crossing distance is the result of outbreeding depression (Price and Waser, 1979; Waser and Price, 1989, 1991, 1994; Waser *et al.*, 2000; Willi *et al.*, 2005; Billingham *et al.*, 2007). However, in most cases, including those for seed germination, an optimum outcrossing distance was not found (see numerous references in the text).
- **Rarity and endemism.** δ is found in both rare and endemic species, but in general the magnitude does not differ from that of common and non-endemic species, respectively (Angeloni *et al.*, 2011), i.e. δ of endemics is similar to that of non-endemics, and δ of rare species is similar to that of common species.

(no epistasis), then fitness is expected to decline exponentially with an increase in F (Fig. 1). This relationship is as follows.

$$R = \text{relative fitness}\,(W_s/W_o)$$

$$W_s = e^{-(A+BF)}$$

$$W_o = e^{-A}$$

$$R = \frac{e^{-(A+BF)}}{e^{-A}} = e^{-BF}$$

A is a decrease in fitness due to environmental causes and genetic damage in a randomly mating population ($F = 0$), i.e. a decrease in fitness not attributed to inbreeding. B is the inbreeding load, i.e. an estimate of the number of lethal equivalents (a group of alleles that would be lethal if homozygous) per gamete. B describes the rate at which fitness declines with inbreeding and is equal to 0 when there is no inbreeding depression.

$$B = -\frac{1}{F}\log_e\left(\frac{W_s}{W_o}\right)$$

$-B$ is the slope of the line ($\Delta y/\Delta x$) (Fig. 1).

$e^{-(A+BF)}$ is a measure of fitness of an inbred trait, e.g. the proportion of inbred seeds that germinates. e^{-A} is a measure of fitness of an outbred trait, e.g. the proportion of outbred seeds that germinates.

F is the coefficient of inbreeding, a mathematical expression of the level of homozygosity (% homozygosity $= F \times 100$) at selected loci for individuals or populations submitted to inbreeding. F values range from 0.0 (no homozygosity) to 1.0 (complete homozygosity).

Thus, the equation for inbreeding depression [$\delta = 1 - \text{relative fitness} = 1 - (W_s/W_o)$] can be written as $1 - (\Delta y/\Delta x)$ ($= 1 - e^{-BF}$).
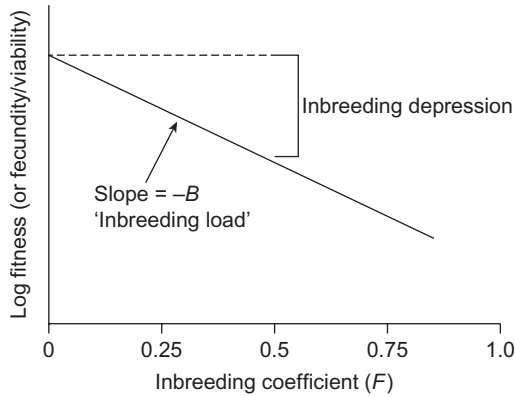
Figure 1. Theoretical decline in fitness (increase in inbreeding depression, δ) with increase in inbreeding coefficient (F). The inbreeding coefficient of progeny of randomly outbred plants ($F = 0$) will be 0.5 after one generation of selfing. From Keller and Waller (2002), with permission.

Now, let us look at the relationship between δ and B. The example given is for selfed progeny ($F = 0.5$) of randomly outbred plants ($F = 0$) that have undergone one generation of selfing.

$$W_s = W_o e^{-BF}$$

$$e^{-BF} = W_s/W_o$$

$$\log_e(e^{-BF}) = \log_e(W_s/W_o)$$

$$-BF = \log_e(W_s/W_o)$$

$$-B = \log_e(W_s/W_o)/F$$

$$B = -\frac{1}{F}\log_e(W_s/W_o)$$

$$B = -\frac{1.0}{0.5}\log_e(W_s/W_o)$$

$B = -2\log_e R$ (i.e. the number of lethal equivalents per gamete).

Number of lethal equivalents per zygote (2B)

$$= -4\log_e R$$

Thus the equation for calculating inbreeding depression for first-generation progeny of outbred plants species is:

$$\delta = 1 - e^{-BF} = 1 - e^{-B(0.5)} = 1 - e^{-B/2}$$

For all other levels of inbreeding, the equation is:

$$\delta = 1 - e^{-B \times F}$$

Effect of level of inbreeding (F) on germination

Germination may or may not decline with an increase in F (Table 2). In the 35 case studies on the 25 species included in Table 2, there was a negative relationship between germinability and F in 12 and no relationship in 23. In a few cases (e.g. Richards, 2000a) the relationship between germination and F was negative-linear, but in none of the cases did germination decline exponentially with increase in F (cf. Fig. 1). Apparently, this indicates that there were epistatic interactions among loci with deleterious mutations affecting germination.

Effect of population genetic diversity on germination

In contrast to what might be expected, germination may not be positively related to population genetic diversity (Table 3). For only four of the ten species listed in this table was there a positive relationship between germination and genetic diversity; for the other six species, there was no relationship between the two characters.

Outbreeding depression and optimum crossing distance

Crosses within (intra) and between (inter) sites or populations could lead to reduced fitness of the hybrid offspring through outbreeding depression (OD). Such a decline in fitness is caused by (1) disruption of segregation and recombination in hybrid offspring of unique co-adapted gene complexes that exist within the genomes of the parents (disruption of favourable epistatic interactions); or (2) loss (dilution with foreign genes) of adaptation in hybrid offspring to the local environment of both parents. In the first case, the decline in fitness may not occur until the F_2 generation, whereas in the second case it can occur in the first generation (i.e. F_1 hybrids) (Price and Waser, 1979; Templeton, 1986; Waser and Price, 1989, 1994; Parker, 1992; Edmands, 2002, 2007). Outbreeding depression (RP$_o$) can be calculated by the following equation (Bermingham and Brody, 2011):

$$RP_0 = (Z_{intra} - Z_{inter})/Z_{max}$$

where Z_{intra} is the mean performance for intrasite hybrid progeny; Z_{inter}, mean performance of intersite hybrid progeny; and $Z_{max} = Z_{intra}$ when $Z_{intra} > Z_{inter}$ and $Z_{max} = Z_{inter}$ when $Z_{inter} > Z_{intra}$. Positive values indicate outbreeding depression.

Since inbreeding depression can occur in offspring from crosses between close neighbours that are relatives and outbreeding depression in offspring

Table 2. Effect of inbreeding coefficient (F) on seed germination

Species	Comments	References
Amsinckia (three species)	Parental inbreeding coefficients of 0.032–1.00 had little effect on ID for germination or seedling emergence of three species from nine populations.	Johnston and Schoen, 1996
Atriplex tatarica	Negative correlation between F and both first-day and final germination percentage of the two diaspore morphs of this heterocarpic species.	Kochánkova and Mandák, 2009
'Caipaira' cucumber	Ranges of RP for germination percentage and speed were only -0.02 to 0.12 and 0.10 to 0.02, respectively, during five generations of inbreeding; no effect on germination from $S_o \rightarrow S_5$.	Godoy *et al.*, 2006
Campanula thyrsoides	F values (0.00–0.25) did not have an effect on germination percentage.	Aegisdóttir *et al.*, 2007
Chamerion (*Epilobium*) *angustifolium*	ID for germination of inbred autotetraploid plants self-pollinated across three successive generations (0.00, 0.17, 0.36) did not differ from that of the outbred line used to control for environmental effects of ID. For both selfed and outcrossed lines, ID for germination decreased with an increase in number of generations ($1 \rightarrow 2 \rightarrow 3$) in a near-linear fashion.	Ozimec and Husband, 2011
Clarkia tembloriensis	Seeds from a population with a selfing rate (s) of 0.74 and an F value of 0.77 germinated to 95%, whereas those from a population with an s value of 0.16 and an F value of 0.10 germinated to 82%.	Holtsford, 1996
Collinsia heterophylla	For four populations, germination percentage declined linearly with an increase in F from 0.00 to 0.75.	Mayer *et al.*, 1996
Crepis sancta	F (0.00–0.25) had no effect on germination of central achenes of this achene-heterocarpic species (peripheral achenes not tested).	Cheptou *et al.*, 2000a
Cucurbita pepo var. *texana*	Germination percentage exhibited a negative-linear decline from *c.* 48% at $F = 0.00$ to *c.* 40% at $F = 0.875$.	Hayes *et al.*, 2005a, b
Epilobium obcordatum	Negative relationship between germination percentage and F (0.00–0.35).	Seavey and Carter, 1994
Gilia achilleifolia	$S_o(F = 0) < [S_1(0.50) = S_2(0.75)]$; a big increase in germination percentage from $S_0 \rightarrow S_1$ generations followed by no change from $S_1 \rightarrow S_2$.	Schoen, 1983
Impatiens capensis	Negative relationship between date of emergence and F (0.00, 0.50, 0.875). Seed mass decreased with F, and smaller seeds emerged later than larger ones.	McCall *et al.*, 1994
Lychnis flos-cuculi	Germination percentage decreased with increase in F from 0.00 to 0.75.	Hauser and Loeschcke, 1995
Lychnis flos-cuculi	Outcrossed seeds ($F = 0$) germinated to 93.3% and inbred seeds ($F = 0.25, 0.50, 0.75$) to 83% to 89.7%. Further, outbred seeds reached maximum germination in 32 d and inbred seeds in 36–45 d.	Hauser and Loeschcke, 1996
Mimulus guttatus	No directional change in germination percentage with increase in F from 0.00 to 0.75.	Willis, 1993a
Plantago coronopus	Germination was not significantly affected by F values of 0.00–0.876.	Koelewijn, 1998
Plantago coronopus	Germination percentage did not differ between selfed hermaphrodites ($F = 0.50$, 91%), outcrossed hermaphrodites ($F = 0.00$, 89%) and females $\times$ hermaphrodites ($F = 0.00$, 86%).	Koelewijn and van Damme, 2005
Raphanus sativus	F values of 0.00–0.25 had no effect on germination.	Nason and Ellstrand, 1995
Rhododendron brachycarpum	No relationship between germination percentage and parental kinship coefficient (parental relatedness).	Hirao, 2010
Sidalcea oregana subsp. *spicata*	Level of inbreeding (outcross, sib-cross, self) had no significant effect on germination.	Ashman, 1992
Silene alba (= *S. latifolia*)	Germination percentage decreased linearly with increase in F, from *c.* 95% at $F = 0.00$ to *c.* 10% at $F = 0.375$, with considerable variation among maternal families.	Richards, 2000b

Table 2. *Continued*

Species	Comments	References
Silene latifolia	Seeds with F values of 0.00, 0.375 and 0.590 germinated to 83.1%, 83.9% and 91.4%, respectively.	Ouborg *et al.*, 2000
Swainsonia recta	Percentage germination was lower in populations with high than with medium and low F values.	Buza *et al.*, 2000
Trifolium hirtum	Germination was not affected by level of inbreeding: S_0 (open-pollinated) $= S_1$ (self-pollinated S_0's) $= S_2$ (self-pollinated S_1's).	Molina-Freaner and Jain, 1993
Vaccinium corymbosum and *V. ashei*	No significant relationship between germination percentage and F.	Hellman and Moore, 1983

ID, inbreeding depression; RP, relative performance; S refers to number of generations of selfing.

between crosses of spatially widely separated individuals that are not closely related, it is not too surprising that an optimal crossing distance between nearby (ID) and far-off (OD) plants has been demonstrated in several studies (e.g. Price and Waser, 1979; Waser and Price, 1989; Fischer and Matthies, 1998; Waser *et al.*, 2000). However, many studies have found no evidence of an optimal outcrossing distance in general (e.g. Newport, 1989; Dudash, 1990; Richter and Weis, 1998). An optimal outcrossing distance for seed germination was found for *Gentianella germanica* (Fischer and Matthies, 1997) and *Zostera marina* (Billingham *et al.*, 2007). For example, in *Z. marina*, the percentage of germination was: intermediate (71%) > near (37%) > far (29%); and for germination rate (speed): intermediate (6 d) > [near (12 d) = far (13 d)]. Germination of field-sown seeds of *Ipomopsis aggregata* had an optimum outcrossing distance in the 1981 cohort but not in the 1987 and 1990 cohorts (Waser *et al.*, 2000). For the tetraploid *Digitalis purpurea*, an optimal outcrossing distance was found for germination speed but not for germination percentage (Grindeland, 2008). On the other hand, an optimal outcrossing distance was not found for germination/emergence in *Agave schottii* (Trame *et al.*, 1995), *Campanula americana* (Galloway and Etterson, 2005), *Chamaecrista fasciculata* (Sork and Schemske, 1992), *Cyclamen* spp. (Affre and Thompson, 1999), *Eupatorium perfoliatum*, *E. resinosum* (Byers, 1998), *Gentiana pneumonanthe* (Oostermeijer *et al.*, 1995), *Impatiens capensis* (McCall *et al.*, 1994), *Lobelia cardinalis* (Schlichting and Devlin, 1992), *Sabatia angularis* (Dudash, 1990), *Scabiosa columbaria* (van Treuren *et al.*, 1993), *Silene acaulis* (Delph, 2004), *Yucca whipplei* subsp. *whipplei* (Richter and Weis, 1998) and several other species.

Table 3. Effect of population genetic diversity on seed germination

Species	Comments	References
Arnica montana	No correlation between germination percentage and genetic diversity.	Luijten *et al.*, 2000
Campanula glomerata	No correlation between germination percentage and genetic diversity; non-germinated seeds were non-viable.	Bachmann and Hensen, 2007
Clarkia pulchella	Germination was significantly higher in populations with high than in those with low genetic effective size.	Newman and Pilson, 1997
Embothrium coccineum	Germination percentage was significantly negatively correlated with log-transformed forest fragment size, which was positively, but not significantly, correlated with gene diversity.	Mathiasen *et al.*, 2007
Gentiana pneumonanthe	No correlation between germination percentage and population genetic diversity, although seed mass was positively correlated with heterozygosity.	Oostermeijer *et al.*, 1994
Gentianella austriaca	Percentage germination was highest in populations with highest genetic diversity.	Greimler and Dobeš, 2000
Lychnis viscaria	No correlation between percentage germination and genetic diversity.	Lammi *et al.*, 1999
Mercurialis perennis	No correlation between germination percentage and genetic diversity.	Vandepitte *et al.*, 2009
Pedicularis palustris	Number of seedlings per flowering plant was significantly higher in populations with higher genetic diversity.	Schmidt and Jensen, 2000
Ranunculus reptans	No significant relationship between germination percentage and long-term population size as measured by allelic diversity.	Willi *et al.*, 2005

Heterosis

Mixing of genes from different sites or populations may also result in heterosis (hybrid vigour), i.e. an increase in offspring fitness due to increased heterozygosity resulting from outcrossing individuals of inbred populations or sites (Luitjen *et al.*, 2002; Busch, 2006). Heterosis (*H*) can be calculated by the following equation (Busch, 2006; Bermingham and Brody, 2011):

$$H = (Z_{inter} - Z_{intra})/Z_{intra}$$

where Z_{intra} is the mean performance of progeny of intrasite (or intrapopulation) crosses and Z_{inter} the mean performance of progeny of intersite (or interpopulation) crosses. Positive values indicate heterosis. An example of hybrid vigour for seed germination is the study by Busch (2006) on the cedar glade endemic *Leavenworthia alabamica*. Seeds from crosses within a small, geographically isolated, self-incompatible population of this species germinated to 38%, whereas those from crosses between this isolated population and other (non-isolated) populations (pollen donors) germinated to 80% (*H* = 1.105), i.e. substantial heterosis. In *Polemonium vanbruntiae*, seeds from intersite crosses germinated to 79% and those from intrasite crosses to 70% (*H* = 0.13) (Bermingham and Brody, 2011).

However, most within-population (WP) and between-population (BP) crosses have not resulted in heterosis for germination. For 40 other such studies, WP < BP (5), WP = BP (29) and WP >BP (6) (see references in Table 1 under 'Within vs. between population crosses'). Five of these 40 cases were on isolated (vs. central) populations. In one of the five cases WP < BP, and in four WP = BP.

Other studies have also included in their crossing scheme near (WP$_{near}$), far (WP$_{far}$) and very far (WP$_{very far}$) distances within populations, and populations within (WR) and between (BR) regions. The results of these studies are as follows: WP$_{near}$ = WP$_{far}$ = WP$_{very far}$ (*Hymenoxys acaulis*) (Moran-Palma and Snow, 1997); WP$_{near}$ > WP$_{far}$ = BP (*Eupatorium perfoliatum, E. resinosum*) (Byers, 1998); WR = BR (*Anthericum liliago, A. ramosum*) (Rosquist, 2001); WP$_{near}$ = WP$_{far}$ (for each of two populations of *Hypericum cumulicola*) (Trager *et al.*, 2005); (WP = BR) > BP (*Hypochoeris radicata*) (Becker *et al.*, 2006); (WP$_{far}$ = BP) > WP$_{near}$ (*Stenocereus eruca*) (Ricardo *et al.*, 2006); WP = BP = BR (*Aster amellus*) (Raabová *et al.*, 2009) and *Polylepis australis* (Seltmann *et al.*, 2009).

RP of germination and lifetime fitness

The effects of inbreeding are cumulative (multiplicative) across the plant life cycle. Lifetime ID is estimated by calculating the product of relative fitness (W_s/W_o) of all stages of the life cycle (= cumulative relative fitness, CRF) and then subtracting CRF from 1.

$$CRF = (W_{s1}/W_{o1}) \times (W_{s2}/W_{o2})$$

$$\times (W_{s3}/W_{o3})...(W_{sx}/W_{ox})$$

$$1 - CRF = total\ inbreeding\ depression.$$

Thus, as a component of multiplicative CRF, low relative fitness for germination can have a big influence on lifetime fitness of plants.

