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REVIEW

Seed germination of gynodioecious species: theoretical considerations and a comparison of females and hermaphrodites

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Abstract

Main conclusion **Better seed germination of females than of hermaphrodites is not a major contributor to the greater geometric lifetime fitness that females require to be maintained in a gynodioecious population.**

Abstract Gynodioecy is a sexually dimorphic breeding system in which females (F, male sterile) and hermaphrodites (H) coexist in the same population. For plants with nuclear (biparental) inheritance of male sterility, theory predicts that except when the product of selfing rate (s) and inbreeding depression (δ) in H is high ($s\delta > 0.50$), F must compensate (female advantage) for the loss of gene transmission via pollen production by producing more or higher-quality offspring than H to be maintained in the population. For species with cytoplasmic (maternal) inheritance of male sterility, the female requires only a small compensation in seed production or some other offspring fitness trait to persist. Reallocation to seeds of resources saved by loss of pollen production is expected to increase the quantity (number) and/or quality (mass, germinability) of seeds produced by F, thus compensating for the lack of pollen production. The primary aim of our study was to compare seed germination of F and H via a literature review. Based on theoretical considerations, we hypothesized that seeds of F should germinate better or equally as well as those of H. We found that of 235 case studies for 47 species $F_{germ} > H_{germ}$ in 48.1%, $F_{germ} = H_{germ}$ in 38.3% and $F_{germ} < H_{germ}$ in 13.6%. Our results are very similar to those of a previously published meta-analysis that included germination of F and H for 12 species. For 162 cases on seed size, F > H in 29.0%, F = H in 63.6% and F < H in 7.4%. Since $[(F_{germ} > H_{germ}) < (F_{germ} \leq H_{germ})]$ and $[(F_{seedsize} > H_{seedsize}) < (F_{seedsize} \leq H_{seedsize})]$, these results suggest that seed quality is not a major fitness component of female advantage.

Keywords Cytoplasmic male sterility · Female advantage · Inbreeding depression · Nuclear male sterility · Reallocation of resources · Seed germination · Seed production · Self-pollination

Introduction

Gynodioecy refers to the coexistence of genetically-determined females (F, male sterile) and hermaphrodites (H) in the same natural interbreeding population (Darwin 1897; Yampolsky and Yampolsky 1922; Lewis 1941; Kaul 1988; Sakai and Weller 1999; Delph et al. 2007; Dufay and Billard 2012). It is the first stage in the gynodioecy pathway from hermaphroditism to dioecy. However, it is not found in all routes from hermaphroditism to dioecy (Arroyo and Raven 1975; Bawa 1980; Charlesworth 1999; Webb 1999; Ashman 2002, 2006; Barrett 2002; Wagner et al. 2005; Ehlers and Bataillon 2007; Spigler and Ashman 2012; Dufay et al. 2014). Gynodioecy is fairly common and taxonomically widespread in angiosperms, and it occurs in eumagnoliids, monocots and eudicots (Dufay et al. 2014). Various estimates of the number of gynodioecious taxa include: 1126 species in 89 families (Godin and Demayanova 2013), 81 of 449 families (Dufay et al. 2014), at least one species in 275 (1.9%) of 14,550 genera (Renner 2014) and 1325 species in 91 families and 36 orders (Caruso et al. 2016). For Hawaii, Sakai et al. (1995) reported that 36 of 971 (3.7%)

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native species of angiosperms are gynodioecious; 23 of these are species of *Bidens* (Asteraceae) or *Hedyotis* (Rubiaceae).

Although some gynodioecious populations consist of pure females (male-sterile) and pure hermaphrodites (McCusker 1962; Jordano 1993; Manicacci et al. 1998; Williams et al. 2000; McCall and Barr 2012), intermediates or a continuum of intermediates between pure females and pure hermaphrodites often are present in the population (Fig. 1). For example, there are many reports of gynomonoecious (perfect flowers + female flowers on the same individual) plants in populations labelled gynodioecious (Baker 1966; Dulberger and Horovitz 1984; Wolff et al. 1988; Klinkhamer et al. 1991; Maurice 1999; Collin and Shykoff 2003; Guitián and Medrano 2000; Lafuma and Maurice 2006; Collin et al. 2009; Dufay et al. 2010). In some studies, gynomonoecious individuals are considered to be a third mating system, whereas in others, they are considered to be hermaphrodites. Various authors have referred to populations consisting of three sex types (i.e. females, gynomonoecious and hermaphrodites) as being gynnodiocious–gynomonoecious (Jolls and Chenier 1989; Desfeux et al. 1996; Collin et al. 2002, 2009; Collin and Shykoff 2003; López-Villavicencio et al. 2005; Dufay et al. 2010; Casimiro-Soriguer et al. 2015). In some sexually dimorphic species, males and females deviate from strict sexually to various degrees, thus forming a continuum of gender maleness and of gender femaleness. These deviants are sometimes referred to as *inconstant males* or *inconstant females*, with inconstant males being more common than inconstant females, i.e. population consists of inconstant males and constant females (e.g. Lloyd 1976; Webb 1999; also see other papers listed after following sentence). Quantitative methods for describing the distribution of gender dimorphism (maleness and femaleness) among individual plants in a population are described by Lloyd (1976, 1979, 1980), Primack and Lloyd (1980), Webb (1981a, b, 1999), Lloyd and Bawa (1984), Pickering and Ash (1993; Maurice et al. 1998).

