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INVITED REVIEW

Pollination intensity and paternity in flowering plants

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- **Background** Siring success plays a key role in plant evolution and reproductive ecology, and variation among individuals creates an opportunity for selection to act. Differences in male reproductive success can be caused by processes that occur during two stages, the pollination and post-pollination phases of reproduction. In the pollination phase, heritable variation in floral traits and floral display affect pollinator visitation patterns, which in turn affect variation among plants in the amount of pollen exported and deposited on recipient stigmas. In the post-pollination phase, differences among individuals in pollen grain germination success and pollen tube growth may cause realized paternity to differ from patterns of pollen receipt. The maternal plant can also preferentially provision some developing seeds or fruits to further alter variation in siring success.
- **Scope** In this review, we describe studies that advance our understanding of the dynamics of the pollination and post-pollination phases, focusing on how variation in male fitness changes in response to pollen limitation. We then explore the interplay between pollination and post-pollination success, and how these processes respond to ecological factors such as pollination intensity. We also identify pressing questions at the intersection of pollination and paternity and describe novel experimental approaches to elucidate the relative importance of pollination and post-pollination factors in determining male reproductive success.
- **Conclusions** The relative contribution of pollination and post-pollination processes to variation in male reproductive success may not be constant, but rather may vary with pollination intensity. Studies that quantify the effects of pollination and post-pollination phases in concert will be especially valuable as they will enable researchers to more fully understand the ecological conditions influencing male reproductive success.

Key words: Floral traits, male reproductive success, paternity, pollen competition, pollen limitation, pollen sorting, pollination, pollination intensity, pollinator, post-pollination, sexual selection, siring success.

INTRODUCTION

> ‘*Meeting the challenge of measuring male reproductive success will permit major advances in our understanding of plant reproductive ecology. … From a male point of view, it is important to father as many viable embryos as possible. This may entail producing and delivering copious sperm, preventing other males from successfully fecundating, and preventing abortion of zygotes by the receiving female. Once sperm has arrived at a receptive site, selection should favor an all-out effort to secure eggs, because at that point the sperm has no other options – it cannot get up and move over to another female, to try again …*’ (Willson, 1983)

Willson (1979, 1983) was among the first to emphasize the key role of siring success for plant evolution and reproductive ecology. Variation among individuals in success through male function is expected to be larger than through female function, enhancing the opportunity for selection to act (Bateman, 1948; Janzen, 1977; Stephenson and Bertin, 1983; Wilson *et al.*, 1994 Briscoe-Runquist *et al.*, 2017). This increased opportunity for selection provides a potential explanation for the elaboration of floral traits and a connection to sexual selection as an evolutionary process (Willson and Burley, 1983; Thomson 2014).

But what are the causes of variation in siring success for flowering plants? It has long been recognized that the behaviour of animal pollinators can play a critical role in floral trait evolution (Grant and Grant, 1965; Harder and Johnson, 2009; Muchhala and Thomson, 2010; Van der Niet *et al.*, 2014), and therefore may contribute to variation in siring success (Minnaar *et al.*, 2019). Because plants cannot directly control pollen export and pollen receipt, most species have evolved floral traits that increase pollinator attraction and promote pollen transport (Simpson and Neff, 1983; Harder and Barrett, 1996; Parachnowitsch *et al.*, 2019; Minnaar *et al.*, 2019). Pollinator-mediated selection on traits that influence female function (seeds mothered) can be strong, and often varies with ecological context (Caruso *et al.*, 2019). For example, selection may be more intense when pollinators are scarce or when there is a strong preference for particular floral morphologies (Sletvold and Agren, 2016; Trunschke *et al.*, 2017; Caruso *et al.*, 2019).

However, in hermaphroditic plants, the opportunity for selection on floral traits depends equally on reproductive success through male function (seeds sired). Unfortunately, this has seldom been measured, let alone compared across ecological contexts, including environments that differ in pollinator abundance, edaphic conditions and the presence of co-flowering species (Broyles and Wyatt, 1990; Meagher, 1991; Devlin and Ellstrand, 1990; Conner *et al.*, 1996; Kulbaba and Worley, 2012, 2013; Briscoe-Runquist *et al.*, 2017).

Variation in siring success can occur at two stages of the reproductive process (Fig. 1). In the pollination phase, pollinator-mediated interactions affect the amount of pollen removed from anthers and transported to recipient stigmas (Stanton *et al.*, 1986; Cayenne Engel and Irwin, 2003; Richards *et al.*, 2009; Minnaar *et al.*, 2019). In the post-pollination phase, differential siring success of pollen from different donors may cause realized paternity to differ from patterns of pollen receipt (Marshall and Folsom, 1991; Harder and Barrett, 1996; Marshall and Diggle, 2001; Sorin *et al.*, 2016). The relative importance of these phases is likely to vary with ecological context (Snow, 1994; Krauss, 2000), and we argue that the amount of pollen arriving on stigmas relative to the amount necessary for full seed set (pollination intensity) is a key aspect of ecological context that affects variation in siring success. Here we highlight the value of combining studies of both phases: pollination phase studies that link floral traits, pollinator visitation and fitness, and post-pollination studies of siring success following controlled pollinations. We also call attention to several exciting questions that can be answered by combining pollination ecology and genetic approaches to the study of paternity.

