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REVIEW ARTICLE

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.

Keywords: dormancy-breaking/germination procedures, endemic species, heterosis, magnitude of inbreeding depression, maternal environmental effects, outbreeding depression, outcrossing distance, seed mass

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

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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:

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

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. [$(\delta_{\text{field}}/\delta_{\text{greenhouse}}) \geq 1.0$ (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; Hiraio, 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 $\delta_{\text{germination}}$ 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 Loeschke, 1995, 1996; Nason and Ellstrand, 1995; Durel *et 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; Hiraio, 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 $\delta = 0.24$), or late, during growth/reproduction ($\delta = 0.25$), but rarely during germination ($\delta = 0.12$), or juvenile survival ($\delta = 0.15$).’
- **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 Loeschke, 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; Dahlgard 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 $1 - (\Delta y/\Delta x) (= 1 - e^{-BF})$.

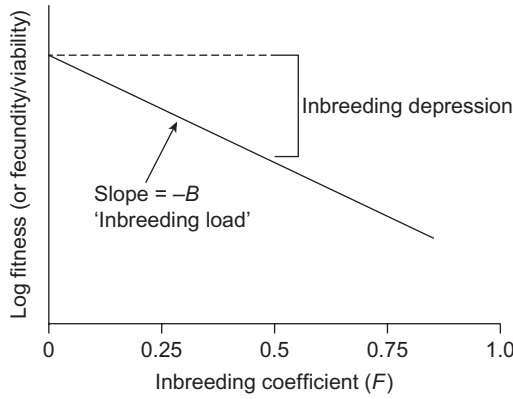


Figure 1. Theoretical decline in fitness (increase in inbreeding depression, δ) with increase in inbreeding coefficient (F). The inbreeding coefficient of progeny of randomly outbred plants ($F = 0$) will be 0.5 after one generation of selfing. From Keller and Waller (2002), with permission.