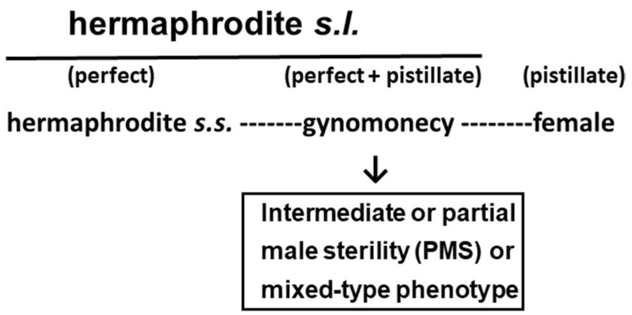

Fig. 1 Conceptual model of gender types in gynodioecious-gynomonoecious populations. Populations of many so-called gynodioecious species are composed of three distinct gender types: hermaphrodites sensu stricto with perfect flowers only; gynomonoecious individuals with perfect and pistillate flowers; and females with pistillate flowers only. Furthermore, the proportion of perfect and pistillate flowers on an individual may vary along a continuum from 100% perfect flowers in pure hermaphrodites to 100% pistillate flowers in pure females. Gynomonoecious individuals are sometimes referred to as “intermediates” or “mixed-type phenotypes.” Some studies on gynodioecy have considered gynomonoecious individuals as hermaphrodites

Mutations (disruption of microsporogenesis and pollen development) responsible for male sterility can be nuclear (biparental transmission, Mendelian inheritance) or only maternally inherited (cytoplasmic male sterility, CMS) (e.g. Lewis 1941; Delph et al. 2007). Mutations of CMS are maternally inherited (via mitochondria), and thus loss of pollen production does not reduce the transmission of cytoplasmic genes. The effect of mutations for CMS can be counteracted by nuclear restorer genes (Bailey and Delph 2007; McCauley and Bailey 2009; Case and Caruso 2010; De Cauwer et al. 2012; Dufay and Billard 2012). Because of the maternal inheritance, mutations leading to loss of the male function (i.e. pollen production) do not influence the cytoplasmic (mitochondrial) genes. Therefore, F resulting from CMS only need a small fitness advantage over the original H (H in population before appearance of F) to invade and persist in a population of H (Lloyd and Bawa 1984). However, the cost (see De Cauwer et al. 2012) is considerable in nuclear male sterility (NMS) because the biparental transmission of nuclear genes is reduced (Lewis 1941; Dufay and Billard 2012).

Because their male fitness is reduced to zero, male-sterile (F) individuals are at a selective disadvantage compared to H in gynodioecious populations. That is, F contribute to their offspring (next generation) via ovules only, whereas H contribute to their offspring via both pollen and ovules. In which case, F must counteract the selective disadvantage of lack of pollen production to be maintained in the population (see e.g. Sun and Ganders 1986). Thus, theory predicts that F fitness should be higher for at least one fitness trait than for H, such as producing more or better quality of seeds, in order for male sterility to be maintained in the population. F also can gain fitness if the product of selfing rate (s) and inbreeding depression (δ) is > 0.0 in H. Some theoretical aspects of persistence of F with *nuclear inheritance* in a gynodioecious species are discussed in the following section.

One fitness trait that has been measured for F and H in numerous studies on gynodioecy is seed germinability. Previous reviews by Shykoff et al. (2003) and Dufay and Billard (2012) on gynodioecious species compared various characteristics of F and H, including seed germination (Appendix 1). However, these two studies (combined) included only 32 case studies (24 species) in which seed germination of F and H was compared, whereas our review for the seed germination stage of the life cycle includes 235 case studies (for 47 species). The primary purpose of this review paper is to compare seed germination of F and H reported in the literature. In other words, the question addressed is: How does the evolutionary transition from male fertility to male sterility affect seed germination?

In tabulating the results of comparisons of F_{germ} vs. H_{germ}, we did not consider the effects of various factors that could have influenced the outcome, such as inbreeding depression in H (or biparental inbreeding depression in F) and mechanism of inheritance (nuclear or nuclear-cytoplasmic) of male sterility, Thus, our results are irrespective of factors influencing seed germination except sex of the plant, i.e. F or H. Our primary aim was to quantify the influence of plant sex on seed germination using the three categories F > H, F = H and F < H.

Theoretical background

To invade a population of hermaphrodites (H), or to persist in the population at frequencies greater than that which can be maintained by mutations for male sterility alone, females (F, male sterile) must compensate ('reproductive compensation' sensu Darwin 1897) for not fathering offspring (i.e. due to loss of viable pollen production) by producing more and/or better quality seeds during their lifetime than the original H (Darwin 1897; Lewis 1941; Charlesworth and Charlesworth 1978, 1981; Charlesworth 1999). Compensation (female advantage) must occur via increased survival, increased female function and/or avoidance of inbreeding depression that occurred in the original H for F to invade and be maintained in the population (Charlesworth and Charlesworth 1978, 1981; Koelewijn 1996; Charlesworth 1999). Female advantage can include differences between F and H (i.e. F > H) in fruit number, fruit set (fruits flower^{-1}), seed set (seeds ovule^{-1}), seeds fruit^{-1}, seeds plant^{-1}, seed mass or size and/or *seed germination* percentage/rate (Shykoff et al. 2003; Dufay and Billard 2012).