In the majority of cases, $W_s < W_o$ for most (or all) life-cycle stages, and total ID will be positive but < 1.0. However, in one or more stage(s) of the life cycle, such as seed germination, survival and flowering, selfed offspring may outperform outcrossed offspring, i.e. $W_s > W_o$. In which case, one could get a CRF of > 1.0 and thus a negative lifetime ID (e.g. Culley *et al.*, 1999; Kephart *et al.*, 1999).

Comparison of inbreeding vs. outcrossing on seed germination

The purpose of this section of the review was to determine the proportion of cases in a large number of plant taxa in which: (1) inbred seeds germinated less well than outbred seeds (I < O); (2) inbred seeds germinated equally well as outbred seeds (I = O); and (3) inbred seeds germinated better than outbred seeds (I > O). We report 743 cases ('case studies') in which germination, based on percentage and/or rate (speed), of inbred seeds were (was) compared to that of outbred seeds. Cross-type (i.e. inbred vs. outbred) comparisons used in selecting inbred vs. outbred cases of seed germination are given in Table 4. The study by Kennedy and Elle (2008) will be used to illustrate what we mean by 'case study'. This study on *Collinsia*

Table 4. Cross-type comparisons used in selecting inbred vs. outbred cases of seed germination

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(1) Selfing (inbred) vs. outcrossing (outbred) in purely hermaphrodite species (most comparisons) and in a few selfed vs. outcrossed hermaphrodites in gynodioecious species.
(2) Crosses with related male, i.e. biparental inbreeding (inbred), vs. crosses with unrelated male (outbred).
(3) Selfing and/or near (inbred) vs. crossing (outbred) with intermediate- and far-distance mates within a population and with mates between populations.
(4) Within (inbred) vs. between (outbred) family crosses.
(5) Within families (inbred) vs. within populations (outbred) crosses.
(6) Zero and low (outbred) vs. high (inbred) coefficient of inbreeding (*F*).
(7) Zero generations of selfing (S_o) (outbred) vs. one or more generations of selfing (S_1, S_2, etc.) (inbred).
(8) High (inbred) vs. low (outbred) autogamous selfing.
(9) Narrow (inbred) vs. wide (outbred) herkogamy (anther–stigma distance) class.

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parviflora included eight populations with two levels of parental plant competition (with and without), thus 16 case studies (see their Appendix S1). Without competition, selfed and outcrossed seeds germinated equally well in all eight populations, thus eight cases of I = O. With competition, selfed seeds germinated better than outcrossed seeds in two populations, thus two cases of I > O; selfed and outcrossed seeds germinated equally well in five populations, thus five more cases of I = O; and selfed seeds germinated less well than outcrossed seeds in one population, thus one case of I < O.

For the 743 case studies (Table 5), inbred seeds germinated less well than outbred seeds in 311 (41.9%); inbred and outbred seeds germinated equally well in 372 (50.1%); and inbred germinated better than outbred seeds in 60 (8.1%). A taxonomic analysis of the data for gymnosperms, angiosperms, monocots, eudicots and the three plant families with the highest number of case studies in the data set is presented in Table 6.

The proportions of I < O, I = O and I > O can vary between plant families; it was much more similar between Asteraceae and Pinaceae than it was between either of these families and Caryophyllaceae (Table 6). The I/O proportions were quite similar between gymnosperms and angiosperms, and they did not differ greatly between monocots and eudicots. Like the entire data set, this analysis found that outbred seeds germinated better than (I < O) or equally well as (I = O) inbred seeds in a high proportion of the cases, and only in a small proportion of the cases did inbred seeds germinate better than outbred ones (I > O). In six of the seven taxonomic groups analysed in Table 6, inbred seeds germinated equally as well or better than outbred seeds in >50% of the cases. The most 'deviant' taxonomic group in this analysis is the Caryophyllaceae, in which (I < O) >> (I = O) > (I > O). For the other taxonomic groups analysed, [(I < O) < (I = O)] >> (I > O) or [(I < O) = (I = O)] >> (I > O) (monocots only).

Relationship between mass and germination in inbred vs. outbred seeds

Here, we report the effect of inbreeding on both seed mass and germination for 216 case studies obtained from papers on the effect of ID on germination (Table 7), which also reported individual seed mass. Mean mass of outbred seeds was greater than that of inbred seeds (I < O) in 107 (49.5%) cases; in 82 (38.0%) cases, I = O; and in 27 (12.5%), I > O. For only 125 (57.9%) cases was there a direct relationship of inbreeding/ outcrossing between seed size and germination, i.e. 54 cases of (I < O, germination) = (I < O, seed mass); 61 cases of (I = O, germination) = (I = O, seed mass);

and 10 cases of (I > O, germination) = (I > O, seed mass). Large seeds germinated better than small ones in 54 (50.0%) of the 107 cases in which outbred seeds were larger than inbred seeds. In the other 53 (50.0%) cases, inbred and outbred seeds germinated equally well in 43 (40.2%) cases, and in 10 (9.3%) cases inbred seeds germinated better than outbred seeds. There was a direct relationship between large seed size and best germination in only 54 (25.0%) of the 216 case studies. In the 54 (67.7%) of the 80 cases in which germination of I < O, mass was I < O. This suggests that ID for germination in these 54 cases may have been mediated by seed size. However, in the other 26 (32.5%) of the 80 cases in which germination of I < O, mass of I = O (15 cases) or mass of I > O (11 cases), thus ID was not mediated by seed size. Outbred seeds were larger than inbred seeds (I < O) in 43 of the 107 cases in which germination of I = O and in 10 of the 27 cases in which germination of I > O.

Magnitude of ID for seed germination

In many cases, ID *per se* for seed germination was not given in a paper. Thus, we calculated these values primarily from information presented by the authors in tables or graphs on percentage and/or speed of germination of selfed vs. outcrossed seeds, based on the methods described under 'Inbreeding depression', above. In a few cases, especially those involving germination and emergence rate, RP was incorrect and needed to be recalculated. For example, in one study RP for speed of germination is given as +0.12. However, since selfed seeds germinated in fewer days (7.923) than outcrossed seeds (9.016), i.e. selfed seeds performed better than outcrossed seeds, the RP should be -0.12, i.e. $(W_s/W_o) - 1$, $(7.923/9.016) - 1 = -0.12$, not $1 - (W_s/W_o) = +0.12$. In another study, RP for days to emergence of selfed vs. outcrossed seedlings with and without competition was reported graphically as -0.12 and $+0.19$, respectively, when in fact they were $+0.12$ and -0.19, respectively. With competition, outcrossed seedlings emerged faster than selfed seedlings, thus the positive value for RP. Without competition, on the other hand, selfed seedlings emerged faster than outcrossed seedlings, thus the negative value for RP.

ID for seed germination covered most of the -1 to $+1$ range possible for RP. The most extreme cases reported for germination in which $W_s < W_o$ are 0.89 for *Silene alba* (= *S. latifolia*) (Richards, 2000a), 0.90 for *Anacamptis morio* (Smithson, 2006) and 1.0 for for *Silene vulgaris* subsp. *maritima* var. *petraea* (Pettersson, 1992), and the most extreme case for $W_s > W_o$ was -0.88 for *Cyclamen repandum* (Affre and Thompson, 1999). For several cases RP $\geq$ 0.50, and in a few cases RP was equal to or more negative than -0.40. On the other

Table 5. A taxonomic survey of the effect of selfing vs. outcrossing on seed germination. I, inbred; O, outbred. The numbers in parentheses indicate the number of case studies for that particular I/O relationship. Nomenclature/taxonomy follows Mabberley (2008) and APG-III (2009). For the few gynodioecious species listed in this table, information is only for hermaphrodites

Taxonomy (family, species)	Selfing vs. outcrossing	References
Acanthaceae		
Stenostephanus obeliiformis	I < O (1)	Stein and Hensen, 2013
Alismataceae		
Sagittaria australis	I < O (2), I = O (3), I > O (1)	Delesalle and Muenchow, 1992
S. latifolia	I < O (3), I = O (2), I > O (1)	Delesalle and Muenchow, 1992
Alliaceae		
Allium schoenoprasum	I < O (1)	Stevens and Bougourd, 1988
Amaranthaceae		
Atriplex tatarica	I < O (2)	Kochánková and Mandak, 2009
Apiaceae		
Trachymene incisa subsp. *incisa*	I = O (1)	Davila and Wardle, 2002
Apocynaceae		
Asclepias exaltata	I < O (1)	Himes and Wyatt, 2005
Nerium oleander	I = O (1)	Herrera, 1991
Araliaceae		
Panax quinquefolius	I = O (1)	Mooney and McGraw, 2007
Asparagaceae		
Agave schottii	I = O (3)	Trame *et al.*, 1995
Anthericum liliago	I = O (1), I > O (1)	Rosquist, 2001
A. ramosum	I < O (4)	Rosquist, 2001
Yucca whipplei subsp. *whipplei*	I < O (3)	Richter and Weis, 1998
Asphodelaceae		
Aloe peglarae	I = O (1)	Arena *et al.*, 2013
Bulbine bulbosa	I = O (1)	Owen *et al.*, 2007
Asteraceae		
Arnica montana	I = O (1)	Luijten *et al.*, 1996
Aster amellus	I = O (2)	Raabová *et al.*, 2009
Carduus pycnocephalus	I = O (1)	Oliviera *et al.*, 1983
C. tenuifolius	I = O (1)	Oliviera *et al.*, 1983
Crepis sancta	I = O (2)	Cheptou *et al.*, 2000b
C. sancta	I < O (2), I = O (2)	Cheptou *et al.*, 2001
Eupatorium perfoliatum	I > O (2)	Byers, 1998
E. resinosum	I = O (2)	Byers, 1998
Fluorensia cernua	I < O (1)	Ferrer *et al.*, 2009
Gaillardia pulchella	I = O (1)	Heywood, 1993
Hymenoxys herbacea	I = O (3)	Moran-Palma and Snow, 1997
Hypochoeris radicata	I = O (2)	Picó *et al.*, 2004a
H. radicata	I < O (3), I = O (1)	Becker *et al.*, 2006
Leontodon autumnalis	I < O (1)[a], I = O (1)[b]	Picó and Koubek, 2003
Olearia adenocarpa	I < O (1)	Heenan *et al.*, 2005
Scalesia affinis	I < O (1)	Nielsen *et al.*, 2007
Scorzonera humilis	I < O (2)	Colling *et al.*, 2004
Senecio integrifolius	I < O (2), I = O (2)	Widén, 1993
S. pterophorus	I < O (1), I = O (1)	Caño *et al.*, 2008
S. squalidus	I < O (1)	Brennan *et al.*, 2005
Tragopogon pratensis	I = O (1)	Picó *et al.*, 2003
Begoniaceae		
Begonia hirsuta	I < O (1)	Ågren and Schemske, 1993
B. semiovata	I = O (1)	Ågren and Schemske, 1993
Blandfordiaceae		
Blandfordia grandiflora	I = O (1)	Ramsey and Vaughton, 1996
B. grandiflora	I < O (11), I = O (9)	Ramsey and Vaughton, 1998
Boraginaceae		
Amsinckia douglasiana	I = O (1)	Cheptou and Schoen, 2003
A. gloriosa	I = O (1)	Cheptou and Schoen, 2003

Table 5. *Continued*

Taxonomy (family, species)	Selfing vs. outcrossing	References
Amsinckia (three spp.)[c]	I = O (18)	Johnston and Schoen, 1996
Anchusa crispa	I < O (1), I = O (3)	Quilichini *et al.*, 2001
Eritrichium aretioides	I < O (1)	Puterbaugh *et al.*, 1997
Hydrophyllum appendiculatum	I < O (1), I = O (1), I > O (1)	Wolfe, 1993
Phacelia dubia	I < O (1)	Del Castillo, 1998
Brassicaceae		
Alliaria petiolata	I = O (2)	Mullarkey *et al.*, 2013
Arabis fecunda	I > O (1)	Hamilton and Mitchell-Olds, 1994
A. petraea	I < O (1)	Kärkkäinen *et al.*, 1999
Brassica cretica	I < O (1)	Rao *et al.*, 2002
B. rapa	I < O (1)	Waller *et al.*, 2008
Cakile edentula var. *lacustris*	I < O (1)	Donohue, 1998
Cochlearia bavarica	I < O (1)	Fischer *et al.*, 2003
Hesperis matronalis	I > O (1)	Susko and Clubb, 2008
Leavenworthia alabamica	I < O (1), I = O (1)	Busch, 2005
L. crassa	I = O (1)	Charlesworth *et al.*, 1994
L. uniflora	I = O (1)	Charlesworth *et al.*, 1994
Raphanus sativus	I = O (1)	Nason and Ellstrand, 1995
Thlaspi alpina	I < O (4), I = O (2)	Riley, 1956
Cactaceae		
Opuntia rastera	I < O (1)	Mandujano *et al.*, 1996
Pachycereus pringlei	I = O (2)	Molina-Freaner *et al.*, 2003
Stenocereus eruca	I < O (1)	Ricardo *et al.*, 2006
Campanulaceae		
Campanula americana	I = O (3)	Galloway *et al.*, 2003
C. americana	I < O (2), I = O (1)	Galloway and Etterson, 2007
C. rapunculoides	I < O (1), I = O (1)	Vogler *et al.*, 1999
C. thyrsoides	I = O (1)	Aegisdóttir *et al.*, 2007
C. uniflora	I = O (2)	Aegisdóttir and Thorhallsóttir, 2006
Lobelia cardinalis	I < O (1), I = O (1)	Johnston, 1992
L. cardinalis	I = O (3)	Schlichting and Devlin, 1992
L. siphilitica	I < O (1)	Johnston, 1992
L. siphilitica	I < O (8), I = O (5), I > O (5)	Mutikainen and Delph, 1998
Caryophyllaceae		
Dianthus guliae	I < O (1)	Gargano *et al.*, 2009
Lychnis flos-cuculi	I < O (3), I = O (5)	Biere, 1991a
L. flos-cuculi	I < O (2), I = O (2)	Biere, 1991b
L. flos-cuculi	I < O (3)	Hauser and Loeschcke, 1994
L. flos-cuculi	I < O (2)	Hauser and Loeschcke, 1995
L. flos-cuculi	I < O (3)	Hauser and Loeschcke, 1996
L. flos-cuculi	I < O (1)	Galeuchet *et al.*, 2005
L. viscaria	I < O (4), I = O (2)	Mustajärvi *et al.*, 2005
Minuartia (*Arenaria*) *uniflora*	I = O (2)	Fishman, 2001
Petrocoptis visosa	I < O (1)	Navarro and Guitián, 2002
Schiedea lydgatei	I < O (10), I > O (1)	Norman *et al.*, 1995
S. membranacea	I < O (10), I > O (1)	Culley *et al.*, 1999
Silene alba (= *S. latifolia*)	I < O (2)	Richards, 2000a, b
S. ciliata	I < O (5), I = O (1)	Garcia-Fernández *et al.*, 2012
S. douglasii var. *oraria*	I < O (6), I = O (2)	Kephart *et al.*, 1999
S. douglasii (two varieties), including *oraria*	I < O (2), I = O (1)	Lofflin and Kephart, 2005
S. latifolia	I = O (1)	Teixeira *et al.*, 2009
S. nutans	I > O (2)	Thiele *et al.*, 2010
S. virginica	I < O (1)	Dudash and Fenster, 2001
S. vulgaris	I < O (1), I = O (2)	Emery and McCauley, 2002
S. vulgaris	I < O (3)	Bailey and McCauley, 2006
S. vulgaris	I < O (2)	Glaettli and Goudet, 2006
S. vulgaris subsp. *maritima* var. *petraea*	I < O (17), I > O (2)	Pettersson, 1992

Table 5. *Continued*

Taxonomy (family, species)	Selfing vs. outcrossing	References
Cistaceae		
Fumana juniperina	I = O (1)	Carrió *et al.*, 2008
Clusiaceae		
Hypericum cumulicola	I = O (2)	Trager *et al.*, 2005
Convolvulaceae		
Ipomoea heteracea var. *integriuscula*	I < O (2)	Hull-Sanders *et al.*, 2005
I. purpurea	I = O (1), I > O (1)	Chang and Rausher, 1999
Crassulaceae		
Sedum pusillum	I = O (5)	Wyatt, 1983
Cucurbitaceae		
Curcurbita maxima subsp. *andreana*	I = O (1)	Ashworth and Galetto, 2001
C. pepo pepo (Caipira cucumber)	I = O (1)	Godoy *et al.*, 2006
C. pepo subsp. *texana*	I < O (1)	Hayes *et al.*, 2005a
C. pepo subsp. *texana*	I = O (1)	Stephenson *et al.*, 2004
C. texana	I = O (1)	Jóhannsson *et al.*, 1998
Cupressaceae		
Metasequoia glyptostroboides	I < O (1)	Kuser, 1983
Sequoia sempervirens	I < O (3), I = O (4)	Libby *et al.*, 1981
Cyperaceae		
Carex madoviana	I > O (1)	Whitkus, 1988
C. pachystachya	I < O (1), I > O (3)	Whitkus, 1988
Dipsacaceae		
Knautia arvensis	I < O (1)	Vange, 2002
Scabiosa columbaria	I < O (1), I = O (1)	van Treuren *et al.*, 1993
S. columbaria	I < O (10), I = O (21), I > O (2)	Picó *et al.*, 2004a
Dipterocarpaceae		
Neobalanocarpus helmii	I < O (1)	Naito *et al.*, 2005
Shorea acuminata	I < O (1)	Naito *et al.*, 2008
S. cordifolia	I = O (4)	Stacy, 2001
Droseraceae		
Drosera anglica	I = O (1)	Murza and Davis, 2005
Ericaceae		
Rhododendron brachycarpum	I = O (1)	Hirao, 2010
R. ponticum	I < O (1)	Stout, 2007
Vaccinium ashei	I = O (1)	El-Agamy *et al.*, 1981
V. ashei	I = O (1)	Hellman and Moore, 1983
V. corymbosa	I = O (1)	El-Agamy *et al.*, 1981
V. corymbosa	I = O (1)	Hellman and Moore, 1983
V. myrtillus	I = O (1)	Guillaume and Jacquemart, 1999
Eriocaulaceae		
Syngonanthus elegans	I < O (1)	Oriani *et al.*, 2009
Euphorbiaceae		
Mercurialis annua	I < O (8), I > O (5)	Eppley and Pannell, 2009
Fabaceae		
Astragalus linifolius	I > O (1)	Karron, 1989
A. lonchocarpus	I = O (1)	Karron, 1989
Chamaecrista fasciculata	I = O (1)	Fenster, 1991
C. fasciculata	I = O (1)	Sork and Schemske, 1992
C. keyensis	I < O (1)	Liu and Koptur, 2003
Crotalaria retusa	I < O (1)	Jacobi *et al.*, 2005
Erythrina crista-galli	I = O (1)	Galetto *et al.*, 2000
Lupinus arboreus	I < O (4), I = O (5), I > O (2)	Kittleson and Maron, 2000
L. perennis	I < O (2)	Shi *et al.*, 2005
L. perennis	I < O (1), I = O (7)	Michaels *et al.*, 2008
L. texensis	I = O (1)	Schaal, 1984
L. texensis	I < O (1), I = O (3), I > O (1)	Helenurm and Schaal, 1996
Sophora microphylla	I < O (1), I > O (1)	Robertson *et al.*, 2011
Trifolium hirtum	I = O (1)	Molina-Freaner and Jain, 1993