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_0) 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
<i>Amsinckia</i> (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
<i>Atriplex tatarica</i>	Negative correlation between F and both first-day and final germination percentage of the two diaspore morphs of this heterocarpic species.	Kochánková 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 $S_0 \rightarrow S_5$.	Godoy <i>et al.</i> , 2006
<i>Campanula thyrsooides</i>	F values (0.00–0.25) did not have an effect on germination percentage.	Aegisdóttir <i>et al.</i> , 2007
<i>Chamerion</i> (<i>Epilobium</i>) <i>angustifolium</i>	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
<i>Clarkia tembloriensis</i>	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%.	Holtford, 1996
<i>Collinsia heterophylla</i>	For four populations, germination percentage declined linearly with an increase in F from 0.00 to 0.75.	Mayer <i>et al.</i> , 1996
<i>Crepis sancta</i>	F (0.00–0.25) had no effect on germination of central achenes of this achene-heterocarpic species (peripheral achenes not tested).	Cheptou <i>et al.</i> , 2000a
<i>Cucurbita pepo</i> var. <i>texana</i>	Germination percentage exhibited a negative-linear decline from c. 48% at $F = 0.00$ to c. 40% at $F = 0.875$.	Hayes <i>et al.</i> , 2005a, b
<i>Epilobium obcordatum</i>	Negative relationship between germination percentage and F (0.00–0.35).	Seavey and Carter, 1994
<i>Gilia achilleifolia</i>	$S_0(F = 0) < [S_1(0.50) = S_2(0.75)]$; 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
<i>Impatiens capensis</i>	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 <i>et al.</i> , 1994
<i>Lychnis flos-cuculi</i>	Germination percentage decreased with increase in F from 0.00 to 0.75.	Hauser and Loeschcke, 1995
<i>Lychnis flos-cuculi</i>	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
<i>Mimulus guttatus</i>	No directional change in germination percentage with increase in F from 0.00 to 0.75.	Willis, 1993a
<i>Plantago coronopus</i>	Germination was not significantly affected by F values of 0.00–0.876.	Koelewijn, 1998
<i>Plantago coronopus</i>	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
<i>Raphanus sativus</i>	F values of 0.00–0.25 had no effect on germination.	Nason and Ellstrand, 1995
<i>Rhododendron</i> <i>brachycarpum</i>	No relationship between germination percentage and parental kinship coefficient (parental relatedness).	Hirao, 2010
<i>Sidalcea oregana</i> subsp. <i>spicata</i>	Level of inbreeding (outcross, sib-cross, self) had no significant effect on germination.	Ashman, 1992
<i>Silene alba</i> (= <i>S. latifolia</i>)	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
<i>Silene latifolia</i>	Seeds with <i>F</i> values of 0.00, 0.375 and 0.590 germinated to 83.1%, 83.9% and 91.4%, respectively.	Ouborg <i>et al.</i> , 2000
<i>Swainsonia recta</i>	Percentage germination was lower in populations with high than with medium and low <i>F</i> values.	Buza <i>et al.</i> , 2000
<i>Trifolium hirtum</i>	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
<i>Vaccinium corymbosum</i> and <i>V. ashei</i>	No significant relationship between germination percentage and <i>F</i> .	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. resinatum* (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
<i>Arnica montana</i>	No correlation between germination percentage and genetic diversity.	Luijten <i>et al.</i> , 2000
<i>Campanula glomerata</i>	No correlation between germination percentage and genetic diversity; non-germinated seeds were non-viable.	Bachmann and Hensen, 2007
<i>Clarkia pulchella</i>	Germination was significantly higher in populations with high than in those with low genetic effective size.	Newman and Pilsen, 1997
<i>Embothrium coccineum</i>	Germination percentage was significantly negatively correlated with log-transformed forest fragment size, which was positively, but not significantly, correlated with gene diversity.	Mathiasen <i>et al.</i> , 2007
<i>Gentiana pneumonanthe</i>	No correlation between germination percentage and population genetic diversity, although seed mass was positively correlated with heterozygosity.	Oostermeijer <i>et al.</i> , 1994
<i>Gentianella austriaca</i>	Percentage germination was highest in populations with highest genetic diversity.	Greimler and Dobeš, 2000
<i>Lychmis viscaria</i>	No correlation between percentage germination and genetic diversity.	Lammi <i>et al.</i> , 1999
<i>Mercurialis perennis</i>	No correlation between germination percentage and genetic diversity.	Vandepitte <i>et al.</i> , 2009
<i>Pedicularis palustris</i>	Number of seedlings per flowering plant was significantly higher in populations with higher genetic diversity.	Schmidt and Jensen, 2000
<i>Ranunculus reptans</i>	No significant relationship between germination percentage and long-term population size as measured by allelic diversity.	Willi <i>et al.</i> , 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):

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

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 ($WP_{\text{very far}}$) distances within populations, and populations within (WR) and between (BR) regions. The results of these studies are as follows: $WP_{\text{near}} = WP_{\text{far}} = WP_{\text{very far}}$ (*Hymenoxys acaulis*) (Moran-Palma and Snow, 1997); $WP_{\text{near}} > WP_{\text{far}} = BP$ (*Eupatorium perfoliatum*, *E. resinosum*) (Byers, 1998); $WR = BR$ (*Anthericum liliago*, *A. ramosum*) (Rosquist, 2001); $WP_{\text{near}} = WP_{\text{far}}$ (for each of two populations of *Hypericum cumulicola*) (Trager *et al.*, 2005); $(WP = BR) > BP$ (*Hypochoeris radicata*) (Becker *et al.*, 2006); $(WP_{\text{far}} = BP) > WP_{\text{near}}$ (*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.

$$\text{CRF} = (W_{s1}/W_{o1}) \times (W_{s2}/W_{o2}) \\ \times (W_{s3}/W_{o3}) \dots (W_{sx}/W_{ox})$$

$$1 - \text{CRF} = \text{total inbreeding depression.}$$

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_0) (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.
-

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

Table 5. Continued

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

Table 5. Continued

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

Table 5. Continued

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

Table 5. Continued

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

Table 5. Continued

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

hand, we found many cases of $RP \leq 0.10$ 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 ≥ 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; Belaousoff 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 outcrossing 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 $\{\delta = 1 - (\text{mean of selfed progeny})/(\text{mean of [legitimate] progeny})\}$ 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 $\geq 70\%$ 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 (KNO₃) and gibberellin (GA). NO₃⁻ 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 ($1 - \text{CRF}$) 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 [$(I < O) < (I = O) \gg (I > O)$].
- 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 GA₃ 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; Clausen 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.

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