Here, we provide a basic theoretical background for a general understanding of the requirements of F with *nuclear (Mendelian) inheritance* for male sterility to persist in an H population. In particular, seed biologists and others not acquainted with gynodioecy and its occurrence in sexually dimorphic plant populations will gain an appreciation of how seed fitness [seed number and/or seed quality (germinability and resulting seedling vigor)] play(s) a role in the invasion and maintenance of F in gynodioecious populations. The examples discussed below are based only on seed number (i.e. seed fitness is the number of seeds produced), thus assuming that F and H seeds have equal chances of success in producing mature plants. Furthermore, it is assumed that seed production by (original) H does not decrease when the hermaphrodite population becomes gynodioecious (i.e. no reallocation of resources from seed production to pollen production) after the appearance of females. At least in some gynodioecious populations, H eventually may be selected to contribute more genes via pollen than ovules, i.e. < 50% of the genetic contribution of H is via seeds and > 50% via pollen. That is, high frequencies of femaleness may select for maleness by decreasing fruit (seed) production (see Lloyd 1974; Wagner et al. 2005).

For F with *nuclear male sterility* to invade an H population, the relationship between reallocation of resources saved from loss of pollen production by F to seed fitness, i.e. increase in seed production by female relative to the original hermaphrodite (k), selfing rate (s) and inbreeding depression (δ) in H is shown by the following inequality (Charlesworth and Charlesworth 1978).

$$1 + k > 2(1 - s\delta). \tag{1}$$

Regardless of the selfing rate (0–100%, i.e. $s = 0$–1) of H, when inbreeding depression is zero, or regardless of the magnitude (0–1) of inbreeding depression when selfing is zero (in both cases $s\delta = 0$), F must produce > 2 × the number of seeds (seed production by female = $1 + k$) relative to seed production by the original H to invade the population. In other words, F must increase seed production (k) by more than 100% (i.e. $k > 1.0$) when $s\delta = 0$, as shown by the following inequality (Charlesworth and Charlesworth 1981; Charlesworth 1999).

$$k > 1 - 2s\delta. \tag{2}$$

When selfing ($s > 0$) and inbreeding depression ($\delta > 0$) in original H are greater than zero (i.e. $s\delta > 0$), F can invade/persist in the population by increasing seed production < 100% (i.e. $k < 1$), and thus by producing < 2 × the number of seeds as the original H. Furthermore, F even can invade an H population by producing the same number of seeds as the original H if $s\delta > 0.50$. Thus, in the absence of reallocation of resources ($k = 0$) saved by the lack of pollen production to ovules (seeds) by F in an H population, $s\delta$ must be > 0.50 for F to invade an H population.

The proportion (p) of F at equilibrium in gynodioecious populations varies (sometimes greatly) between populations (Connor 1963; Stevens and Richards 1985; Wolff et al. 1988; Widen 1992; Koelewijn and Van Damme 1996; Wolfe and Shmida 1997; Gigord et al. 1998; Thompson and Tarayre 2000; Williams et al. 2000; Olson et al. 2005; Nilsson and Ågren 2006; Dufay et al. 2009; Adhikari et al. 2019); sites (patches) within populations (Kohn 1989; Dinnétz and Jerling 1998; Graff 1999; Nilsson and Ågren 2006; McCauley and Bailey 2009); age (successional stage) of colonizing population (Belhassen et al. 1989; Manicacci et al. 1996); ecology (abiotic and biotic factors and their interactions, including along environmental gradients, i.e. "ecological context" sensu Ashman 2006) (Darwin 1897; Krohne et al. 1980; Delph 1990; Wolfe and Shmida 1997;

Delph and Carroll 2001; Ashman 2002, 2006; Collin et al. 2002; Barr 2004; Case and Barrett 2004; Vaughton and Ramsey 2004; Doubleday and Adler 2017) [However, see Svoen et al. (2019) who found that female frequency in *Silene acaulis* in the high Arctic did not differ between closed and open habitats, i.e. female frequency was not influenced by density of the vegetation.]; and years and seasons (Kikuzawa 1989; Ashman 1999; Klinkhamer et al. 1991; Molina-Freaner and Jain 1992; Williams et al. 2000; Koelewijn and Van Damme 1996). p can be estimated by the following equation (Marshall and Ganders 2001):

$$p = \frac{(1 - 2f + 2fs\delta)}{(2 - 2f + 2fs\delta)}, \quad (3)$$

where f is seed production of H relative to seed production by F (i.e. H/F ratio), and s and δ are as defined above. Thus, the frequency of F increases as s and δ increase or as f decreases.