Table 5. *Continued*

Taxonomy (family, species)	Selfing vs. outcrossing	References
Gentianaceae		
Gentiana newberryi	I = O (2)	Barnes and Rust, 1994
G. pneumonanthe	I < O (1), I = O (2), I > O (5)	Oostermeijer *et al.*, 1995
Gentianella germanica	I < O (1), I = O (2)	Fischer and Matthies, 1997
Sabatia angularis	I = O (2)	Dudash, 1990
Swertia perennis	I = O (1)	Lienert and Fischer, 2004
Geraniaceae		
Erodium cazorlanum	I < O (1)	Alonzo and García-Sevilla, 2013
Gesneriaceae		
Besleria melancholica	I > O (1)	Stein and Henson, 2013
Lamiaceae		
Salvia pratensis	I < O (1)	Ouborg and van Treuren, 1994
Lythraceae		
Decodon verticillatus	I < O (2)	Eckert and Barrett, 1994
Diplusodon hirsutus	I > O (1)	Jacobi *et al.*, 2000
D. orbiculatus	I < O (1)	Jacobi *et al.*, 2000
Lagerstroemia (2 spp.)	I < O (4)	Pounders *et al.*, 2006
Lythrum salicaria	I < O (2)	O'Neil, 1994
Magnoliaceae		
Magnolia obovata	I < O (1)	Ishida, 2006
Malvaceae		
Dombeya acutangula subsp. *acutangula*	I < O (2)	Gigord *et al.*, 1998
Hibiscus laevis	I = O (1)	Klips and Snow, 1997
H. moscheutos	I < O (1), I = O (3)	Snow and Spira, 1993
H. moscheutos	I < O (2), I = O (10), I > O (3)	Liu and Spira, 2001
H. trionum var. *trionum*	I = O (1)	Ramsey *et al.*, 2003
H. trionum var. *vesicarius*	I = O (1)	Lhamo *et al.*, 2006
H. trionum var. *vesicarius*	I = O (1)	Seed *et al.*, 2006
Kosteletzyka virginica	I < O (6)	Ruan *et al.*, 2009
Sidalcea hendersonii	I < O (1), I = O (1)	Marshall and Ganders, 2001
Marantaceae		
Calathea micans	I = O (1)	Le Corff, 1996
Melanthiaceae		
Chionographis japonica var. *kurohimensis*	I < O (2), I = O (1)	Maki, 1993
Menyanthaceae		
Nymphoides peltata	I = O (1)	Takagawa *et al.*, 2006
Moraceae		
Ficus aurea	I = O (3)	Hossaert-McKey and Bronstein, 2001
Myrtaceae		
Eucalyptus globulus subsp. *globulus*	I = O (1)	Hardner and Potts, 1995
Myrtus communis	I < O (8), I > O (2)	González-Varo and Traveset, 2010
Syzygium rubicundum	I = O (5)	Stacy, 2001
Onagraceae		
Clarkia concinna	I < O (2), I = O (10)	Groom and Preuninger, 2000
C. tembloriensis	I = O (5)	Holtsford and Ellstrand, 1990
C. tembloriensis	I < O (1), I = O (1)	Holtsford, 1996
Clarkia (four spp.)[d]	I < O (2), I = O (2)	Barringer and Geber, 2008
Epilobium angustifolium	I < O (1)	Husband and Schemske, 1995
E. angustifolium	I < O (1)	Parker *et al.*, 1995
E. angustifolium	I < O (4), I = O (1)	Husband and Schemske, 1997
E. angustifolium	I < O (1)	Husband and Gurney, 1998
E. ciliatum	I = O (1)	Parker *et al.*, 1995
E. obcordatum	I = O (1)	Seavey and Carter, 1994
Orchidaceae		
Anacamptis fragrans	I < O (1)	Smithson, 2006
A. morio	I < O (1), I = O (1)	Smithson, 2006
Barlia robertiana	I < O (2)	Smithson, 2006
Caladenia behrii	I = O (1)	Petit *et al.*, 2009

Table 5. *Continued*

Taxonomy (family, species)	Selfing vs. outcrossing	References
C. tentactulata	I = O (1)	Peakall and Beattie, 1996
Dactylorhiza praetermissa	I < O (2), I > O (1)	Ferdy *et al.*, 2001
D. sambucina	I < O (2)	Juillet *et al.*, 2007
Encyclia cochleata	I = O (1), I > O (1)	Ortiz-Barney and Ackerman, 1999
Eulophia alta	I = O (1)	Johnson *et al.*, 2009
Platanthera leucophaea	I = O (1)	Bowles *et al.*, 2002
Paeoniaceae		
Paeonia spontanea	I < O (1)	Jing and Zheng, 1999
Passifloraceae		
Turnera ulmifolia	I = O (9)	Belaouoff and Shore, 1995
Phrymaceae		
Mimulus guttatus	I = O (2)	Willis, 1993a
M. guttatus	I < O (2)	Willis, 1993b
M. guttatus	I < O (2)	Carr and Dudash, 1995
M. guttatus	I < O (2)	Carr and Dudash, 1996
M. guttatus	I = O (3)	Carr *et al.*, 1997
M. guttatus	I < O (2)	Dudash *et al.*, 1997
M. luteus var. *luteus*	I = O (1), I > O (1)	Carvallo and Medel, 2010
M. micranthus	I < O (2)	Carr and Dudash, 1996
Mimulus (four spp.)[e]	I < O (2), I = O (13)	Latta and Ritland, 1994
Pinaceae		
Abies procera	I = O (1)	Sorensen *et al.*, 1976
Larix (five spp.)	I < O (4), I > O (1)	Franklin, 1970
Picea glauca	I = O (1)	Mergen *et al.*, 1965
P. glauca	I < O (2)	Coles and Fowler, 1976
P. glauca	I < O (6), I = O (11), I > O (3)	Fowler and Park, 1983
Picea (two spp.)[f]	I < O (1), I > O (1)	Franklin, 1970
Pinus banksiana	I = O (5)	Fowler, 1965b
P. monticola	I = O (2), I > O (1)	Squillace and Bingham, 1958
P. monticola	I < O (4)	Barnes *et al.*, 1962
P. ponderosa	I = O (1)	Sorensen and Miles, 1974
P. resinosa	I = O (1)	Fowler, 1965a
P. strobus	I > O (1)	Fowler, 1965b
Pinus (ten spp.)[g,h]	I < O (8), I > O (2)	Franklin, 1970
Pseudotsuga mengiesii	I < O (1)	Franklin, 1970
P. menziesii [h]	I = O (3)	Piesch and Stettler, 1971
P. menziesii	I = O (5)	Sorensen, 1971
P. menziesii	I = O (1)	Sorensen and Miles, 1974
Plantaginaceae		
Collinsia heterophylla	I < O (4)	Mayer *et al.*, 1996
C. parviflora	I < O (1), I = O (13), I > O (2)	Kennedy and Elle, 2008
C. verna	I < O (1)	Kalisz, 1989
Digitalis purpurea	I = O (3)	Grindeland, 2008
Penstemon tenuiflorus	I < O (1), I = O (4)	Clements *et al.*, 1999
Plantago coronopus	I = O (1)	Koelewijn, 1998
P. coronopus	I = O (1)	Koelewijn, 2004
P. lanceolata	I = O (1)	van Damme and van Delden, 1984
Poaceae		
Spartina alterniflora	I = O (1)	Daehler, 1999
Polemoniaceae		
Gilia achilleifolia	I > O (1)	Schoen, 1983
Linanthus bicolour	I = O (3)	Goodwillie, 2000
L. jepsonii	I = O (3)	Goodwillie, 2000
Leptosiphon (*Linanthus*) *jepsonii*	I = O (3)	Goodwillie and Knight, 2006
Phlox drummondii	I = O (3)	Levin and Bulonska-Radomska, 1988
Polemonium vanbruntiae	I = O (3)	Bermingham and Brody, 2011
Primulaceae		
Cyclamen balearicum	I < O (1)	Affre and Thompson, 1999
C. creticum	I > O (1)	Affre and Thompson, 1997

Table 5. *Continued*

Taxonomy (family, species)	Selfing vs. outcrossing	References
C. creticum	I > O (1)	Affre and Thompson, 1999
C. hederifolium	I = O (1)	Affre and Thompson, 1999
C. repandum	I > O (1)	Affre and Thompson, 1999
Primula sieboldii	I < O (1)	Watanabe *et al.*, 2003
Proteaceae		
Banksia ilicifolia	I < O (1)	Heliyanto *et al.*, 2005
Grevillea mucronata	I = O (1)	Forrest *et al.*, 2011
Ranunculaceae		
Aquilegia caerulea	I < O (1), I = O (1)	Montalvo, 1994
A. canadensis	I = O (1)	Routley *et al.*, 1999
Nigella degenii	I = O (1)	Ellmer and Andersson, 2004
Pulsatilla patens subsp. *multifida*	I = O (1)	Brock and Peterson, 1975
Rosaceae		
Fragaria × *ananassa*	I < O (1)	Melville *et al.*, 1980
Polylepis australis	I < O (2), I = O (2)	Seltman *et al.*, 2009
Rubiaceae		
Diodia teres	I = O (3)	Hereford, 2009
Rutaceae		
Dictamus albus	I = O (1)	Hensen and Wesche, 2006
Sarraceniaceae		
Sarracenia flava	I < O (2)	Sheridan and Karowe, 2000
Saxifragaceae		
Saxifraga granulata	I < O (1)	Walisch *et al.*, 2012
S. hirculus	I < O (1)	Dahlgaard and Warncke, 1995
Solanaceae		
Datura stramonium	I = O (1)	Nuñez-Farfán *et al.*, 1996
Solanum carolinense	I = O (1)	Mena-Ali *et al.*, 2008
Xyridaceae		
Xyris tennesseensis	I > O (1)	Boyd *et al.*, 2011
Zingiberaceae		
Costus allenii	I < O (1), I > O (1)	Schemske, 1983
C. laevis	I = O (2)	Schemske, 1983
C. allenii	I = O (4)	Schemske and Paulter, 1984
Costus (three spp.)[i]	I = O (3)	Shemske, 1983
Zosteraceae		
Zostera marina	I < O (2), I = O (1), I > O (1)	Billingham *et al.*, 2007

[a] Central achenes
[b] Peripheral achenes
[c] One species not otherwise on list
[d] None of four species otherwise on list
[e] Three species not otherwise on list
[f] Neither species otherwise on list
[g] Seven species not otherwise on list
[h] Only filled seeds used in germination tests
[i] All three species on list

hand, we found many cases of RP ≤ 0.10 and a considerable number of cases in which it is less negative than −0.10. RP values for germination in the study by Husband and Schemske (1996) (calculated from their mean relative fitness values) ranged from −0.36 to +0.40.

The magnitude of ID is relative, thus by themselves values generated for ID and RP do not necessarily tell us anything about actual performance, i.e. seed size, percentage of seeds germinating, grams of biomass accumulated, etc. For example, the level of ID will be the same (0.20) for inbred vs. outbred seeds that germinated to 8% and 10%, respectively, as it would be for inbred vs. outbred seeds that germinated to 80% and 100%, respectively.

We scored the case studies of I < O, I = O and I > O based on the results of statistical tests on germination percentage/rate (speed) by the authors of the papers and/or on RP values. It should be pointed out that in some cases *P* values and RP values for comparison of

Table 6. Partial analysis of the I/O data by taxonomic group; I, inbred; O, outbred

Taxonomic group	Number and per cent of cases in I/O category		
	I < O	I = O	I > O
Gymnosperms	27 (38.6%)	35 (50.0%)	8 (11.4%)
Pinaceae	23 (37.1%)	31 (50.0%)	8 (12.9%)
Angiosperms	284 (42.2%)	337 (50.1%)	52 (7.7%)
Monocots	39 (43.8%)	38 (42.7%)	12 (13.5%)
Eudicots	245 (42.0%)	299 (51.2%)	40 (6.9%)
Asteraceae	15 (37.5%)	23 (57.5%)	2 (5.0%)
Caryophyllaceae	79 (76.7%)	18 (17.5%)	6 (5.8%)

germination data on crossed vs. selfed seeds seem to merit a different interpretation with regard to significance. Three examples of the difficulty of making assignments to I/O categories will be given. In the study by Dudash and Fenster (2001) on *Silene virginica*, the average family mean for germination of selfed seeds from two populations was 39% and that of outcrossed seeds 49%. The P value for this comparison was 0.125, i.e. non-significant. Yet, the RP value calculated for these means is 0.204, i.e. average family mean for ID in the germination stage of the life cycle was 20.4%, which would seem to be biologically significant. Thus, we have scored this case as I < O. In the study by Takagawa *et al.* (2006) on *Nymphoides peltata,* mean germination percentages for legitimate and selfed families of this heterostylous species were 96.1 and 91.0%, respectively, which was significant ($P = 0.006$), but the RP was only 0.05; we recorded this as I = O. In the study by Kennedy and Elle (2008) on *Collinsia parviflora* mentioned earlier, there was a significant difference ($P < 0.05$) in germination in one case of selfed vs. outcrossed seeds in which ID was 0.08. Yet, in another case of selfed vs. outcrossed seeds in the same paper the germination difference was not significant ($P > 0.05$), but ID was 0.11. For this study, we have made assignments based on statistical significance of the data. Thus, it is obvious that some case-by-case decisions had to be made on how to score the I/O relationship. For most assignments to I/O categories based on RP only, the following values were used: RP $\geq$ 0.10, I < O; $-0.10 <$ RP < 0.10, I = O; and RP ≤ -0.10, I > O.

Below, we discuss the different categories about ID and seed germination. See Table 1 for additional information on topics discussed in this section.

Congeneric species

ID for germination may (e.g. Schemske, 1983; Latta and Ritland, 1994; Affre and Thompson, 1999) or may not (e.g. Ågren and Schemske, 1993; Carr and Dudash, 1996; Johnston and Schoen, 1996) vary considerably

between congeneric species. RP was 0.02 for *Begonia hirsuta* and 0.05 for *B. semiovata* (Ågren and Schemske, 1993), whereas it was -0.44 for *Diplusodon hirsutus* and 0.62 for *D. orbiculatus*. RP for germination of four species of *Cyclamen* ranged from -0.88 to 0.45 (Affre and Thompson, 1997).

Populations

Considerable variation in ID for germination has been found between populations of some species (e.g. Levin and Bulinska-Radomska, 1988; Latta and Ritland, 1994; Belaoussoff and Shore, 1995; Ferdy *et al.*, 2001; Lofflin and Kephart, 2005) but not of others (e.g. Willis, 1993a; Eckert and Barrett, 1994; Johnston and Schoen, 1996; Goodwillie and Knight, 2006). RP values in populations A, B and C of the orchid *Dactylorhiza pratermissa* were 0.140, 0.382 and -0.778, respectively (Ferdy *et al.*, 2001). However, the range of RP values for three populations of *Linanthus* (*Leptosiphon*) *bicolor* was only 0.00–0.03 (Goodwillie, 2000). In *Chionographis japonica* var. *kurohimensis,* ID for seed germination in the same population was 0.34 in 1989 and 0.05 in 1990 (Maki, 1993). ID for germination of central populations of *Clarkia concinna* ranged from 0.28 to 0.32 and that of isolated populations from 0.22 to 0.27 (Groom and Preuninger, 2000). ID for seed germination was -0.01 and 0.37 for self-compatible and self-incompatible populations, respectively, of the cedar glade endemic *Leavenworthia alabamica* (Busch, 2005), whereas it was 0.05 and -0.03 for germination in selfing and out-crossing populations, respectively, of the rock-outcrop endemic *Minuartia* (*Arenaria*) *uniflora* (Fishman, 2001).

Maternal families

Maternal families of many taxa seem to exhibit a wide range of among-family variation in ID (e.g. Pettersson, 1992; Husband and Schemske, 1995; Kephart *et al.*, 1999). RP for germination of eight families of *Silene douglasii* var. *oraria* ranged from 0.00 to 0.80 (Kephart *et al.*, 1999). For three maternal fig trees, on the other hand, progeny ID for germination was only 0.04 to 0.06 (Hossaert-McKey and Bronstein, 2001). Furthermore, ID can carry over to the next generation in the form of

Table 7. Relationship between percentage/rate of germination and mass of inbred (I) and outbred (O) seeds in 216 case studies

Germination	Seed mass		
	I < O	I = O	I > O
I < O (80)	54	15	11
I = O (110)	43	61	6
I > O (26)	10	6	10

maternal effects (Vogler *et al.*, 1999; Hayes *et al.*, 2005a). Thus, germination of progeny may be due to maternal inbreeding (δ_m), although $F = 0$ for progeny via maternal outcrossing.