When $s\delta = 0$, F must produce > 2 × the number of seeds as H to be maintained at equilibrium in the population. For example, when H/F (relative seed production) = 0.50 $p = 0\%$ (i.e. F produces 2 × the number as H), and when H/F = 0.49 (i.e. F produces 2.04 × the number of seeds as H) $p = 2\%$. When $s\delta > 0.50$, F can be maintained at equilibrium in the population by producing the same number of seeds as H (i.e. $f = 1.0$). For example, when $s\delta = 0.50$, $p = 0\%$, and $s\delta = 0.51$, $p = 2\%$.

Materials and methods

To compare seed germination of F and H, we used the relative performance (RP) index:

$$\mathrm{RP} = \left(W_F - W_H\right)/W_{\max}\left[W_F \text{ or } W_H\right], \quad (4)$$

where W_F and W_H are the germination percentages or rates (speed) of F and H, respectively, and $W_{\max}$ the highest of the two values. Values for RP range from − 1 to 1. A positive value indicates that F germinated to a higher percentage or rate than H and a negative value that H germinated to a higher percentage or rate than F. The closer the value is to 1.0 (W_F) or − 1.0 (W_H), the greater the RP between F and H, respectively. When $W_F = W_H$, RP = 0, i.e. F and H germinated to the same percentage or rate. We used three categories in comparing germination of F and H: F > H, F = H and F < H. For assignment to F > H, RP had to be ≥ 0.10, and for assignment to F < H, RP had to be ≤ − 0.10, i.e. − 0.10 or more negative than − 0.10. Thus, RP values between − 0.10 and 0.10 were used for assignment to the F = H category.

These three categories were arbitrarily chosen and may or may not be concordant with results of statistical tests by the author(s) of the respective papers. For example, an RP of 0.11 indicates that $F_{germ} > H_{germ}$, whereas the statistical test used by the authors (Ramsey and Vaughton 2002; see "Appendix 2") indicated that germination percentage of seeds of F and H did not differ significantly (i.e. $F_{germ} = H_{germ}$). On the other hand, a small difference in germination percentage of F and H may differ statistically but not differ based on the limits we set for RP. For example, in a study by Dalton et al. (2013; see "Appendix 2"), F seeds of *Fragaria vesca* germinated to 97% and outcrossed seeds of H (H_{ox}) to 93% ($p < 0.05$; i.e. F > H), whereas RP = (97 − 93)/97 = 4/97 = 0.04, i.e. F = H_{ox}. See "Appendix 2" for the results of additional comparisons of agreements/disagreements of our results using RP and those of authors of respective papers using statistical tests.

We define a case study as a treatment combination comparing germination of F and H. For example, comparing germination of F and H of a species from each of five populations in each of 2 years would give ten case studies (5 populations × 2 years). Considering the variation that can occur in germination (and other plant functional traits) across, for example, years, genotypes and populations as well as interactions among the three effects, results of case studies would seem to be more representative of the reality of the outcome of F vs. H. than averages across years, genotypes and/or populations.

Results and discussion

We identified 235 case studies of F vs. H in a total of 47 species in 34 genera and 23 families (three monocots, 20 eudicots) (Table 1). The species, genus and family with the most case studies were *Thymus vulgaris* (42), *Silene* (64) and Caryophyllaceae (85), respectively. There are 32 case studies for *Silene acaulis* and 31 for *S. vulgaris*. A diversity of sexual systems occurs in the genus *Silene*, and thus it is a model system for the study of reproductive systems in plants (Desfeux et al. 1996; Bernasconi et al. 2009; Casimiro-Sorguer et al. 2015). For germination, F > H in 113 of the 235 case studies in which F and H were compared, F = H in 90 and F < H in 32. Thus, the (F > H):(F = H) ratio is 1.26, (F > H):(F < H) ratio 3.53 and (F = H):(F < H) ratio 2.81. Furthermore, the [(F > H) + (F = H)]:(F < H) ratio is 6.34, and the (F > H):[(F = H) + (F < H)] ratio is 0.93. A main point here is that $F_{germ} > H_{germ}$ in < 50% of the case studies.

There are 11 species entries in Table 1 for which all of the two or more case studies (two to eight per species entry, total = 33) are F > H. However, there is only one species entry for which all of the case studies (two, and thus total = 2) are F < H. For eight species entries, all of the two or more case studies (two to 22 per species entry, total = 49), F = H. Thus, 20 of the species entries showed uniformity within species between case studies, whereas 21 did not (Table 1).

Table 1 Comparison of the germination of seeds produced by females and hermaphrodites (235 case studies)

Family/species	Germination	References
Amaranthaceae		
Beta vulgaris ssp. *maritima*	$[F_{cms}=H_{restored\ cms}\ (1);\ F_{cms}=H_{non\text{-}cms}\ (1)]$	De Cauwer et al. (2011)
Apicaceae		
Gingidia montana	[F = H (1)] F = (inconstant) male	Webb (1981a)
Scandia geniculata	[F < H (1)] F < (inconstant) male	Webb (1981b)
Asteraceae		
Bidens sandvicensis	$[F_{open}>H_{open}\ (1),\ F_{open}=H_{ox}\ (1),\ F_{open}>H_{s}\ (1)]$	Schultz and Ganders (1996)
Cirsium arvense	[F > H (1)]; F > (inconstant) male	Lloyd and Myall (1976)
Cirsium arvense	[a][F > H (1)]; F > (inconstant) male	Kay (1985)
Boraginaceae		
Echium vulgare	[F = H (1)]	Klinkhamer et al. (1994)
Eritrichium aretioides	[F > H (1)]	Puterbaugh et al. (1997)
Phacelia dubia	[F < H (1)]	del Castillo (1993)
P. linearis	[F > H (8), F = H (2), F < H (6)]	Eckhart (1992a, b)
Brassicaceae		
Raphanus sativus	$[F_{cms}=H_{cms}\ (1),\ F_{cms}<H_{non\text{-}cms}\ (1)]$	Miyake et al. (2009)
Cactaceae		
Pachycereus pringlei	[F = H (1)]	Fleming et al. (1994)
P. pringlei	$[F=H_{ox}\ (1),\ F=H_{s}\ (1)]$	Sosa and Fleming (1999)
Campanulaceae		
Lobelia siphilitica	$F_{lineages}=H_{lineages}$	Mutikainen and Delph (1998)
L. spicata	[b][F > H (4); F < H (5)]	Ruffatto et al. (2015)
Caryophylaceae		
Dianthus sylvestris	[F = H (1)]	Collin et al. (2002)
Gypsophila repens	$[F<H_{ox}\ (2)]$	López-Villavicencio et al. (2005)
Minuartia obtusiloba	$[F=H_{ox}\ (1),\ F>H_{s}\ (1),\ F=H\ (1),\ F>H\ (3)]$	Schrader (1986)
Schiedea adamantis	[F > H (2)]	Sakai et al. (1997)
S. salicaria	[F > H (8)]	Weller and Sakai (2005)
Stellaria longipes	[F = H (1)]	Philipp (1980)
Silene acaulis	$[F=H_{ox}\ (1),\ F=H_{s}\ (1)]$	Shykoff (1988)
S. acaulis	[F = H (2)]	Delph and Mutikainen (2003)
S. acaulis	$[F=H_{ox}\ (8),\ F=H_{s}\ (8),\ F_{ox}=H_{s}\ (1),\ F_{FS}=H_{s}\ (1),\ F_{HS}=H_{s}\ (1),\ F_{ox}=H_{ox}\ (1),\ F_{FS}=H_{ox}\ (1),\ F_{HS}=H_{ox}\ (1)]$	Delph (2004)
S. acaulis	$[F>H_{ox}\ (2),\ F=H_{ox}\ (1),\ F>H_{s}\ (3)]$	Keller and Schwaegerle (2006)
S. nutans	[F = H (1)]	Dufay et al. (2010)
S. vulgaris	$[F<H_{ox}\ (1),\ F>Hs\ (1)]$	Jolls and Chenier (1989)
S. vulgaris	[F = H (11)]	McCauley and Brock (1998)
S. vulgaris	[F > H (2), F = H (2)]	Taylor et al. (1999)
S. vulgaris	[F > H (1)]	McCauley et al. (2000)
S. vulgaris	$[F>H_{ox}\ (6),\ F=H_{ox}\ (2),\ F<H_{s}\ (2)]$	Emery and McCauley (2002)
S. vulgaris	[F > H (2)]	Olson et al. (2006)
S. vulgaris	[F = H (1)]	Miyake and Olson (2009)
S. vulgaris subsp. *maritima* var. *petraea*	[F = H (1)]	Pettersson (1992)
Celastraceae		
Euonymous europaeus	[c][F = H (1)]	Webb (1979)
Celastraceae		
Wurmbea biglandulosa subsp. *biglandulosa*	[F > H (3)]	Ramsey and Vaughton (2002)

Table 1 (continued)