Physical environment

The physical environment of parental parents may (e.g. Schemske, 1983) or may not (e.g. Dudash, 1990; Groom and Preuninger, 2000) have a considerable effect on ID for germination of progeny. RP values for germination of progeny of *Clarkia tembloriensis* grown in a lath house and in the field were −0.01 to 0.08 and −0.04 to 0.03, respectively (Holtsford and Ellstrand, 1990). On the other hand, RPs for germination of *Costus laevis* grown in sun and in shade in the field and in a greenhouse were 0.09, 0.27 and −0.09, respectively (Schemske, 1983).

Competition

Competition among parental plants may or may not increase ID of progeny. For germination (emergence date) of *Hydrophyllum appendiculatum* seeds, RP increased from −0.19 without competition to 0.11 with competition (Wolfe, 1993). However, there was little or no effect of competition on ID for germination of seeds of *Collinsia parviflora* (Kennedy and Elle, 2008). For eight populations of this species, RP for germination with competition ranged from −0.14 to 0.08 and that without competition from −0.04 to 0.11.

Heterostyly and heterocarpy

For the two heterostylous species *Lythrum salicaria* (O'Neil, 1994) and *Nymphoides peltata* (Takagawa *et al.*, 2006), magnitudes of ID for seed germination {$\delta = 1 −$ (mean of selfed progeny)/(mean of [legitimate] progeny)} were relatively low. RP values for two populations of *L. salicaria* were 0.11 and 0.14. Mean germination percentages were 96.1% and 91.0% for legitimate and selfed families, respectively, of *N. peltata*, a mean RP of 0.05. There was essentially no ID for germination for either of two heterostylous populations of *Amsinckia douglasiana* or of *A. spectabilis* (Johnston and Schoen, 1996).

ID for germination of central achenes (%, 0.26 and speed, 0.10) of the heterocarpic species *Leontodon autumnalis* was higher than it was for peripheral achenes (%, −0.21 and speed, 0.02) (Picó and Koubek, 2003).

Ploidy level

In general, there does not seem to be much difference in germination of diploids and tetraploids, especially for the same cross type, i.e. selfing or outcrossing. ID for seed germination was 0.00 for two populations of the tetraploid species *Amsinckia gloriosa*; 0.00 and 0.012 for two populations of the diploid species *A. douglasiana*; and 0.00 to 0.087 for five diploid populations of *A. spectabilis* (Johnston and Schoen, 1996). The mean ID values for seed germination of diploid and tetraploid cytotypes of *Epilobium angustifolium* were 0.22 and 0.11, respectively. In all five populations, selfed seeds germinated to a lower percentage than outcrossed seeds (Husband and Schemske, 1997). For germination percentage in four species of *Clarkia*: [diploid outcrossing species (ID 41) = polyploid outcrossing species (0.33)] > [diploid selfing species (0.06) = polyploid selfing species (0.05)]. There was no effect of inbreeding on days to germination: diploid outcrossing species = diploid selfing species = polyploid outcrossing species = polyploid selfing species (Barringer and Geber, 2008).

Herkogamy class

RP values for narrow and wide herkogamy classes of *Mimulus guttatus* were 0.05 and 0.06, respectively, in one population and 0.17 and 0.04, respectively, in another population (Carr *et al.*, 1997).

Endemics

ID for germination was low or non-existent for most endemics, e.g. 0.07 for *Amsinckia douglasiana* (Cheptou and Schoen, 2002); −0.08 for *Anchusa crispa* (Quilichini *et al.*, 2001); −0.03 and 0.05 for outcrossing and selfing populations, respectively, of *Minuartia* (*Arenaria*) *uniflora* (Fishman, 2001); −0.20 for *Astragalus linifolius* (Karron, 1989); −0.04 for *Brassica cretica* (Rao *et al.*, 2002); 0.00 for *Hymenoxys herbacea* (Moran-Palma and Snow, 1997); 0.001 (%) and 0.03 (speed) for *Leavenworthia crassa* (Charlesworth *et al.*, 1994); 0.00 to 0.04 for *Linanthus* (*Leptosiphon*) *jepsonii* (Goodwillie and Knight, 2006); and −0.02 for *Sedum pusillum* (Wyatt, 1983). However, ID for germination is not low for all endemic species. It was 0.42 (Kephart *et al.*, 1999) and 0.34 (Lofflin and Kephart, 2005) for *Silene douglasii* var. *oraria*. RP values for 19 families of the Öland (Sweden) alvar endemic *Silene vulgaris* subsp. *maritima* var. *petraea* ranged from −0.27 to 1.0 (Pettersson, 1992), and it was 0.37 for self-incompatible populations of the narrow Alabama cedar glade endemic *Leavenworthia alabamica* (Busch, 2005).

Endemic vs. common species

Several studies on endemic species also included one or more congeners that are more geographically

widespread than the narrow endemics, thus presenting an opportunity to compare ID values between these two groups. Some results are: *Amsinckia douglasiana* (endemic) 0.00 to 0.013 vs. *A. spectabilis* (widespread) −0.087 to 0.097 (Johnston and Schoen, 1996); *Astragalus linifolius* (endemic) −0.20 vs. *A. lonchocarpus* (widespread) −0.03 (Karron, 1989); *Leavenworthia crassa* (endemic) 0.001 (%) and 0.03 (speed) vs. *L. uniflora* (widespread) 0.05 (%) and 0.08 (speed) (Charlesworth *et al.*, 1994); *Linanthus* (*Leptosiphon*) *jepsonii* (endemic) vs. *L. bicolor* (widespread), in which ID in all populations studied was 0.00 or nearly so (Goodwillie, 2000); *Mimulus micranthus* (endemic) 0.19 (within population) and 0.20 (between populations) vs. *M. guttatus* (widespread) 0.21 (within population) and 0.29 (between populations) (Carr and Dudash, 1996); and *Silene douglasii* var. *oraria* (endemic) 0.34 vs. *S. douglasii* var. *douglasii* (widespread) 0.44 (Cascades Jack Creek population) and 0.04 (Cascades Cove Creek population) (Lofflin and Kephart, 2005).

Procedures used in germinating seeds in studies on inbreeding depression

Dormancy occurs in seeds of a high proportion of the species in all major vegetation zones on Earth (Baskin and Baskin, 2003, 2014), and dormancy, along with temperature and light, are three of the most important factors regulating seed germination (Baskin and Baskin, 2014). Further, seeds of nearly all of the families and genera containing species for which germination of inbred and outbred seeds have been compared (Table 5) have some kind of dormancy (most of them non-deep physiological) at maturity (Baskin and Baskin, 2014). Thus, since germination percentage and/or rate (speed) are used as (a) measure(s) of fitness in inbred vs. outbred seeds in studies of ID in this stage of the plant life cycle, it is essential that careful attention be given to how to break dormancy and germinate the seeds.

Percentage of germination/seedling emergence in the case studies in our survey ranged from very low/low (e.g. Wolfe, 1993; Mandujano *et al.*, 1996; Puterbaugh, 1997; Affre and Thompson, 1999; Routley *et al.*, 1999) to high/very high (e.g. Schoen, 1983; Hauser and Loescheke, 1995; Johnston and Schoen, 1996; Cheptou *et al.*, 2000b; Goodwillie, 2000). In many of the papers, there was no mention of giving the seeds a dormancy-breaking treatment. Except in a few cases, e.g. those of the three species of Dipterocarpaceae, the seeds cannot necessarily be considered to have been (fully) non-dormant, even though germination percentage was high in the limited range of conditions in which they were tested/sown. They may have been conditionally dormant, i.e. in a state of dormancy between 'true dormancy' and non-dormancy (Vegis,

1964; Baskin and Baskin, 2004, 2014). In the paper by Seltmann *et al.* (2009) on *Polylepis australis* (Rosaceae), it is stated that the seeds were non-dormant. However, when the seeds were tested for germination they were 1 month old, having been stored under ambient laboratory (afterripening) conditions during this time. Furthermore, highest germination was 30%; viability of non-germinated seeds was not tested. We suggest that the seeds were physiologically dormant at maturity and that many of them were still dormant at the time they were tested, i.e. the ≥70% that did not germinate, assuming they were viable.

A wide variety of storage conditions used in the studies can be included under the 'storage/afterripening' dormancy-breaking category, e.g. seeds afterripened at room temperature and then maintained at approximately 4°C with a desiccant; seeds stored in paper bags from spring 1999 to December 1999; seeds afterripened for 1 month; seeds stored at room temperature for 6 months; seeds stored dry in laboratory at 40°C; and seeds stored for 13–14 months in screw-capped vials at 4°C. While in some cases 'afterripening/storage' was definitely planned as a dormancy-breaking treatment, it appears that in others the seeds were stored simply for the sake of keeping them until a later date, i.e. until they could be used in a study.

For cold-stratified seeds, the length of the cold-stratification period ranged from 5 d, which is a very short period of cold stratification and unlikely to be effective in breaking dormancy in seeds of most species, to 12 weeks, usually at 4 or 5°C. In some cases, we could not determine whether the seeds were moist-cold treated or simply dry-cold stored. In the former case, water-permeable, but not water-impermeable, seeds would have been cold stratified, whereas in the latter case neither water-permeable nor water-impermeable seeds would have been cold stratified, but water-permeable seeds might have afterripened.

Perhaps the most unnatural dormancy-breaking treatment was soaking seeds of an orchid in a calcium hypochlorite solution to chemically scarify the seed coat (Ferdy *et al.*, 2001), and the most natural one was sowing seeds in the field/outdoors, where they are exposed to warm and/or cold temperatures between dispersal and germination. Other chemicals used in dormancy-breaking treatments included potassium nitrate (KNO_3) and gibberellin (GA). NO_3^- has been reported to break seed dormancy in nature, and GAs are natural plant growth regulators known to be intimately involved in the biochemical mechanism(s) of breakage of physiological dormancy in seeds (Finch-Savage and Leubner-Metzger, 2006; Footitt *et al.*, 2011; Graeber *et al.*, 2012). Moist cold-stratification and dry-storage (afterripening) treatments simulate dry, warm and moist, cold conditions, respectively, that seeds are exposed to in nature (Baskin and Baskin, 2004, 2014).

However, scarification is not a treatment that simulates a dormancy-breaking process in nature (Baskin and Baskin, 2000, 2014). In our survey, dormancy was broken in most of the case studies in the hardseeded (i.e. water-impermeable seed coat) families Cistaceae, Convolvulaceae, Fabaceae, Geraniaceae and Malvaceae (Baskin *et al.*, 2000) by mechanical scarification. In a few of the studies, even seeds with a water-permeable seed coat were scarified or 'pricked'. In two of these cases, the whole seed coat was removed, and only the embryo was tested for 'germination'. Scarifying seeds with non-deep physiological dormancy allows the seed to germinate by lowering the mechanical restraint of the seed coat on embryo growth (radicle emergence) and not by creating an opening for the entrance of water (Baskin and Baskin, 2004). Scarification of neither water-impermeable nor water-permeable seed coats has been demonstrated to be a way in which seed dormancy is overcome in nature.

We suggest that the scarification treatment is a good one to use to learn about viability of seeds with water-impermeable seed coats but not about dormancy, or thus seed germination, in nature, which may take up to two decades or longer to be completed by a seed population (or lot) (Baskin and Baskin, 2014). In the great majority of seeds with physical dormancy, the fully developed embryo is non-dormant, and thus when the seed coat is made water permeable the radicle emerges, usually within a few days. In nature, physical dormancy is broken by high (including heat from fires) and fluctuating temperatures (including low fluctuating temperatures) (Van Assche *et al.*, 2003; Moreira and Pausas, 2012; Baskin and Baskin, 2014).

A few of the papers did not include any description of germination procedures. Many of the papers reported both temperature and light conditions for germination; most such studies were done in controlled growth cabinets. In a high percentage of these studies, seeds were germinated under a single temperature regime. A high percentage of the studies in which seeds were germinated in the laboratory or greenhouse did not provide information on either temperature or light conditions. Some studies provided information on either temperature or light but not on both.

Conclusions, recommendations and remarks

- We recommend using the equation for RP to calculate values for traits, such as percentage germination, in studies on the effects of inbreeding vs. outbreeding in plants. When $W_o \geq W_s$, equations for δ and RP will give the same positive value (to +1). When $W_o < W_s$, however, $\delta \neq$ RP.

That is, whereas the RP equation can give a negative value to only -1, the equation for δ can give a negative value to $-\infty$. Thus, the equation for RP gives equal weight to the same phenotype trait value for the best and worst performer, whereas the equation for δ does not. Using RP in cases where $W_s > W_o$ certainly would make it easier to compare the effects of selfing and outcrossing.

- Keep in mind that in studies of rates (speed) of a process or of an event in the plant life cycle, such as days to germinate, the higher number means lower performance. Thus, use the equation $1 - (W_o/W_s)$ when number of days for outcrossed seeds to germinate is fewer than that for inbred seeds, and the equation $(W_s/W_o) - 1$ when the number of days for inbred seeds to germinate is fewer than that for outcrossed seeds.

- Relative fitness values in the multiplicative fitness portion (CRF) of the equation for calculating cumulative (lifetime) inbreeding depression $(1-CRF)$ will be >1 when inbreeders outperform outbreeders. Thus, one may get either a positive or a negative value for events across the life cycle in selfers vs. outcrossers. If the speed of an event in the life cycle is used in this equation, when $W_s > W_o$ (in terms of number of days) relative fitness should be expressed as (W_o/W_s) and when $W_o > W_s$ as (W_s/W_o).

- 'Optimal outcrossing distance' for germination has been reported for only a few taxa. Most studies that have tested the effect of various distances between the seeds' parents on germination (and also other stages in the plant life cycle) have found no evidence for it. That is, in most studies there was no evidence that seeds germinate better at some intermediate distance between the parents than at far distances from them. Neither outbreeding depression nor heterosis for germination appears to be common for crosses between populations. However, crosses between different populations can sometimes reduce the performance of hybrid offspring via outbreeding depression (OD). Thus, transfer of genes into a population via pollen, seeds or transplants could lead to reduced fitness through disruption of gene complexes or by disruption of local adaptation. Conservationists need to be aware of the possibility of these negative consequences when obtaining seeds for restoration [see Johnson *et al.* (2004), who discuss the concept and use of 'tree seed zones' in research and management of forests; but also see Broadhurst *et al.* (2008), who, while accepting the existence of local adaptation and outbreeding depression, challenge the view among restoration ecologists that *local is best* as a guiding principle for seed sourcing].

- Outbred seeds germinate better than, equal to or less well than inbred seeds. In 50.1% of the cases

surveyed, inbred seeds germinated as well as outbred seeds, and in 8.1% inbred seeds germinated better than outbred seeds. Our results for 743 cases of germination of inbred vs. outbred seeds differ considerably from those of Darwin's (1876) very limited study on 21 comparisons of speed of germination of inbred vs. outbred seeds. For I < O, I = O and I > O, Darwin reported 47.6%, 4.8% and 47.6%, respectively, whereas we report 41.9%, 50.1% and 8.1%, respectively. Black (2009) does not mention this part of Darwin's research on seeds, and although Owens and Miller (2009) say that Darwin recorded time from planting to seed germination, they do not give any results of his observations.

- Proportional relationships of I < O, I = O and I > O for germination of gymnosperms and angiosperms are quite similar; in both groups $[(I < O) < (I = O)] >> (I > O)$.

- There does not seem to be a strong relationship between decrease in germination with increase in F, or between increase in germination and increase in population genetic diversity.

- There is a huge range of variation in the magnitude of ID for seed germination, and the level of ID may depend on species, population, maternal family, year, breeding system, degree of inbreeding, number of pollen parents, degree of seed-set autogamy, herkogamy class, physical environment or degree of competition in which seeds were produced, outcrossing distance, crosses within vs. among populations, seed morph in seed/fruit heteromorphic species, ploidy level, degree of relatedness of parents and dormancy-breaking treatment and germination conditions; and probably several other things.

- There is not a particularly strong relationship between seed size and germination in inbred vs. outbred seeds. In some cases of ID for seed germination, small seeds may germinate equally well or even better than large seeds; also, for seeds of equal size, W_s may be greater than W_o. In which cases, ID for seed germination is not mediated by large seed size. Our results of 216 case studies on size of inbred vs. outbred seeds do not agree with those of Darwin's (1876) 16 comparisons of seed size in inbred and outbred seeds. For I < O, I = O and I > O, Darwin's relative proportions are 6, 0 and 10, respectively, and ours are 107, 82 and 27, respectively. Both Black (2009) and Owens and Miller (2009) note that for 10 of the 16 species Darwin (1876) examined for seed mass, mass of inbred seeds was greater than that of outbred seeds.

- ID for seed germination for the majority of narrow endemics in our survey was low and, in general, did differ substantially from that of geographically widespread congeners.

- In general, more attention needs to be given to seed dormancy and germination in studies of the effects of inbreeding in plants. In particular, germinating/testing seeds at near-natural field conditions would allow one to extrapolate the results to the real world.

- We recommend that before beginning a study of ID on a species the investigator first become familiar with its natural history, thus following the advice of Bernhardt (1999, p. 69): 'If you want to find, grow, or study any living thing you must first become familiar with its season of activity.' In the case of seed germination, the investigator needs to become familiar with the seasons of dormancy break and germination. In sum, researchers need to incorporate a stronger element of whole-seed physiology and plant life cycle phenology into their studies on ID that include seed germination.

- Furthermore, plants obtained from seeds whose dormancy is broken by artificial, non-natural treatments (e.g. GA) may differ in growth and morphology from those obtained from seeds whose dormancy is broken by natural means (Baskin and Baskin, 1975; Fox et al., 1995; Evans et al., 1996). This being the case, then, it is easy to imagine that the results for ID, not only for germination but also of other stages of the plant life cycle, would not be representative of what is happening in the real world. Additionally, 'forced' germination may affect families (Fox et al., 1995; Evans et al., 1996), and perhaps even inbred and outbred progeny, differently. In the study by Evans et al. (1996), 'The magnitude of the GA_3 effect was strongly influenced by both germination environment and maternal sibship.'