Family/species	Germination	References
Ericaceae		
Leucopogon melaleucoides	[d][F = H (1)]	McCusker (1962)
Fabaceae		
Trifolium hirtum	[F = H (4)]	Molina-Freaner and Jain (1992)
Geraniaceae		
Geranium maculatum	[F = H (1), F < H (1)]	Chang (2006)
G. maculatum	[F > H (2)]; $F_{lineages} > H_{lineages}$	Chang (2007)
G. sylvaticum	[F > H (1), F < H (1)]	Vaarama and Jääskeläinen (1967)
G. sylvaticum	[F > H (1)]	Asikainen and Mutikainen (2003)
G. sylvaticum	[F = H (1)]	Ramula et al. (2007)
Iridaceae		
Iris douglasiana	[e][F = H (1)]	Uno (1982)
Lamiaceae		
Thymus mastichina	[F > H (3), F = H (1), F < H (2)]	Manicacci et al. (1998)
T. vulgaris	[F > H (1), F > H_{ox} (1), F > Hs (1)]	Assouad et al. (1978)
T. vulgaris	[f][F > H (2), F = H (2), F < H (2)]	Bonnemaison et al. (1979)
T. vulgaris	[F > H (6), F < H (1)]	Dommée and Jaquard (1985)
T. vulgaris	[g][F > H (5)]	Couvet et al. (1986)
T. vulgaris	[h][F > H (1), F < H (1)	Belhassen et al. (1989)
T. vulgaris	[F > H (5), F = H (1)]	Manicacci et al. (1998)
T. vulgaris	[F > H (1)]	Gigord et al. (1999)
T. vulgaris	[F > H (11), F < H (1)]	Thompson and Taratye (2000)
T. zygis	[F > H (4), F = H (1), F < H (1)]	Manicacci et al. (1998)
Malvaceae		
Sidalcea hendersonii	[F > H_{ox} (1), F > H_{s} (1)]	Marshall and Ganders (2001)
S. oregana subsp. *spicata*	[F > H (1), F = H (1)]	Ashman (1992)
Onagraceae		
Fuchsia excorticata	[F = H_{ox} (1),F = H_{s} (2), F < H_{ox} (1)]	Robertson et al. (2011)
Plantaginaceae		
Plantago coronopus f. *pygmaea*	[F > H (3), F = H (4), F < H (1)]	Schat (1981)
P. coronopus	[F = H_{ox} (2), F = H_{s} (2)	Koelewijn and Van Damme (2005)
P. lanceolata	[F = H (1)]	van Damme and Van Delden (1984)
P. maritima	[F < H (1)]	Dinnétz and Jerling (1997)
P. maritima	[I][F > H(1)]	Dinnétz and Jerling (1998)
Poaceae		
Cortaderia richardii	[F > H (1), F = H (1)]	Connor (1965)
C. richardii	[F > H (1)]	Connor (1973)
C. selloana	[F > H (1)]	Connor (1973)
Resedaceae		
Ochradenus baccatus	[j][F > H (1)]; F > (inconstant) male	Wolfe and Shmida (1997)
O. baccatus	[F > H (2)]	Wolfe and Burns (2001)
Rosaceae		
Fragaria vesca subsp. *bracteata*	[F = $H_{ox,}$ (1)]	Dalton et al. (2013)
Prunus mahaleb	[F = H (1)]	Jordano (1993)
Saxifragaceae		

Table 1 (continued)

Family/species	Germination	References
Saxifraga granulata	[F > H (2)]	Stevens 1988)
Thymelaeaceae		
Daphne laureola	[F > H_{ox}(1), F > H_s (1)]	Alonso and Herrera (2001)

Number of case studies is shown in parentheses

F female (male-sterile), F_{FS} female germinated from full-sib offspring seeds, F_{HS} female germinated from half-sib offspring seeds, *H* hermaphrodite, H_{ox} hermaphrodite outcrossed, H_s hermaphrodite selfed, *inconstant male* produces some seeds but most of fitness is via pollen production (see text for a more detailed explanation), *cms* cytoplasmic male sterility, *non-cms* hermaphrodite that does not have cms, *restored cms* hermaphrodite has been restored from female via interaction of cms and nuclear restorer genes

[a] Germination without 'seed coat'; seed coat removed. Germination of intact seeds was low in all samples

[b] In 13 of 22 case studies (11 populations × 2 years), germination ranged from 0% to *c*. 12% for F and from 0% to *c*. 6% for H. Since the germination percentages were low for both F and H in these 13 cases, we did not include them in our tabulations for germination of F vs. H. In the other nine cases (shown here), the highest germination in a case study (i.e. comparison of germination percentages for a given year and population) was 31.5–64.0%. Thus, in all of these nine comparisons for F and H germination was ≥ 31.5% for one or the other of the pair

[c] No seeds of either F or H germinated. Webb (1979) stated that "…attempts to germinate seeds from male and female plants were completely unsuccessful."

[d] McCusker stated that, "Several attempts to germinate seeds dissected from ripe fruits were unsuccessful." However, the tetrazolium test indicted that "… all the embryos stained brightly after 15 h." Thus, the seeds were viable but dormant

[e] Only 5 of 500 viable seeds (tetrazolium test) germinated "under a variety of test conditions."

[f] Based on [(number of established seedlings) / (number of seeds sown)] × 100

[g] Based on F producing 3.1 to 12.4 more germinating seeds than H in three populations in 1978 and in one population in 1978 and 1982, i.e. $(3\times 1) + (1\times 2) = 5$

[h] Based on [(number of "viable" (i.e. germinated) seeds per plant)/(total number of seeds per plant)]. Authors assumed that nongerminated seeds were not viable; however, they did not test viability. We suggest that the nongerminated seeds could have been dormant. The conditions under which the seeds were germinated (temperature, light, etc.) were not specified. Belhassen et al. (1989) merely state (caption for their Table 5) that "Numbers of viable [i.e. germinated] seeds per plant were determined by germinating the seeds in petri dishes."