- Our overall impression of the thinking of many researchers who do studies on ID in plants is that at a given time it is better for a seed to germinate than not to germinate, i.e. not to remain dormant and thus delay germination until a later date. Thus, seeds that germinate to high percentages are more beneficial to the plant (via increased fitness) than are seeds that germinate to low percentages. However, undoubtedly in many cases/circumstances the plant would gain more long-term fitness by some of the seeds delaying germination than it would by all of them germinating at the same time. Importantly, delaying germination in an unpredictable environment such as deserts can be an adaptive bet-hedging strategy, i.e. increasing the geometric mean fitness of the genotype over generations (Cohen, 1966; Venable, 1985; Mandák and Pyšek, 1999; Clauss and Venable, 2000; Simons, 2011; Gremer and Venable, 2014). Considering the long term, then, at least for annual species in temporally stochastic environments, low germination (high dormancy) percentages of selfed seeds

compared to those of outcrossed seeds may be more beneficial to the species.

- With some exceptions (e.g. Schoen, 1983; Norman *et al.*, 1995; Ferdy *et al.*, 2001; Heenan *et al.*, 2005; Ferrer *et al.*, 2009), information on seed viability was not reported in the studies included in our survey. In which cases, germination percentages were based on the total number of seeds, a portion of which may have been non-viable when sown/incubated. This raises a question: should the non-viable seeds be included in the germination or in the seed development (or seed production) stage of the life cycle? We suggest that non-viability in fresh seeds be considered to have occurred during seed development, and loss of viability thereafter, e.g. during dormancy-breaking treatment, in the seed-germination stage. Further, in many cases inbred seeds are more likely to lose viability during development than are outcrossed seeds (Husband and Schemske, 1996). Thus, including freshly matured non-viable seeds in the seed development stage of the plant life cycle should lower the magnitude of ID for seed germination, since non-viable seeds that cannot germinate regardless of treatment are 'replaced' by viable seeds that can germinate either with (dormant) or without (non-dormant) dormancy-breaking treatments.

Note added in proof

A recently published paper [Carta, A., Bedini, G., Giannotti, A., Savio, L. and Peruzzi, L. (2015) Mating system modulates degree of seed dormancy in *Hypericum elodes* L. (Hypericaceae). *Seed Science Research* **25**, 299–305] also calls for persons doing research on inbreeding depression in plants to pay attention not only to seed germination but also to seed dormancy. These authors found that, for germination, I > O for seeds cold-stratified for 0 and 3 weeks, whereas I = O for seeds cold-stratified for 8 weeks. They concluded that, '... seed germination alone is not an appropriate fitness measure for inbreeding depression estimates, unless dormancy is removed'. Otherwise, lack of germination may be related to dormancy and not to ID.

Conflicts of interest

None.

References

Aegisdóttir, H.H. and Thorhallsdóttir, T.E. (2006) Breeding system evolution in the Arctic: a comparative study of *Campanula uniflora* in Greenland and Iceland. *Arctic, Antarctic, and Alpine Research* **38**, 305–312.

Aegisdóttir, H.H., **Jespersen, D.**, **Kuss, P. and Stöcklin, J.** (2007) No inbreeding depression in an outcrossing alpine species: the breeding system of *Campanula thyrsoides*. *Flora* **202**, 218–225.

Affre, L. and Thompson, J.D. (1997) Population genetic structure and levels of inbreeding depression in the Mediterranean island endemic *Cyclamen creticum* (Primulaceae). *Biological Journal of the Linnean Society* **60**, 527–549.

Affre, L. and Thompson, J.D. (1999) Variation in self-fertility, inbreeding depression and levels of inbreeding in four *Cyclamen* species. *Journal of Evolutionary Biology* **12**, 113–122.

Ågren, J. and Schemske, D.W. (1993) Outcrossing rate and inbreeding depression in two annual monoecious herbs, *Begonia hirsuta* and *B. semiovata*. *Evolution* **47**, 125–135.

Alonzo, C. and Garcia-Sevilla, M. (2013) Strong inbreeding depression and individually variable mating system in the narrow endemic *Erodium cazorlanum* (Geraniaceae). *Anales del Jardin Botánico de Madrid* **70**, 72–80.

Anderson, N.O., **Ascher, P.D. and Widmer, R.E.** (1992) Lethal equivalents and genetic load. *Plant Breeding Reviews* **10**, 93–127.

Angeloni, F., **Ouborg, N.J. and Leimu, R.** (2011) Meta-analysis on the association of population size and life history with inbreeding depression in plants. *Biological Conservation* **144**, 35–43.

APG-III (The Angiosperm Phylogeny Group) (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG-III. *Botanical Journal of the Linnean Society* **161**, 105–121.

Arena, G., **Symes, C.T. and Witkowski, E.T.F.** (2013) The birds and the seeds: opportunistic avian nectarivores enhance reproduction in an endemic montane aloe. *Plant Ecology* **214**, 35–47.

Armbruster, P. and Reed, D.H. (2005) Inbreeding depression in benign and stressful environments. *Heredity* **95**, 235–242.

Ashman, T.-L. (1992) The relative importance of inbreeding and maternal sex in determining progeny fitness in *Sidalcea oregana* ssp. *spicata*, a gynodioecious plant. *Evolution* **46**, 1862–1874.

Ashworth, L. and Galetto, L. (2001) Pollinators and reproductive success of the wild cucurbit *Cucurbita maxima* ssp. *andreana* (Cucurbitaceae). *Plant Biology* **3**, 398–404.

Bachmann, U. and Hensen, I. (2007) Is declining *Campanula glomerata* threatened by genetic factors? *Plant Species Biology* **22**, 1–10.

Bailey, M.F. and McCauley, D.E. (2006) The effects of inbreeding, outbreeding and long-distance gene flow on survivorship in North American populations of *Silene vulgaris*. *Journal of Ecology* **94**, 98–109.

Barnes, B.V., **Bingham, R.T. and Squillace, A.E.** (1962) Selective fertilization in *Pinus monticola* Dougl. *Silvae Genetica* **11**, 103–111.

Barnes, M.E. and Rust, R.W. (1994) Seed production in *Gentiana newberryi* (Gentianaceae). *Great Basin Naturalist* **54**, 351–358.

Barringer, B.C. and Geber, M.A. (2008) Mating system and ploidy influence levels of inbreeding depression in *Clarkia* (Onagraceae). *Evolution* **62**, 1040–1051.

Baskin, C.C. and Baskin, J.M. (2014) *Seeds: Ecology, biogeography, and evolution of dormancy and germination* (2nd edition). San Diego, Elsevier/Academic Press.

Baskin, J.M. and Baskin, C.C. (1975) Growth of *Ruellia humilis* plants from embryos of chilled, GA₃-treated and laboratory-stored seeds. *Botanical Gazette* **136**, 299–305.

Baskin, J.M. and Baskin, C.C. (2000) Evolutionary considerations of claims for physical dormancy-break by microbial action and abrasion by soil particles. *Seed Science Research* **10**, 409–413.

Baskin, J.M. and Baskin, C.C. (2003) Classification, biogeography, and phylogenetic relationships of seed dormancy. pp. 518–544 *in* Smith, R.D.; Dickie, J.B.; Linington, S.H.; Pritchard, H.W.; Probert, R.J. (Eds) *Seed conservation: Turning science into practice*. Kew, The Royal Botanic Gardens.

Baskin, J.M. and Baskin, C.C. (2004) A classification system for seed dormancy. *Seed Science Research* **14**, 1–16.

Baskin, J.M., **Baskin, C.C and Li, X.** (2000) Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biology* **15**, 139–152.

Becker, U., **Reinhold, T. and Matthies, D.** (2006) Effects of pollination distance on reproduction and offspring performance in *Hypochoeris radicata*: experiments with plants from three European regions. *Biological Conservation* **132**, 109–118.

Belaoussoff, S. and Shore, J.S. (1995) Floral correlates and fitness consequences of mating-system variation in *Turnera ulmifolia*. *Evolution* **49**, 545–556.

Bermingham, L.H. and Brody, A.K. (2011) Pollen source affects female reproductive success and early offspring traits in the rare endemic plant *Polemonium vanbruntiae* (Polemoniaceae). *Plant Species Biology* **26**, 244–253.

Bernhardt, P. (1999) *The rose's kiss: A natural history of flowers*. Chicago, University of Chicago Press.

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.

Billingham, M.R., **Simões, T.**, **Reusch, T.B.H. and Serrão, E.A.** (2007) Genetic sub-structure and intermediate optimal outcrossing distance in the marine angiosperm *Zostera marina*. *Marine Biology* **152**, 793–801.

Black, M. (2009) Darwin and seeds. *Seed Science Research* **19**, 193–199.

Bowles, M.L., **Jacobs, K.A.**, **Zettler, L.W. and Delaney, T.W.** (2002) Crossing effects on seed viability and experimental germination of the federal threatened *Platanthera leucophaea* (Orchidaceae). *Rhodora* **104**, 14–30.

Boyd, R.S., **Teem, A. and Wall, M.A.** (2011) Floral biology of an Alabama population of the federally endangered plant, *Xyris tennesseensis* Kral (Xyridaceae). *Castanea* **76**, 255–265.

Brennan, A.C., **Harris, S.A. and Hiscock, S.J.** (2005) Modes and rates of selfing and associated inbreeding depression in the self-incompatible plant *Senecio squalidus* (Asteraceae): a successful colonizing species in the British Isles. *New Phytologist* **168**, 475–486.

Broadhurst, L.M., **Lowe, A.**, **Coates, D.J.**, **Cunningham, S.A.**, **McDonald, M.**, **Vesk, P.A. and Yates, C.** (2008) Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications* **1**, 587–597.

Brock, J.H. and Peterson, S.J. (1975) Reproductive biology of *Pulsatilla patens* (Ranunculaceae). *The American Midland Naturalist* **94**, 476–478.

Busch, J.W. (2005) Inbreeding depression in self-incompatible and self-compatible populations of *Leavenworthia alabamica*. *Heredity* **94**, 159–165.

Busch, J.W. (2006) Heterosis in an isolated, effectively small, and self-fertilizing population of the flowering plant *Leavenworthia alabamica*. *Evolution* **60**, 184–191.

Buza, L., **Young, A. and Thrall, P.** (2000) Genetic erosion, inbreeding and reduced fitness in fragmented populations of the endangered tetraploid pea *Swainsonia recta*. *Biological Conservation* **93**, 177–186.

Byers, D.L. (1998) Effect of cross proximity on progeny fitness in a rare and a common species of *Eupatorium* (Asteraceae). *American Journal of Botany* **85**, 644–653.

Byers, D.L. and Waller, D.M. (1999) Do plant populations purge their genetic load? Effects of population size and mating history on inbreeding depression. *Annual Review of Ecology and Systematics* **30**, 479–513.

Caño, L., **Escarré, J.**, **Blanco-Moreno, J.M. and Sans, F.X.** (2008) Assessing the effect of inbreeding and long-distance gene flow on the invasive potential of *Senecio pterophorus* (Asteraceae). *Australian Journal of Botany* **56**, 539–549.

Carr, D.E. and Dudash, M.R. (1995) Inbreeding depression under a competitive regime in *Mimulus guttatus*: consequences for potential male and female function. *Heredity* **75**, 437–445.

Carr, D.E. and Dudash, M.R. (1996) Inbreeding depression in two species of *Mimulus* (Scrophulariaceae) with contrasting mating systems. *American Journal of Botany* **83**, 586–593.

Carr, D.E. and Eubanks, M.D. (2002) Inbreeding alters resistance to insect herbivory and host plant quality in *Mimulus guttatus* (Scrophulariaceae). *Evolution* **56**, 22–30.

Carr, D.E., **Fenster, C.B. and Dudash, M.R.** (1997) The relationship between mating-system characters and inbreeding depression in *Mimulus guttatus*. *Evolution* **51**, 363–372.

Carrió, E., **Herreros, R.**, **Bacchetta, G. and Güemes, J.** (2008) Evidence of delayed selfing in *Fumana juniperina* (Cistaceae). *International Journal of Plant Sciences* **169**, 761–767.

Carvallo, G.O. and Medel, R. (2010) Effects of herkogamy and inbreeding on the mating system of *Mimulus luteus* in the absence of pollinators. *Evolutionary Ecology* **24**, 509–522.

Chang, S.-M. and Rausher, M.D. (1999) The role of inbreeding depression in maintaining the mixed mating system of the common morning glory, *Ipomoea purpurea*. *Evolution* **53**, 1366–1376.

Charlesworth, D. and Charlesworth, B. (1987) Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* **18**, 237–268.

Charlesworth, D. and Willis, J.H. (2009) The genetics of inbreeding depression. *Nature Reviews Genetics* **10**, 783–796.

Charlesworth, D., **Lyons, E.E. and Litchfield, L.B.** (1994) Inbreeding depression in two highly inbreeding populations of *Leavenworthia*. *Proceedings of the Royal Society of London B* **258**, 209–214.

Cheptou, P.-O. and Donohue, K. (2011) Environment-dependent inbreeding depression: its ecological and evolutionary significance. *New Phytologist* **189**, 395–407.

Cheptou, P.-O. and Schoen, D.J. (2003) Frequency-dependent inbreeding depression in *Amsinckia*. *The American Naturalist* **162**, 744–753.

Cheptou, P.-O., **Berger, A.**, **Blanchard, A.**, **Collin, C. and Escarré, J.** (2000a) The effect of drought stress on inbreeding depression in four populations of the Mediterranean outcrossing plant *Crepis sancta* (Asteraceae). *Heredity* **85**, 294–302.

Cheptou, P.-O., **Imbert, E.**, **Lepart, J. and Escarré, J.** (2000b) Effects of competition on lifetime estimates of inbreeding depression in the outcrossing plant *Crepis sancta* (Asteraceae). *Journal of Evolutionary Biology* **13**, 522–531.

Cheptou, P.-O., **Lepart, J. and Escarré, J.** (2001) Inbreeding depression under intraspecific competition in a highly outcrossing population of *Crepis sancta* (Asteraceae): evidence for frequency-dependent variation. *American Journal of Botany* **88**, 1424–1429.

Clauss, M.J. and Venable, D.L. (2000) Seed germination in desert annuals: an empirical test of adaptive bet hedging. *The American Naturalist* **155**, 168–186.

Clements, R.K., **Baskin, J.M. and Baskin, C.C.** (1999) The comparative biology of the two closely-related species *Penstemon tenuiflorus* Pennell and *P. hirsutus* (L.) Willd. (Scrophulariaceae, section *Graciles*): II. Reproductive biology. *Castanea* **64**, 299–309.

Cohen, D. (1966) Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* **12**, 119–129.

Coles, J.F. and Fowler, D.P. (1976) Inbreeding in neighboring trees in two white spruce populations. *Silvae Genetica* **25**, 29–34.

Colling, G., **Reckinger, C. and Matthies, D.** (2004) Effects of pollen quantity and quality on reproduction and offspring vigor in the rare plant *Scorzonera humilis* (Asteraceae). *American Journal of Botany* **91**, 1774–1782.

Culley, T.M., **Weller, S.G.**, **Sakai, A.K. and Rankin, A.E.** (1999) Inbreeding depression and selfing rates in a self-compatible, hermaphroditic species, *Schiedea membranacea* (Caryophyllaceae). *American Journal of Botany* **86**, 980–987.

Daehler, C.C. (1999) Inbreeding depression in smooth cordgrass (*Spartina alterniflora*, Poaceae) invading San Francisco Bay. *American Journal of Botany* **86**, 131–139.

Dahlgaard, J. and Warncke, E. (1995) Seed set and germination in crosses within and between two geographically isolated small populations of *Saxifraga hirculus* in Denmark. *Nordic Journal of Botany* **15**, 337–341.

Darwin, C. (1876) *The effects of cross and self fertilization in the vegetable kingdom*. London, John Murray.

Davila, Y.C. and Wardle, G.M. (2002) Reproductive ecology of the Australian herb *Trachymene incisa* subsp. *incisa* (Apiaceae). *Australian Journal of Botany* **50**, 619–626.

Davis, H.G., **Taylor, C.M.**, **Civille, J.C. and Strong, D.R.** (2004) An Allee effect at the front of a plant invasion: *Spartina* in a Pacific estuary. *Journal of Ecology* **92**, 321–327.

Del Castillo, R.F. (1998) Fitness consequences of maternal and nonmaternal components of inbreeding in the gynodioecious *Phacelia dubia*. *Evolution* **52**, 44–60.

Delesalle, V.A. and Muenchow, G.E. (1992) Opportunities for selfing and inbreeding depression in *Sagittaria* congeners (Alismataceae) with contrasting sexual systems. *Evolutionary Trends in Plants* **6**, 81–91.

Delph, L.F. (2004) Testing for sex differences in biparental inbreeding and its consequences in a gynodioecious species. *American Journal of Botany* **91**, 45–51.

de Vere, N., **Jongejans, E.**, **Plowman, A. and Williams, E.** (2009) Population size and habitat quality affect genetic diversity and fitness in the clonal herb *Cirsium dissectum*. *Oecologia* **159**, 59–68.

Donohue, K. (1998) Effects of inbreeding on traits that influence dispersal and progeny density in *Cakile edentula* var. *lacustris* (Brassicaceae). *American Journal of Botany* **85**, 661–668.

Dudash, M.R. (1990) Relative fitness of selfed and outcrossed progeny in a self-compatible, protandrous species, *Sabatia angularis* L. (Gentianaceae): a comparison in three environments. *Evolution* **44**, 1129–1139.

Dudash, M.R. and Fenster, C.B. (2001) The role of breeding system and inbreeding depression in the maintenance of an outcrossing mating strategy in *Silene virginica* (Caryophyllaceae). *American Journal of Botany* **88**, 1953–1959.

Dudash, M.R., **Carr, D.E. and Fenster, C.B.** (1997) Five generations of enforced selfing and outcrossing in *Mimulus guttatus*: inbreeding depression variation at the population and family level. *Evolution* **51**, 54–65.

Durel, C.E., **Bertin, P. and Kremer, A.** (1996) Relationship between inbreeding depression and inbreeding coefficient in maritime pine (*Pinus pinaster*). *Theoretical and Applied Genetics* **92**, 347–356.