[i] Based on percentage of seedlings that germinated from seeds of F and H dispersed different distances (i.e. 0.1–0.8 m) from seed source, i.e. F succeeded in establishing more seedlings per m^{-2} than did H

[j] Germination did not differ among the six populations, presumably germination did not differ for F or for H among the six populations

Our results for germination of F vs. H agree well with analyses by Shykoff et al. (2003) and Dufay and Billard (2012) on gynodioecious species (Appendix 1). Of the 47 species for which we compared germination of F and H, germination of 12 of them was included in the analysis by Shykoff et al. (2003) and 17 in the analysis by Dufay and Billard (2012). Altogether, germination of F and H of 24 of the 47 species (51.1%) in our survey was compared in the two analyses. For the 32 cases of seed germination reported in the two analyses combined, 40.6%, 50.0% and 9.4% were in the categories F > H, F = H and F < H, respectively, which compares fairly well with our 48.1, 38.3% and 13.6%, respectively, for the three categories in 235 cases. Percentages for the meta-analysis by Shykoff et al. (2003) were 46.2, 38.5 and 15.4, respectively, and for the analysis by Dufay and Billard (2012) 36.8, 57.9 and 5.3, respectively. In particular, the results of the meta-analysis by Shykoff et al. (2003) are very similar to our results.

Size/mass is another seed trait that often differs between F and H in gynodioecious species. Shykoff et al. (2003) reported 17, 10 and 2 cases of seed size in which F > H, F = H and F < H, respectively, and Dufay and Billard (2012) 14, 9 and 1, respectively. We sorted out 162 cases for seed size from 61 published papers including one Ph.D. thesis (Ågren and Willson 1991; Barrett et al. 1999; Delph et al. 1999; Molina-Freaner et al. 2003; Ramula and Mutikainen 2003; Schultz 2003; Van Etten et al. 2008; Varga 2014; Varga et al. 2015; plus

Table 2 A matrix table of 42 case studies on seed size vs. germination of females (F) and hermaphrodites (H)

Seed size	Germination		
	F > H	F = H	F < H
F > H	6, 5	11, 3	0, 0
F = H	1, 2	2, 4	1, 1
F < H	1, 0	0, 2	2, 1

First number is based on Shykoff et al. (2003) or Dufay and Billard (2012) and second number on other literature cited in present study references marked with an asterisk in "References"). Based on results of seed size categories determined by the same procedure used to assign seed germination of F vs. H to the three categories (see "Materials and methods"), our results for seed size are as follows: F > H (47), F = H (103) and F < H (12). Thus, the proportion of seeds in our F > H category (29.0%) is much smaller and that of the F = H category (63.6%) much larger than reported for these two size categories by Shykoff et al. (2003) and Dufay and Billard (2012).

Theoretically, large seeds are predicted to be less dormant (and thus to germinate better) than small ones (Venable and Brown 1988; Rees 1993, 1994, 1996); however, this often is not the case (Leishman and Westoby 1994; Bu et al. 2008; Norden et al. 2009 and literature cited therein; Baskin and Baskin 2014). Based on data in Shykoff et al. (2003) and Dufay and Billard (2012) and on 18 cases we could clearly sort out in our literature review, the results for nine possible combinations [(F > H, F = H, F < H) x (F > H, F = H, F < H)] of seed size and seed germination (i.e. seed size/seed germination) are shown in Table 2. Thus, data for gynodioecious species suggest that seed size might have an influence on germination in some cases (e.g. F > H/F > H) and that it might not have had an influence on germination in other cases (e.g. F > H/F = H). For the three studies combined, the most frequent seed size/seed germination category (14 of 42 cases) was F > H/F = H, thus casting some doubt on the general importance of seed size in the lifetime fitness advantage of females in gynodioecious species. Additionally, for 22 case studies of germination of seeds of *Silene acaulis* (Delph 2004), F = H (Table 1). Seed size was not given, and thus we could not calculate RP for seed size. However, Delph (2004) stated that "Seed mass was not found to affect germination or survival of seedlings…" This further suggests that production of larger seeds by F may not be an important determinant of female advantage.

Considering seed production by females ($1 + k$) and selfing (s)/inbreeding depression (δ) in hermaphrodites, the theoretical reasons why seeds of F might germinate better or at least equally as well as those of H can be obtained from information included above on "Theoretical background". That is, F might be favored due to selfing/inbreeding depression in H and reallocation to seeds of resources saved by not producing pollen. On the other hand, the reason(s) why $F_{germ} < H_{germ}$ in 13.6% of the cases in our survey and 9.4% of the cases in the analyses by Shykoff et al. (2003) and Dufay and Billard (2012) is (are) not so obvious. Perhaps biparental inbreeding depression (δ_{bip}) for germination of F seeds plays a role in cases of $F_{germ} < H_{germ}$ (e.g. see Schultz and Ganders 1996; Sun and Ganders 1988; Thompson and Tarayre 2000; Dufay et al. 2010).

Furthermore, in a year or location other than the one in which the study was done (i.e. when $F_{germ} < H_{germ}$), germination percentage/rate of F seeds might be greater than or equal to that of H. This could be due, for example, to year and locality differences in environmental effects either on F during seed development (maternal effect) and/or on post-dispersal germination environment into which the seeds are dispersed. Various environmental factors that could vary between years and localities differentially affect the ecology, life history and sex ratio of F and H in gynodioecious populations, include habitat quality (Krohne et al. 1980; Case and Barrett 2001; Delph and Carroll 2001; Vaughton and Ramsay 2004), herbivory (Uno 1982; Ashman 2002; Cole and Ashman 2005; Doubleday and Adler 2017; McCall and Barr 2012), mycorrhizae (Koide 2010; Varga and Kytöviita 2010a, b; Varga et al. 2013), pollinator (pollen) limitation (Ashman and Stanton 1991; Fleming et al. 1994; McCauley and Brock 1998; Ashman 2000; Case and Ashman 2009; De Cauwer et al. 2010; Dornier and Dufay 2013) and predators-pathogens (Marshall and Ganders 2001; Collin et al. 2002; Ashman 2006; Marr 2006; Miyake et al. 2018).