Eckert, C.G. and Barrett, S.C.H. (1994) Inbreeding depression in partially self-fertilizing *Decodon verticillatus* (Lythraceae): population-genetic and experimental analyses. *Evolution* **48**, 952–964.

Edmands, S. (2002) Does parental divergence predict reproductive compatibility? *Trends in Ecology and Evolution* **17**, 520–527.

Edmands, S. (2007) Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Molecular Ecology* **16**, 463–475.

El-Agamy, S.Z.A., **Sherman, W.B. and Lyrene, P.M.** (1981) Fruit set and seed number from self- and cross-pollinated highbush (4x) and rabbiteye (6x) blueberries. *Journal of the American Society for Horticultural Science* **106**, 443–445.

Ellmer, M. and Andersson, S. (2004) Inbreeding depression in *Nigella degenii* (Ranunculaceae): fitness components compared with morphological and phenological characters. *International Journal of Plant Sciences* **165**, 1055–1061.

Emery, S.N. and McCauley, D.E. (2002) Consequences of inbreeding for offspring fitness and gender in *Silene vulgaris*, a gynodioecious plant. *Journal of Evolutionary Biology* **15**, 1057–1066.

Eppley, S.M. and Pannell, J.R. (2009) Inbreeding depression in dioecious populations of the plant *Mercurialis annua*: comparisons between outcrossed progeny and the progeny of self-fertilized feminized males. *Heredity* **102**, 600–608.

Evans, A.S., **Mitchell, R.J. and Cabin, R.J.** (1996) Morphological side effects of using gibberellic acid to induce germination: consequences for the study of seed dormancy. *American Journal of Botany* **83**, 543–549.

Fenster, C.B. (1991) Gene flow in *Chamaecrista fasciculata* (Leguminosae). II. Gene establishment. *Evolution* **45**, 410–422.

Ferdy, J.-B., **Loriot, S.**, **Sandmeier, M.**, **Lefranc, M. and Raquin, C.** (2001) Inbreeding depression in a rare

deceptive orchid. *Canadian Journal of Botany* **79**, 1181–1188.

Ferrer, M.M., Good-Avila, S.V., Montaña, C., Domínguez, C.A. and Eguiarte, L.E. (2009) Effect of variation in self-incompatibility on pollen limitation and inbreeding depression in *Flourensia cernua* (Asteraceae) scrubs of contrasting density. *Annals of Botany* **103**, 1077–1089.

Finch-Savage, W.E. and Leubner-Metzger, G. (2006) Seed dormancy and the control of germination. *New Phytologist* **171**, 501–523.

Fischer, M. and Matthies, D. (1997) Mating structure and inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (Gentianaceae). *American Journal of Botany* **84**, 1685–1692.

Fischer, M. and Matthies, D. (1998) RAPD variation in relation to population size and plant fitness in the rare *Gentianella germanica* (Gentianaceae). *American Journal of Botany* **85**, 811–819.

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.

Fishman, L. (2001) Inbreeding depression in two populations of *Arenaria uniflora* (Caryophyllaceae) with contrasting mating systems. *Heredity* **86**, 184–194.

Footitt, S., Douterelo-Soler, I., Clay, H. and Finch-Savage, W.E. (2011) Dormancy cycling in *Arabidopsis* seeds is controlled by seasonally distinct hormone-signaling pathways. *Proceedings of the National Academy of Sciences of the United States of America* **198**, 20236–20241.

Forrest, C.N., Ottewell, K.M., Whelan, R.J. and Ayre, D.J. (2011) Tests for inbreeding and outbreeding depression and estimation of population differentiation in the bird-pollinated shrub *Grevillea mucronulata*. *Annals of Botany* **108**, 185–195.

Fowler, D.P. (1965a) Effects of inbreeding in red pine, *Pinus resinosa* Ait. III. Factors affecting natural selfing. *Silvae Genetica* **14**, 37–46.

Fowler, D.P. (1965b) Effects of inbreeding in red pine, *Pinus resinosa* Ait. IV. Comparison with other northeastern *Pinus* species. *Silvae Genetica* **14**, 76–81.

Fowler, D.P. and Park, Y.S. (1983) Population studies of white spruce. I. Effects of self-pollination. *Canadian Journal of Forest Research* **13**, 1133–1138.

Fox, C.W., Scheibly, K.L. and Reed, D.H. (2008) Experimental evolution of the genetic load and its implications for the genetic basis of inbreeding depression. *Evolution* **62**, 2236–2249.

Fox, G.A., Evans, A.S. and Keefer, C.J. (1995) Phenotypic consequences of forcing germination: a general problem of intervention in experimental design. *American Journal of Botany* **82**, 1264–1270.

Franklin, E.C. (1970) Survey of mutant forms and inbreeding depression in species of the family Pinaceae. *USDA Forest Service Research Paper* **SE-61**, 1–21.

Galetto, L., Bernardello, G., Isele, I.C., Vesprin, J., Speroni, G. and Berduc, A. (2000) Reproductive biology of *Erythrina crista-galli* (Fabaceae). *Annals of the Missouri Botanical Garden* **87**, 127–145.

Galeuchet, D.J., Perret, C. and Fischer, M. (2005) Performance of *Lychnis flos-cuculi* from fragmented populations under experimental biotic interactions. *Ecology* **86**, 1002–1011.

Galloway, L.F. and Etterson, J.R. (2005) Population differentiation and hybrid success in *Campanula americana*: geography and genome size. *Journal of Evolutionary Biology* **18**, 81–89.

Galloway, L.F. and Etterson, J.R. (2007) Inbreeding depression in an autotetraploid herb: a three cohort field study. *New Phytologist* **173**, 383–392.

Galloway, L.F., Etterson, J.R. and Hamrick, J.L. (2003) Outcrossing rate and inbreeding depression in the herbaceous autotetraploid, *Campanula americana*. *Heredity* **90**, 308–315.

Garcia-Fernández, A., Iriondo, J.M. and Escudero, A. (2012) Inbreeding at the edge: does inbreeding depression increase under more stressful conditions? *Oikos* **121**, 1435–1445.

Gargano, D., Gullo, T. and Bernardo, L. (2009) Do inefficient selfing and inbreeding depression challenge the persistence of the rare *Dianthus guliae* Janka (Caryophyllaceae)? Influence of reproductive traits on a plant's proneness to extinction. *Plant Species Biology* **24**, 69–76.

Gigord, L., Lavigne, C. and Shykoff, J.A. (1998) Partial self-incompatibility and inbreeding depression in a native tree species of La Réunion (Indian Ocean). *Oecologia* **117**, 342–352.

Glaettli, M. and Goudet, J. (2006) Variation in the intensity of inbreeding depression among successive life-cycle stages and generations in gynodioecious *Silene vulgaris* (Caryophyllaceae). *Journal of Evolutionary Biology* **19**, 1995–2005.

Godoy, A.R., Oviedo, V.R.S., Castro, M.M. and Cardoso, A.I.I. (2006) Efeito da endogamia na produção de sementes de pepino caipira. *Bragantia* **65**, 569–573.

González-Varo, J.P. and Traveset, A. (2010) Among-individual variation in pollen limitation and inbreeding depression in a mixed-mating shrub. *Annals of Botany* **106**, 999–1008.

Goodwillie, C. (2000) Inbreeding depression and mating systems in two species of *Linanthus* (Polemoniaceae). *Heredity* **84**, 283–293.

Goodwillie, C. and Knight, M.C. (2006) Inbreeding depression and mixed mating in *Leptosiphon jepsonii*: a comparison of three populations. *Annals of Botany* **98**, 351–360.

Graeber, K., Nakabayashi, K., Miatton, E., Leubner-Metzger, G. and Soppe, W.J.J. (2012) Molecular mechanisms of seed dormancy. *Plant, Cell & Environment* **35**, 1769–1786.

Greimler, J. and Dobeš, Ch. (2000) High genetic diversity and differentiation in relict lowland populations of *Gentianella austriaca* (A. and J. Kern.) Holub (Gentianaceae). *Plant Biology* **2**, 628–637.

Gremer, J.R. and Venable, D.L. (2014) Bet hedging in desert winter annual plants: optimal germination strategies in a variable environment. *Ecology Letters* **17**, 380–387.

Grindeland, J.M. (2008) Inbreeding depression and outbreeding depression in *Digitalis purpurea*: optimal outcrossing distance in a tetraploid. *Journal of Evolutionary Biology* **21**, 716–726.

Groom, M.J. (1998) Allee effects limit population viability of an annual plant. *The American Naturalist* **151**, 487–496.

Groom, M.J. and Preuninger, T.E. (2000) Population type can influence the magnitude of inbreeding depression in *Clarkia concinna* (Onagraceae). *Evolutionary Ecology* **14**, 155–180.

Guillaume, P. and Jacquemart, A.-L. (1999) Early-inbreeding depression in *Vaccinium myrtillus* and *V. vitis-idaea*. *Protoplasma* **208**, 107–114.

Hamilton, M.B. and Mitchell-Olds, T. (1994) The mating system and relative performance of selfed and outcrossed progeny in *Arabis fecunda* (Brassicaceae). *American Journal of Botany* **81**, 1252–1256.

Hardner, C.M. and Potts, B.M. (1995) Inbreeding depression and changes in variation after selfing in *Eucalyptus globulus* ssp. *globulus*. *Silvae Genetica* **44**, 46–54.

Hauser, T.P. and Loeschcke, V. (1994) Inbreeding depression and mating-distance dependent offspring fitness in large and small populations of *Lychnis flos-cuculi* (Caryophyllaceae). *Journal of Evolutionary Biology* **7**, 609–622.

Hauser, T.P. and Loeschcke, V. (1995) Inbreeding depression in *Lychnis flos-cuculi* (Caryophyllaceae): effects of different levels of inbreeding. *Journal of Evolutionary Biology* **8**, 589–600.

Hauser, T.P. and Loeschcke, V. (1996) Drought stress and inbreeding depression in *Lychnis flos-cuculi* (Caryophyllaceae). *Evolution* **50**, 1119–1126.

Hayes, C.N., **Winsor, J.A. and Stephenson, A.G.** (2005a) Multigenerational effects of inbreeding in *Cucurbita pepo* ssp. *texana* (Cucurbitaceae). *Evolution* **59**, 276–286.

Hayes, C.N., **Winsor, J.A. and Stephenson, A.G.** (2005b) Environmental variation influences the magnitude of inbreeding depression in *Cucurbita pepo* ssp. *texana* (Cucurbitaceae). *Journal of Evolutionary Biology* **18**, 147–155.

Heenan, P.B., **Smissen, R.D. and Dawson, M.I.** (2005) Self-incompatibility in the threatened shrub *Olearia adenocarpa* (Asteraceae). *New Zealand Journal of Botany* **43**, 831–841.

Helenurm, K. and Schaal, B.A. (1996) Genetic and maternal effects on offspring fitness in *Lupinus texensis* (Fabaceae). *American Journal of Botany* **83**, 1596–1608.

Heliyanto, B., **Veneklaas, E.J.**, **Lambers, H. and Krauss, S.L.** (2005) Preferential outcrossing in *Banksia ilicifolia* (Proteaceae). *Australian Journal of Botany* **53**, 163–170.

Hellman, E.W. and Moore, J.N. (1983) Effect of genetic relationship to pollinizer on fruit, seed, and seedling parameters in highbush and rabbiteye blueberries. *Journal of the American Society for Horticultural Science* **108**, 401–405.

Hensen, I. and Oberprieler, C. (2005) Effects of population size on genetic diversity and seed production in the rare *Dictamnus albus* (Rutaceae) in central Germany. *Conservation Genetics* **6**, 63–73.

Hensen, I. and Wesche, K. (2006) Relationships between population size, genetic diversity and fitness components in the rare plant *Dictamnus albus* in central Germany. *Biodiversity Conservation* **15**, 2249–2261.

Hereford, J. (2009) Postmating/prezygotic isolation, heterosis, and outbreeding depression in crosses within and between populations of *Diodia teres* (Rubiaceae) Walt. *International Journal of Plant Sciences* **170**, 301–310.

Herrera, J. (1991) The reproductive biology of a riparian Mediterranean shrub, *Nerium oleander* L. (Apocynaceae). *Botanical Journal of the Linnean Society* **106**, 147–172.

Heschel, M.S., **Hausmann, N. and Schmitt, J.** (2005) Testing for stress-dependent inbreeding depression in *Impatiens capensis* (Balsaminaceae). *American Journal of Botany* **92**, 1322–1329.

Heywood, J.S. (1993) Biparental inbreeding depression in the self-incompatible annual plant *Gaillardia pulchella* (Asteraceae). *American Journal of Botany* **80**, 545–550.

Himes, S.L. and Wyatt, R. (2005) Costs and benefits of self-fertility in *Asclepias exaltata* (Apocynaceae). *Journal of the Torrey Botanical Society* **132**, 24–32.

Hirao, A.S. (2010) Kinship between parents reduces offspring fitness in a natural population of *Rhododendron brachycarpum*. *Annals of Botany* **105**, 637–646.

Hirayama, K., **Ishida, K.**, **Setsuko, S. and Tomaru, N.** (2007) Reduced seed production, inbreeding, and pollen shortage in a small population of a threatened tree, *Magnolia stellata*. *Biological Conservation* **136**, 315–323.

Holtsford, T.P. (1996) Variation in inbreeding depression among families and populations of *Clarkia tembloriensis* (Onagraceae). *Heredity* **76**, 83–91.

Holtsford, T.P. and Ellstrand, N.C. (1990) Inbreeding effects in *Clarkia tembloriensis* (Onagraceae) populations with different natural outcrossing rates. *Evolution* **44**, 2031–2046.

Hooftman, D.A., **van Kleunen, M. and Diemer, M.** (2003) Effects of habitat fragmentation on the fitness of two common wetland species, *Carex davalliana* and *Succisa pratensis*. *Oecologica* **134**, 350–359.

Hossaert-McKey, M. and Bronstein, J.L. (2001) Self-pollination and its costs in a monoecious fig (*Ficus aurea*, Moraceae) in a highly seasonal subtropical environment. *American Journal of Botany* **88**, 685–692.

Hull-Sanders, H.M., **Eubanks, M.D. and Carr, D.E.** (2005) Inbreeding depression and selfing rate of *Ipomoea hederacea* var. *integriuscula* (Convolvulaceae). *American Journal of Botany* **92**, 1871–1877.

Husband, B.C. and Gurney, J.E. (1998) Offspring fitness and parental effects as a function of inbreeding in *Epilobium angustifolium* (Onagraceae). *Heredity* **80**, 173–179.

Husband, B.C. and Schemske, D.W. (1995) Magnitude and timing of inbreeding depression in a diploid population of *Epilobium angustifolium* (Onagraceae). *Heredity* **75**, 206–215.

Husband, B.C. and Schemske, D.W. (1996) Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution* **50**, 54–70.

Husband, B.C. and Schemske, D.W. (1997) The effect of inbreeding in diploid and tetraploid populations of *Epilobium angustifolium* (Onagraceae): implications for the genetic basis of inbreeding depression. *Evolution* **51**, 737–746.

Ishida, K. (2006) Maintenance of inbreeding depression in a highly self-fertilizing tree, *Magnolia obovata* Thunb. *Evolutionary Ecology* **20**, 173–191.

Jacobi, C.M., **do Carmo, R.M. and Oliveira, R.S.** (2000) The reproductive biology of two species of *Diplusodon* Pohl (Lythraceae) from Serra do Cipo, southeastern Brazil. *Plant Biology* **2**, 670–676.

Jacobi, C.M., **Ramalho, M. and Silva, M.** (2005) Pollination biology of the exotic rattleweed *Crotalaria retusa* L. (Fabaceae) in NE Brazil. *Biotropica* **37**, 357–363.

Jing, X.-M. and Zheng, G.-H. (1999) The characteristics in seed germination and dormancy of four wild species of tree peonies and their bearing on endangerment. *Acta Phytophysiologica Sinica* **25**, 214–221.

Jóhannsson, M.H., **Gates, M.J. and Stephenson, A.G.** (1998) Inbreeding depression affects pollen performance in

Cucurbita texana. *Journal of Evolutionary Biology* **11**, 579–588.

Johnson, G.R., **Sorensen, F.C.**, **St. Clair, J.B. and Cronn, R.C.** (2004) Pacific northwest forest tree seed zones: a template for native plants? *Native Plants Journal* **5**, 131–140.

Johnson, T.R., **Stewart, S.L.**, **Kauth, P.**, **Kane, M.E. and Philman, N.** (2009) Confronting assumptions about spontaneous autogamy in populations of *Eulophia alta* (Orchidaceae) in south Florida: assessing the effect of pollination treatments on seed formation, seed germination and seedling development. *Botanical Journal of the Linnean Society* **161**, 78–88.

Johnston, M.O. (1992) Effects of cross and self-fertilization on progeny fitness in *Lobelia cardinalis* and *L. siphilitica*. *Evolution* **46**, 688–702.

Johnston, M.O. and Schoen, D.J. (1996) Correlated evolution of self-fertilization and inbreeding depression: an experimental study of nine populations of *Amsinckia* (Boraginaceae). *Evolution* **50**, 1478–1491.

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.

Juillet, N., **Dunand-Martin, S. and Gigord, L.D.B.** (2007) Evidence for inbreeding depression in the food-deceptive colour-dimorphic orchid *Dactylorhiza sambucina* (L.) Soò. *Plant Biology* **9**, 147–151.

Kahman, S. and Poschold, P. (2000) Population size, plant performance, and genetic variation in the rare plant *Arnica montana* L. in Rhön, Germany. *Basic and Applied Ecology* **1**, 43–51.

Kalisz, S. (1989) Fitness consequences of mating system, seed weight, and emergence date in a winter annual, *Collinsia verna*. *Evolution* **43**, 1263–1272.

Kärkkäinen, K., **Koski, V. and Savolainen, O.** (1996) Geographical variation in the inbreeding depression of Scots pine. *Evolution* **50**, 111–119.

Kärkkäinen, K., **Kuittinen, H.**, **van Treuren, R.**, **Vogl, C.**, **Oikarinen, S. and Savolainen, O.** (1999) Genetic basis of inbreeding depression in *Arabis petraea*. *Evolution* **53**, 1354–1365.

Karron, J.D. (1989) Breeding systems and levels of inbreeding depression in geographically restricted and widespread species of *Astragalus* (Fabaceae). *American Journal of Botany* **76**, 331–340.

Keller, L.F. and Waller, D.M. (2002) Inbreeding effects in wild populations. *Trends in Ecology and Evolution* **17**, 230–241.

Kennedy, B.F. and Elle, E. (2008) The inbreeding depression cost of selfing: importance of flower size and population size in *Collinsia parviflora* (Veronicaceae). *American Journal of Botany* **95**, 1596–1605.

Kephart, S.R., **Brown, E. and Hall, J.** (1999) Inbreeding depression and partial selfing: evolutionary implications of mixed-mating in a coastal endemic, *Silene douglasii* var. *oraria* (Caryophyllaceae). *Heredity* **82**, 543–554.

Kittleson, P.M. and Maron, J.L. (2000) Outcrossing rate and inbreeding depression in the perennial yellow bush lupine, *Lupinus arboreus* (Fabaceae). *American Journal of Botany* **87**, 652–660.

Klips, R.A. and Snow, A.A. (1997) Delayed autonomous self-pollination in *Hibiscus laevis* (Malvaceae). *American Journal of Botany* **84**, 48–53.

Kochánková, J. and Mandák, B. (2009) How do population genetic parameters affect germination of the heterocarpic species *Atriplex tatarica* (Amaranthaceae)? *Annals of Botany* **103**, 1303–1313.

Koelewijn, H.P. (1998) Effects of different levels of inbreeding on progeny fitness in *Plantago coronopus*. *Evolution* **52**, 692–702.

Koelewijn, H.P. (2004) Sibling competition, size variation and frequency-dependent outcrossing advantage in *Plantago coronopus*. *Evolutionary Ecology* **18**, 51–74.

Koelewijn, H.P. and van Damme, J.M.M. (2005) Effects of seed size, inbreeding and maternal sex on offspring fitness in gynodioecious *Plantago coronopus*. *Journal of Ecology* **93**, 373–383.

Koelewijn, H.P., **Koski, V. and Savolainen, O.** (1999) Magnitude and timing of inbreeding depression in Scots pine (*Pinus sylvestris* L.). *Evolution* **53**, 758–768.

Kuser, J. (1983) Inbreeding depression in *Metasequoia*. *Journal of the Arnold Arboretum* **64**, 475–481.

Lammi, A., **Siikamäki, P. and Mustajärvi, K.** (1999) Genetic diversity, population size, and fitness in central and peripheral populations of a rare plant *Lychnis viscaria*. *Conservation Biology* **13**, 1069–1078.

Lande, R. and Schemske, D.W. (1985) The evolution of self-fertilization and inbreeding depression in plants. I. Genetic models. *Evolution* **39**, 24–40.

Latta, R. and Ritland, K. (1994) The relationship between inbreeding depression and prior inbreeding among populations of four *Mimulus* taxa. *Evolution* **48**, 806–817.

Le Cadre, S., **Tully, T.**, **Mazer, S.J.**, **Ferdy, J.-B.**, **Moret, J. and Machon, N.** (2008) Allee effects within small populations of *Aconitum napellus* ssp. *lusitanicum*, a protected species in northern France. *New Phytologist* **179**, 1171–1182.

Le Corff, J. (1996) Establishment of chasmogamous and cleistogamous seedlings of an ant-dispersed understory herb, *Calathea micans* (Marantaceae). *American Journal of Botany* **83**, 155–161.

Leimu, R. and Mutikainen, P. (2005) Population history, mating system, and fitness variation in a perennial herb with a fragmented distribution. *Conservation Biology* **19**, 349–356.

Levin, D.A. and Bulinska-Radomska, Z. (1988) Effects of hybridization and inbreeding on fitness in *Phlox*. *American Journal of Botany* **75**, 1632–1639.

Lhamo, N., **Ramsey, M. and Vaughton, G.** (2006) Density- and frequency-dependent inbreeding depression in the Australian annual *Hibiscus trionum* var *vesicarius*. *Evolutionary Ecology Research* **8**, 717–730.

Libby, W.J., **McCutchan, B.G. and Millar, C.I.** (1981) Inbreeding depression in selfs of redwood. *Silvae Genetica* **30**, 15–25.

Lienert, J. and Fischer, M. (2004) Experimental inbreeding reduces seed production and germination independent of fragmentation of populations of *Swertia perennis*. *Basic and Applied Ecology* **5**, 43–52.

Liu, H. and Koptur, S. (2003) Breeding system and pollination of a narrowly endemic herb of the Lower Florida Keys: impacts on the urban-wildland interface. *American Journal of Botany* **90**, 1180–1187.

Liu, H. and Spira, T.P. (2001) Influence of seed age and inbreeding on germination and seedling growth in *Hibiscus moscheutos* (Malvaceae). *Journal of the Torrey Botanical Society* **128**, 16–24.

Lofflin, D.L. and Kephart, S.R. (2005) Outbreeding, seedling establishment, and maladaptation in natural and reintroduced populations of rare and common *Silene douglasii* (Caryophyllaceae). *American Journal of Botany* **92**, 1691–1700.

Luijten, S.H., **Oostermeijer, J.G.**, **van Leeuwen, N.C. and den Nijs, H.C.M.** (1996) Reproductive success and clonal genetic structure of the rare *Arnica montana* (Compositae) in The Netherlands. *Plant Systematics and Evolution* **201**, 15–30.

Luijten, S.H., **Dierick, S.**, **Oostermeijer, J.G.B.**, **Raijmann, L.E.L. and den Nijs, H.C.M.** (2000) Population size, genetic variation and reproductive success in the rapidly declining self-incompatible *Arnica montana* in The Netherlands. *Conservation Biology* **14**, 1776–1787.

Luijten, S.H., **Kéry, M.**, **Oostermeijer, J.G. and den Nijs, H.C.M.** (2002) Demographic consequences of inbreeding and outbreeding in *Arnica montana*: a field experiment. *Journal of Ecology* **90**, 593–603.

Mabberley, D.J. (2008) *Mabberley's plant-book. A portable dictionary of plants, their classification and uses* (3rd edition). Cambridge, Cambridge University Press.

Maki, M. (1993) Outcrossing and fecundity advantage of females in gynodioecious *Chionographis japonica* var *kurohimensis* (Liliaceae). *American Journal of Botany* **80**, 629–634.

Mandák, B. and Pyšek, P. (1999) Effects of plant density and nutrient levels on fruit polymorphism in *Atriplex sagittata*. *Oecologia* **119**, 63–72.

Mandujano, M.C., **Montana, C. and Eguiarte, L.E.** (1996) Reproductive ecology and inbreeding depression in *Opuntia rastrera* (Cactaceae) in the Chihuahuan Desert: why are sexually derived recruitments so rare? *American Journal of Botany* **83**, 63–70.

Marshall, M. and Ganders, F.R. (2001) Sex-biased seed predation and the maintenance of females in a gynodioecious plant. *American Journal of Botany* **88**, 1437–1443.

Mathiasen, P., **Rovere, A.E. and Premoli, A.C.** (2007) Genetic structure and early effects of inbreeding in fragmented temperate forests of a self-incompatible tree, *Embothrium coccineum*. *Conservation Biology* **21**, 232–240.

Mayer, S.S., **Charlesworth, D. and Meyers, B.** (1996) Inbreeding depression in four populations of *Collinsia heterophylla* Nutt. (Scrophulariaceae). *Evolution* **50**, 879–891.

McCall, C., **Waller, D.M. and Mitchell-Old, T.** (1994) Effects of serial inbreeding on fitness components in *Impatiens capensis*. *Evolution* **48**, 818–827.

Meier, C. and Holderegger, R. (1998) Breeding system, germination, and phenotypic differences among populations of *Saxifraga aizoides* (Saxifragaceae) at the periphery of its alpine distribution. *Nordic Journal of Botany* **18**, 681–688.

Melville, A.H., **Galletta, G.J. and Draper, A.D.** (1980) Seed germination and early seedling vigor in progenies of inbred strawberry selections. *HortScience* **15**, 749–750.

Mena-Ali, J.I., **Keser, L.H. and Stephenson, A.G.** (2008) Inbreeding depression in *Solanum carolinense* (Solanaceae), a species with a plastic self-incompatibility response. *BMC Evolutionary Biology* **8**, 10. doi:10.1186/1471-2148-8-10.

Menges, E.S. (1991) Seed germination percentage increases with population size in a fragmented prairie species. *Conservation Biology* **5**, 158–164.

Mergen, F., **Burley, J. and Furnival, G.M.** (1965) Embryo and seedling development in *Picea glauca* (Moench) Voss after self-, cross- and wind-pollination. *Silvae Genetica* **14**, 188–194.

Michaels, H.J., **Shi, X.J. and Mitchell, R.J.** (2008) Effects of population size on performance and inbreeding depression in *Lupinus perennis*. *Oecologia* **154**, 651–661.

Molina-Freaner, F. and Jain, S.K. (1993) Inbreeding effects in a gynodioecious population of the colonizing species *Trifolium hirtum* All. *Evolution* **47**, 1472–1479.

Molina-Freaner, F., **Cervantes-Salas, M.**, **Morales-Romero, D.**, **Buchmann, S. and Fleming, T.H.** (2003) Does the pollinator abundance hypothesis explain geographic variation in the breeding system of *Pachycereus pringlei*? *International Journal of Plant Sciences* **164**, 383–393.

Montalvo, A.M. (1994) Inbreeding depression and maternal effects in *Aquilegia caerulea*, a partially selfing plant. *Ecology* **75**, 2395–2409.

Mooney, E.H. and McGraw, J.B. (2007) Effects of self-pollination and outcrossing with cultivated plants in small natural populations of American ginseng, *Panax quinquefolius* (Araliaceae). *American Journal of Botany* **94**, 1677–1687.

Moran-Palma, P. and Snow, A.A. (1997) The effect of interplant distance on mating success in federally-threatened, self-incompatible *Hymenoxys herbacea* = *H. acaulis* var *glabra* (Asteraceae). *American Journal of Botany* **84**, 233–238.

Moreira, B. and Pausas, J.G. (2012) Tanned or burned: the role of fire in shaping physical seed dormancy. *PLoS ONE* **7**(12), e51523.

Morgante, M., **Vendramin, G.G.**, **Rossi, P. and Olivieri, A.M.** (1993) Selection against inbreds in early life-cycle phases in *Pinus leucodermis* Ant. *Heredity* **70**, 622–627.

Mullarkey, A.A., **Byers, D.L. and Anderson, R.C.** (2013) Inbreeding depression and partitioning of genetic load in the invasive biennial *Alliaria petiolata* (Brassicaceae). *American Journal of Botany* **100**, 509–518.

Murza, G.L. and Davis, A.R. (2005) Flowering phenology and reproductive biology of *Drosera anglica* (Droseraceae). *Botanical Journal of the Linnean Society* **147**, 417–426.

Mustajärvi, K., **Siikamäki, P. and Åkerberg, A.** (2005) Inbreeding depression in perennial *Lychnis viscaria* (Caryophyllaceae): effects of population mating history and nutrient availability. *American Journal of Botany* **92**, 1853–1861.

Mutikainen, P. and Delph, L.F. (1998) Inbreeding depression in gynodioecious *Lobelia siphilitica*: among-family differences override between-morph differences. *Evolution* **52**, 1572–1582.

Naito, Y., **Konuma, A.**, **Iwata, H.**, **Suyama, Y.**, **Seiwa, K.**, **Okuda, T.**, **Lee, S.L.**, **Muhammad, N. and Tsumura, Y.** (2005) Selfing and inbreeding depression in seeds and seedlings of *Neobalanocarpus heimii* (Dipterocarpaceae). *Journal of Plant Research* **118**, 423–430.

Naito, Y., **Kanzaki, M.**, **Iwata, H.**, **Obayashi, K.**, **Lee, S.L.**, **Muhammad, N.**, **Okuda, T. and Tsumura, Y.** (2008) Density-dependent selfing and its effects on seed performance in a tropical canopy tree species, *Shorea acuminata* (Dipterocarpaceae). *Forest Ecology and Management* **256**, 375–383.

Nason, J.D. and Ellstrand, N.C. (1995) Lifetime estimates of biparental inbreeding depression in the self-incompatible annual plant *Raphanus sativus*. *Evolution* **49**, 307–316.

Navarro, L. and Guitián, J. (2002) The role of floral biology and breeding system on the reproductive success of the narrow endemic *Petrocoptis viscosa* Rothm. (Caryophyllaceae). *Biological Conservation* **103**, 125–132.

Newman, D. and Pilson, D. (1997) Increased probability of extinction due to decreased genetic effective population size: experimental populations of *Clarkia pulchella*. *Evolution* **51**, 354–362.

Newport, M.E.A. (1989) A test for proximity-dependent outcrossing in the alpine skypilot, *Polemoniun viscosum*. *Evolution* **43**, 1110–1113.

Nielsen, L.R., Siegismund, H.R. and Hansen, T. (2007) Inbreeding depression in the partially self-incompatible endemic plant species *Scalesia affinis* (Asteraceae) from Galápagos islands. *Evolutionary Ecology* **21**, 1–12.

Norman, J.K., Sakai, A.K., Weller, S.G. and Dawson, T.E. (1995) Inbreeding depression in morphological and physiological traits of *Schiedea lydgatei* (Caryophyllaceae) in two environments. *Evolution* **49**, 297–306.

Nuñez-Farfán, J., Cabrales-Vargas, R.A. and Dirzo, R. (1996) Mating system consequences on resistance to herbivory and life history traits in *Datura stramonium*. *American Journal of Botany* **83**, 1041–1049.

Oliviera, I., Swan, M. and Gouyon, P.-H. (1983) Reproductive system and colonizing strategy of two species of *Carduus* (Compositae). *Oecologia* **60**, 114–117.

O'Neil, P. (1994) Genetic incompatibility and offspring quality in the tristylous plant *Lythrum salicaria* (Lythraceae). *American Journal of Botany* **81**, 76–84.

Oostermeijer, J.G.B., van Eijek, M.W. and den Nijs, J.C.M. (1994) Offspring fitness in relation to population size and genetic variation in the rare perennial plant species *Gentiana pneumonanthe* (Gentianaceae). *Oecologia* **97**, 289–296.

Oostermeijer, J.G.B., Altenburg, R.G.M. and den Nijs, J.C.M. (1995) Effects of outcrossing distance and selfing on fitness components in the rare *Gentiana pneumonanthe* (Gentianaceae). *Acta Botanica Neerlandica* **44**, 257–268.

Oriani, A., Sano, P.T. and Scatena, V.L. (2009) Pollination biology of *Syngonanthus elegans* (Eriocaulaceae - Poales). *Australian Journal of Botany* **57**, 94–105.

Ortiz-Barney, E. and Ackerman, J.D. (1999) The cost of selfing in *Encyclia cochleata* (Orchidaceae). *Plant Systematics and Evolution* **219**, 55–64.

Ouborg, N.J. and van Treuren, R. (1994) The significance of genetic erosion in the process of extinction. IV. Inbreeding load and heterosis in relation to population size in the mint *Salvia pratensis*. *Evolution* **48**, 996–1008.

Ouborg, N.J., Biere, A. and Mudde, C.L. (2000) Inbreeding effects on resistance and transmission-related traits in the *Silene-Microbotryum* pathosystem. *Ecology* **81**, 520–531.

Owen, K., Vaughton, G. and Ramsey, M. (2007) Facilitated autogamy and costs of selfing in the perennial herb *Bulbine bulbosa* (Asphodelaceae). *International Journal of Plant Sciences* **168**, 579–585.

Owens, S.J. and Miller, R. (2009) Cross- and self-fertilization of plants – Darwin's experiments and what we know now. *Botanical Journal of the Linnean Society* **161**, 357–395.

Ozimec, B. and Husband, B.C. (2011) Effect of recurrent selfing on inbreeding depression and mating system evolution in an autopolyploid plant. *Evolution* **65**, 2038–2049.

Parker, I.M., Nakamura, R.R. and Schemske, D.W. (1995) Reproductive allocation and the fitness consequences of selfing in two sympatric species of *Epilobium* (Onagraceae) with contrasting mating systems. *American Journal of Botany* **82**, 1007–1016.

Parker, M.A. (1992) Outbreeding depression in a selfing annual. *Evolution* **46**, 837–841.

Peakall, R. and Beattie, A.J. (1996) Ecological and genetic consequences of pollination by sexual deception in the orchid *Caladenia tentactulata*. *Evolution* **50**, 2207–2220.

Petit, S., Jusaitis, M. and Bickerton, D. (2009) Effect of pollen load, self-pollination and plant size on seeds and germination in the endangered pink-lipped spider orchid, *Caladenia behrii*. *Australian Journal of Botany* **57**, 307–314.

Pettersson, M.W. (1992) Advantages of being a specialist female in nodioecious *Silene vulgaris* s.l. (Caryophyllaceae). *American Journal of Botany* **79**, 1389–1395.

Picó, F.X. and Koubek, T. (2003) Inbreeding effects on fitness traits in the heterocarpic herb *Leontodon autumnalis* L. (Asteraceae). *Acta Oecologica* **24**, 289–294.

Picó, F.X., Ouborg, N.J. and van Groenendael, J.M. (2003) Fitness traits and dispersal ability in the herb *Tragopogon pratensis* (Asteraceae): decoupling the role of inbreeding depression and maternal effects. *Plant Biology* **5**, 522–530.

Picó, F.X., Ouborg, N.J. and van Groenendael, J.M. (2004a) Influence of selfing and maternal effects on life-cycle traits and dispersal ability in the herb *Hypochaeris radicata* (Asteraceae). *Botanical Journal of the Linnean Society* **146**, 163–170.