Concluding remarks

It seems doubtful that $F_{germ} > H_{germ}$ is overall a major contributor to the female advantage required for the maintenance/spread of F in populations of gynodioecious species. However, seed germination is only one component of lifetime fitness. Thus, even if $F_{germ} < H_{germ}$, some other fitness trait(s), such as number of seeds produced plant^{-1} and/or survival to reproductive maturity, could give F the advantage it needs to coexist with H. In fact, based on theory, if $F_{germ} \leq H_{germ}$, some other fitness trait(s) and geometric lifetime fitness must be greater for F than for H in order for F to be maintained in the population.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix 1

Comparison of the F/H relationships for seed germination of 24 species in present study with those included in reviews by Shykoff et al. (2003) and Dufay and Billard (2012). *F* female, *H* hermaphrodite, *cms* cytoplasmic male sterility. For present study, numbers in parentheses indicate number of case studies.

Family/species	Shykoff et al. (2003)	Dufay and Billard (2012)	This study
Amaranthaceae			
Beta vulgaris subsp. *maritima*	–	F = H	$F_{cms}=H_{restored\ cms}$ (1)$F_{cms}=H_{non\text{-}cms}$ (1)
Boraginaceae			
Echium vulgare	–	F = H	F = H (1)
Eritichium aretioides	–	F > H	F > H (1)
Phacelia dubia var. *dubia*	F < H	–	F < H (1)
Phacelia linearis	–	F = H	F > H (8), F = H (2), F < H (6)
Brassicaceae			
Raphanus sativus	–	F < H	$F_{cms}=H_{cms}$ (1), $F_{cms}<H_{non\text{-}cms}$ (1)
Caryophyllaceae			
Dianthus sylvestris	F = H	F = H	F = H (1)
Schiedea adamantis	F > H, F = H	F = H	F > H (2)
Schiedea salicaria	–	F > H, F = H	F > H (8)
Silene acaulis	F = H	–	F = H (12)
Silene vulgaris	–	F = H	F > H (12), F = H (17), F < H (3)
Colchicaceae			
Wurmbea biglandulosa subsp. *biglandulosa*	–	F > H	F > H (3)
Fabaceae			
Trifolium hirtum	F = H	–	F = H (4)
Geraniaceae			
Geranium maculatum	–	F > H, F = H	F > H (2), F = H (1), F < H (1)
Geranium sylvaticum	–	F = H	F > H (2), F = H (1), F < H (1)
Lamiaceae			
Thymus vulgaris	F > H	F > H	F > H (34), F = H (3), F < H (5)
Plantaginaceae			
Plantago lanceolata	–	F = H	F = H (1)
Plantago maritima	F < H	–	F < H (1), F < H (1)
Poaceae			
Cortaderia richardii	F > H	F > H	F > H (2), F = H (1)
Cortaderia selloana	F > H	–	F > H (1)
Rosaceae			
Prunus mahaleb	F = H	F = H	F = H (1)
Saxifragaceae			
Saxifraga granulata	–	F > H	F > H (2)
Resedaceae			
Ochradenus baccatus	F > H	–	F > H (3)
Thymelaeaceae			
Daphnus laureola	F = H	–	F > H (2)

Appendix 2

A selected sample of comparisons of our results using relative performance (RP, as described in "Materials and methods") and results (*ns* nonsignificant, *s* significant) of statistical tests (*p*) by authors of 11 papers (21 case studies) for germination of females and males; agree (yes or no), do RP and *p* agree?

Paper	RP	*p*	Agree
Alonzo and Herrera (2001)	0.36	ns	No
Ashman (1992)			
Greenhouse	0.26	s	Yes
Field	−0.08	ns	Yes
Dalton et al. (2013)	0.04	s	No
Dinnétz and Jerling (1997)	−0.12	s	Yes
Jordano (1993)	−0.04	ns	Yes
Lopez-Villavicencio et al. (2005)	−0.10	s	Yes
McCauley et al. (2000)	0.14	ns	No
Ramsey and Vaughton (2002)	0.11	ns	No
Stevens (1988)			
Experiment 1	0.24	ns	No
Experiment 2	0.26	ns	No
Webb (1981b)			
Species 1	0.08	ns	Yes
Species 2	−0.13	ns	No
Weller and Sakai (2005)			
Population 1[a]	0.57	s	Yes
Population 2	0.20	ns	No
Population 3	0.34	ns	No
Population 4	0.23	ns	No

Paper	RP	*p*	Agree
Population 5	0.23	s	Yes
Population 6	0.20	ns	No
Population 7	0.48	s	Yes
Population 8	0.32	s	Yes

[a]Populations of *Schiedea salicaria*

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