Picó, F.X., Ouborg, N.J. and van Groenendael, J.M. (2004b) Evaluation of the extent of among-family variation in inbreeding depression in the perennial herb *Scabiosa columbaria* (Dipsacaceae). *American Journal of Botany* **91**, 1183–1189.

Piesch, R.F. and Stettler, R.F. (1971) The detection of good selfers for haploid induction in douglar-fir. *Silvae Genetica* **20**, 144–148.

Platenkamp, G.A.J. and Shaw, R.G. (1993) Environmental and genetic maternal effects on seed characters in *Nemophila menziesii*. *Evolution* **47**, 540–555.

Pluess, A.R. and Stöcklin, J. (2004) Genetic diversity and fitness in *Scabiosa columbaria* in the Swiss Jura in relation to population size. *Conservation Genetics* **5**, 145–156.

Pounders, C., Reed, S. and Pooler, M. (2006) Comparison of self- and cross-pollination on pollen tube growth, seed development, and germination in crapemyrtle. *HortScience* **41**, 575–578.

Price, M.V. and Waser, N.M. (1979) Pollen dispersal and optimal outcrossing in *Delphinium nelsonii*. *Nature* **277**, 294–297.

Prill, N., Bullock, J.M., van Dam, N.M. and Leimu, R. (2014) Loss of heterosis and family-dependent inbreeding depression in plant performance against multiple herbivores under drought stress. *Journal of Ecology* **102**, 1497–1505.

Pujol, B. and McKey, D. (2006) Size asymmetry in intraspecific competition and the density-dependence of inbreeding depression in a natural plant population: a case study in cassava (*Manihot esculenta* Crantz, Euphorbiaceae). *Journal of Evolutionary Biology* **19**, 85–96.

Puterbaugh, M.N., Wied, A. and Galen, C. (1997) The functional ecology of gynodioecy in *Eritrichium aretioides* (Boraginaceae), the alpine forget-me-not. *American Journal of Botany* **84**, 393–400.

Quilichini, A., **Debussche, M. and Thompson, J.D.** (2001) Evidence for local outbreeding depression in the Mediterranean island endemic *Anchusa crispa* Viv. (Boraginaceae). *Heredity* **87**, 190–197.

Raabová, J., **Münzbergová, Z. and Fischer, M.** (2009) Consequences of near and far between-population crosses for offspring fitness in a rare herb. *Plant Biology* **11**, 829–836.

Ramsey, M. and Vaughton, G. (1996) Inbreeding depression and pollinator availability in a partially self-fertile perennial herb *Blandfordia grandiflora* (Liliaceae). *Oikos* **76**, 465–474.

Ramsey, M. and Vaughton, G. (1998) Effect of environment on the magnitude of inbreeding depression in seed germination in a partially self-fertile perennial herb (*Blandfordia grandiflora*, Liliaceae). *International Journal of Plant Sciences* **159**, 98–104.

Ramsey, M., **Seed, L. and Vaughton, G.** (2003) Delayed selfing and low levels of inbreeding depression in *Hibiscus trionum* (Malvaceae). *Australian Journal of Botany* **51**, 275–281.

Rao, G.-Y., **Widen, B. and Andersson, S.** (2002) Patterns of inbreeding depression in a population of *Brassica cretica* (Brassicaceae): evidence from family-level analyses. *Biological Journal of the Linnean Society* **76**, 317–325.

Ricardo, C.T., **Corrado, C.A.**, **Mandujano, M.C. and Molina-Freaner, F.** (2006) Reproductive consequences of clonal growth in *Stenocereus eruca*, a rare clonal cactus of the Sonoran Desert. *Evolutionary Ecology* **20**, 131–142.

Richards, C.M. (2000a) Inbreeding depression and genetic rescue in a plant metapopulation. *The American Naturalist* **155**, 383–394.

Richards, C.M. (2000b) Genetic and demographic influences on population persistence: gene flow and genetic rescue in *Silene alba*. pp. 271–291 *in* Young, A.G.; Clarke, G.M. (Eds) *Genetics, demography and viability of fragmented populations*. Cambridge, Cambridge University Press.

Richter, K.S. and Weis, A.E. (1998) Inbreeding and outcrossing in *Yucca whipplei*: consequences for the reproductive success of plant and pollinator. *Ecology Letters* **1**, 21–24.

Riley, R. (1956) The influence of the breeding system on the genecology of *Thlaspi alpestre* L. *New Phytologist* **55**, 319–330.

Robertson, A.W., **Kelly, D. and Ladley, J.J.** (2011) Futile selfing in the trees *Fuchsia excorticata* (Onagraceae) and *Sophora microphylla* (Fabaceae): inbreeding depression over 11 years. *International Journal of Plant Sciences* **172**, 191–198.

Rosquist, G. (2001) Reproductive biology in diploid *Anthericum ramosum* and tetraploid *A. liliago* (Anthericaceae). *Oikos* **92**, 143–152.

Routley, M.B., **Mavraganis, K. and Eckert, C.G.** (1999) Effect of population size on the mating system in a self-compatible, autogamous plant, *Aquilegia canadensis* (Ranunculaceae). *Heredity* **82**, 518–528.

Ruan, C.-J., **Li, H. and Mopper, S.** (2009) *Kosteletzkya virginica* displays mixed mating in response to the pollinator environment despite strong inbreeding depression. *Plant Ecology* **203**, 183–193.

Ruckelshaus, M.H. (1995) Estimates of outcrossing rates and of inbreeding depression in a population of the marine angiosperm *Zostera marina*. *Marine Biology* **123**, 583–593.

Schaal, B.A. (1984) Life-history variation, natural selection, and maternal effects in plant populations. pp. 188–206 *in* Dirzo, R.; Sarukhan, J. (Eds) *Perspectives on plant population ecology*. Sunderland, MA, Sinauer Associates.

Schemske, D.W. (1983) Breeding system and habitat effects on fitness components in three neotropical *Costus* (Zingiberaceae). *Evolution* **37**, 523–539.

Schemske, D.W. and Pautler, L.P. (1984) The effects of pollen composition on fitness components in a neotropical herb. *Oecologia* **62**, 31–36.

Schlichting, C.D. and Devlin, B. (1992) Pollen and ovule sources affect seed production of *Lobelia cardinalis* (Lobeliaceae). *American Journal of Botany* **79**, 891–898.

Schmidt, K. and Jensen, K. (2000) Genetic structure and AFLP variation in remnant populations in the rare plant *Pedicularis palustris* (Scrophulariaceae) and its relation to population size and reproductive components. *American Journal of Botany* **87**, 678–689.

Schoen, D.J. (1983) Relative fitnesses of selfed and outcrossed progeny in *Gilia achilleifolia* (Polemoniaceae). *Evolution* **37**, 292–301.

Seavey, S.R. and Carter, S.K. (1994) Self-sterility in *Epilobium obcordatum* (Onagraceae). *American Journal of Botany* **81**, 331–338.

Seed, L., **Vaughton, G. and Ramsey, M.** (2006) Delayed autonomous selfing and inbreeding depression in the Australian annual *Hibiscus trionum* var. *vesicarius* (Malvaceae). *Australian Journal of Botany* **54**, 27–34.

Seltmann, P., **Cocucci, A.**, **Renison, D.**, **Cierjacks, A. and Hensen, I.** (2009) Mating system, outcrossing distance effects and pollen availability in the wind-pollinated treeline species *Polylepis australis* BITT (Rosaceae). *Basic and Applied Ecology* **10**, 52–60.

Sheridan, P.M. and Karowe, D.N. (2000) Inbreeding, outbreeding, and heterosis in the yellow pitcher plant, *Sarracenia flava* (Sarraceniaceae), in Virginia. *American Journal of Botany* **87**, 1628–1633.

Shi, X.J., **Michaels, H.J. and Mitchell, R.J.** (2005) Effects of self-pollination and maternal resources on reproduction and offspring performance in the wild lupine, *Lupinus perennis* (Fabaceae). *Sexual Plant Reproduction* **18**, 55–64.

Simons, A.M. (2011) Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proceedings of the Royal Society B* **279**, 1601–1609.

Smithson, A. (2006) Pollinator limitation and inbreeding depression in orchid species with and without nectar rewards. *New Phytologist* **169**, 419–430.

Snow, A.A. and Spira, T.P. (1993) Individual variation in the vigor of self pollen and selfed progeny in *Hibiscus moscheutos* (Malvaceae). *American Journal of Botany* **80**, 160–164.

Sorensen, F. (1969) Embryonic genetic load in coastal douglas-fir, *Pseudotsuga menziesii* var. *menziesii*. *The American Naturalist* **103**, 389–398.

Sorensen, F. (1971) Estimate of self-fertility in coastal douglas-fir from inbreeding studies. *Silvae Genetica* **20**, 115–120.

Sorensen, F.C. and Miles, R.S. (1974) Self-pollination effects of douglas-fir and ponderosa pine seeds and seedlings. *Silvae Genetica* **23**, 135–138.

Sorensen, F., **Franklin, J.F. and Wollard, R.** (1976) Self-pollination effects on seed and seedling traits in noble fir. *Forest Science* **22**, 155–159.

Sork, V.L. and Schemske, D.W. (1992) Fitness consequences on mixed-donor pollen loads in the annual legume *Chamaecrista fasciculata*. *American Journal of Botany* **79**, 508–515.

Squillace, A.E. and Bingham, R.T. (1958) Selective fertilization in *Pinus monticola* Dougl. *Silvae Genetica* **7**, 188–196.

Stacy, E.A. (2001) Cross-fertility in two tropical tree species: evidence of inbreeding depression within populations and genetic divergence among populations. *American Journal of Botany* **88**, 1041–1051.

Stein, K. and Hensen, I. (2013) The reproductive biology of two understory plants in the Atlantic rain forest, Brazil. *Ecological Research* **28**, 593–602.

Stephenson, A.G., Leyshon, B., Travers, S.E., Haynes, C.N. and Winsor, J.A. (2004) Interrelationships among inbreeding, herbivory, and disease on reproduction in a wild gourd. *Ecology* **85**, 3023–3034.

Stevens, J.P. and Bougourd, S.M. (1988) Inbreeding depression and the outcrossing rate in natural populations of *Allium schoenoprasum* L. (wild chives). *Heredity* **60**, 257–261.

Stout, J. (2007) Reproductive biology of the invasive exotic shrub, *Rhododendron ponticum* L. (Ericaceae). *Botanical Journal of the Linnean Society* **155**, 373–381.

Susko, D.J. and Clubb, M. (2008) Pollination effects on patterns of ovule fate in *Hesperis matronalis* (Brassicaceae). *Botany* **86**, 466–474.

Takagawa, S., Washitani, I., Uesugi, R. and Tsumura, Y. (2006) Influence of inbreeding depression on a lake population of *Nymphoides peltata* after restoration from the soil seed bank. *Conservation Genetics* **7**, 705–716.

Taylor, D.R., Trimble, S. and McCauley, D.E. (1999) Ecological genetics and gynodioecy in *Silene vulgaris*: relative fitness of females and hermaphrodites during the colonization process. *Evolution* **53**, 745–751.

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.

Templeton, A.R. (1986) Coadaptation and outbreeding depression. pp. 105–116 *in* Soulé, M.E. (Ed.) *Conservation biology. The science of scarcity and diversity*. Sunderland, MA, Sinauer Associates.

Thiele, J., Hansen, T., Siegismund, H.R. and Hauser, T.P. (2010) Genetic variation in inbreeding depression among floral and fitness traits in *Silene nutans*. *Heredity* **104**, 52–60.

Trager, M.D., Menges, E.S, Quintana-Ascencio, P.F. and Weekley, C.W. (2005) Outcrossing effects on the reproductive performance of *Hypericum cumulicola*, an endangered Florida scrub endemic. *Journal of the Torrey Botanical Society* **132**, 204–213.

Trame, A.-M., Coddington, A.J. and Paige, K.N. (1995) Field and genetic studies testing optimal outcrossing in *Agave schottii*, a long-lived clonal plant. *Oecologia* **104**, 93–100.

Van Assche, J.A., Debucquoy, K.L.A. and Rommens, W.A.F. (2003) Seasonal cycles in the germination capacity of buried seeds of some Leguminosae (Fabaceae). *New Phytologist* **158**, 315–323.

van Damme, J.M.M. and van Delden, W. (1984) Gynodioecy in *Plantago lanceolata* L. IV. Fitness components of sex types in different life cycle stages. *Evolution* **38**, 1326–1336.

Vandepitte, K., Roldán-Ruiz, I. and Honnay, I. (2009) Reproductive consequences of mate quantity versus mate diversity in a wind-pollinated plant. *Acta Oecologica* **35**, 548–553.

Vange, V. (2002) Breeding system and inbreeding depression in the clonal plant species *Knautia arvensis* (Dipsacaceae): implications for survival in abandoned grassland. *Biological Conservation* **108**, 59–67.

van Treuren, R., Bijlsma, R., Ouborg, N.J. and van Delden, W. (1993) The significance of genetic erosion in the process of extinction. IV. Inbreeding depression and heterosis effects caused by selfing and outcrossing in *Scabiosa columbaria*. *Evolution* **47**, 1669–1680.

Vegis, A. (1964) Dormancy in higher plants. *Annual Review of Plant Physiology* **15**, 185–224.

Venable, D.L. (1985) The evolutionary ecology of seed heteromorphism. *The American Naturalist* **126**, 577–595.

Vogler, D.W., Filmore, K. and Stephenson, A.G. (1999) Inbreeding depression in *Campanula rapunculoides* L. I. A comparison of inbreeding depression in plants derived from strong and weak self-incompatibility phenotypes. *Journal of Evolutionary Biology* **12**, 483–494.

Wagenius, S., Hangelbroek, H.H., Ridley, C.E. and Shaw, R.G. (2009) Biparental inbreeding and inter-remnant mating in a perennial prairie plant: fitness consequences for progeny in their first eight years. *Evolution* **64**, 761–771.

Walisch, T.J., Colling, G., Poncelet, M. and Matthies, D. (2012) Effects of inbreeding and interpopulation crosses on performance and plasticity of two generations of offspring of a declining grassland plant. *American Journal of Botany* **99**, 1300–1313.

Wallace, L.E. (2003) The cost of inbreeding in *Platanthera leucophaea* (Orchidaceae). *American Journal of Botany* **90**, 235–242.

Waller, D.M., Dole, J. and Bersch, A.J. (2008) Effects of stress and phenotypic variation on inbreeding depression in *Brassica rapa*. *Evolution* **62**, 917–931.

Wang, T., Hagqvist, R. and Tigerstedt, P.M.A. (1999) Inbreeding depression in three generations of selfed families of silver birch (*Betula pendula*). *Canadian Journal of Forest Research* **29**, 662–668.

Waser, N.M. and Price, M.V. (1989) Optimal outcrossing in *Ipomopsis aggregata*: seed set and offspring fitness. *Evolution* **43**, 1097–1109.

Waser, NM. and Price, M.V. (1991) Outcrossing distance effects in *Delphinium nelsonii*: pollen load, pollen tubes, and seed set. *Ecology* **72**, 171–179.

Waser, N.M. and Price, M.V. (1994) Crossing-distance effects in *Delphinium nelsonii*: outbreeding and inbreeding depression in progeny fitness. *Evolution* **48**, 842–852.

Waser, N.M., Price, M.V. and Shaw, R.G. (2000) Outbreeding depression varies among cohorts of *Ipomopsis aggregata* planted in nature. *Evolution* **54**, 485–491.

Watanabe, A., Goka, K. and Washitani, I. (2003) Effects of population spatial structure on the quantity and quality of seeds set by *Primula sieboldii* (Primulaceae). *Plant Species Biology* **18**, 107–121.

Whitkus, R. (1988) Experimental hybridizations among chromosome races of *Carex pachystachya* and the related species *C. macloviana* and *C. preslii* (Cyperaceae). *Systematic Botany* **13**, 146–153.

Widén, B. (1993) Demographic and genetic effects on reproduction as related to population size in a rare perennial herb, *Senecio integrifolius*. *Biological Journal of the Linnean Society* **50**, 179–195.

Willi, Y., **Van Buskirk, J. and Fischer, M.** (2005) A three-fold genetic allee effect: population size affects cross-compatibility, inbreeding depression and drift load in the self-incompatible *Ranunculus reptans*. *Genetics* **169**, 2255–2265.

Willi, Y., **Dietrich, S.**, **van Kleunen, M. and Fischer, M.** (2007) Inter-specific competitive stress does not affect the magnitude of inbreeding depression. *Evolutionary Ecology Research* **9**, 959–974.

Willis, J.H. (1993a) Effects of different levels of inbreeding on fitness components in *Mimulus guttatus*. *Evolution* **47**, 864–876.

Willis, J.H. (1993b) Partial self-fertilization and inbreeding depression in two populations of *Mimulus guttatus*. *Heredity* **71**, 145–154.

Willis, J.H. (1999a) The role of genes of large effect on inbreeding depression in *Mimulus guttatus*. *Evolution* **53**, 1678–1691.

Willis, J.H. (1999b) Inbreeding load, average dominance and the mutation rate for mildly deleterious alleles in *Mimulus guttatus*. *Genetics* **153**, 1885–1898.

Winn, A.A., **Elle, E.**, **Kalisz, S.**, **Cheptou, P.-O.**, **Eckert, C.G.**, **Goodwillie, C.**, **Johnston, M.O.**, **Moeller, D.A.**, **Ree, R.H.**, **Sargent, R.D. and Vallejo-Marin, M.** (2011) Analysis of inbreeding depression in mixed-mating plants provides evidence for selective interference and stable mixed mating. *Evolution* **65**, 3339–3359.

Wolfe, L.M. (1993) Inbreeding depression in *Hydrophyllum appendiculatum*: role of maternal effects, crowding, and parental mating history. *Evolution* **47**, 374–386.

Wyatt, R. (1983) Reproductive biology of the granite outcrop endemic *Sedum pusillum* (Crassulaceae). *Systematic Botany* **8**, 24–28.