INFLUENCE OF FLORAL TRAITS AND POLLINATION ECOLOGY ON VARIANCE IN SIRING SUCCESS

Reproduction in flowering plants has been engaging researchers since the late 18th century (Sprengel, 1793). Pioneering ecological studies described interactions of plants and pollinators, and how floral morphology influences pollen removal, pollen deposition and seed production (female reproductive success) (Darwin, 1862; 1877; Müller, 1883; Robertson, 1895). More recently, researchers have sought to characterize the effect of floral traits and pollination ecology on plant fitness through female function. However, these early efforts did not explicitly recognize the importance of evaluating effects on siring success. It was not until a century later that Janzen (1977) and Willson (1983) explicitly explored the critical role of paternity in floral trait evolution.

Floral traits such as shape, size, petal colour, nectar production and fragrance often vary widely within and among populations and can play a critical role in pollinator attraction and in the frequency and quality of pollinator visits (Fig. 1; Waser and Price, 1983; Galen and Newport, 1987; Raguso, 2008; Harder and Johnson, 2009; Parachnowitsch *et al.*, 2019; van der Kooi *et al.*, 2019). In hermaphroditic plants, rates of pollinator visitation are strongly associated with both pollen receipt (female function) and pollen export (male function) (Fig. 1; Campbell, 1989; Campbell *et al.*, 1991, 2012; Mitchell and Waser, 1992; Rojas-Nossa *et al.*, 2015). Selection on traits influencing female reproductive success has been studied much more extensively than selection on male reproductive success (Kulbaba and Worley, 2013). However, floral traits are hypothesized to be under stronger selection through male function because siring success is mate-limited, while seed production is often resource-limited (Bateman's principle; Bateman, 1948). In this section we briefly review previous studies exploring how floral trait variation influences male reproductive success and highlight how pollination intensity and pollinator identity can affect this relationship.

Flower shape influences the orientation of a pollinator's body as it probes a flower, which may affect the location of pollen placement on the pollinator as well as the quantity of pollen removed by the pollinator (Kulbaba and Worley, 2012; Anderson *et al.*, 2016; Minnaar *et al.*, 2019; de Jager and Peakall, 2019). For example, Kulbaba and Worley (2012) found that following visitation by hawkmoths, male reproductive success in *Polemonium brandegeei* was higher for plants with narrow corollas, which may reflect the likelihood that floral sexual organs contact the hawkmoth's proboscis. In *Ipomopsis aggregate*, selection through male function favours flowers with wide corollas (Campbell *et al.*, 1996, 1997). Hummingbirds can probe flowers with wide corollas more deeply, and therefore

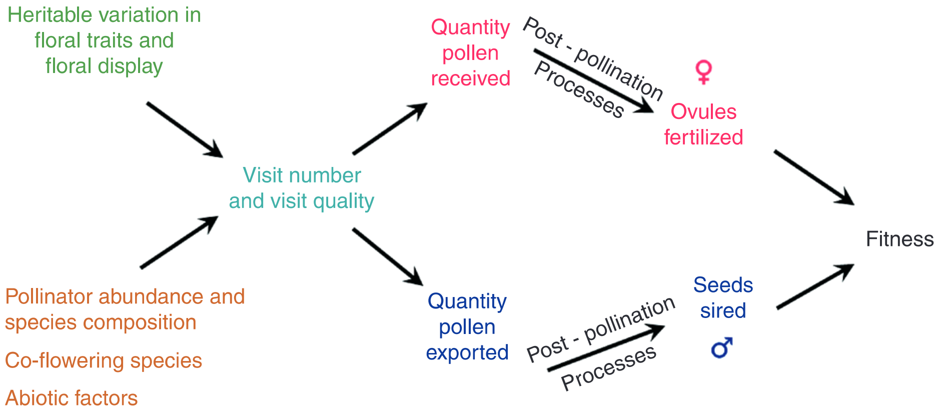

Fig. 1. Genetic and ecological factors influencing pollination and post-pollination processes in hermaphroditic flowering plants. The relative importance of each of these processes in determining plant fitness depends on a variety of factors and the interplay between them. These factors may include: pollinator abundance, amount of pollen transferred, resource availability and maternal seed provisioning. These factors are discussed in detail throughout this review.

remove more pollen. In *Clarkia xantiana*, larger flowers attract more pollinator visits and have higher outcross siring success (Briscoe Runquist *et al.*, 2017). In these examples, the specific traits under selection vary between systems; however, we see a pattern indicating that floral morphology is important to siring success.

Different floral trait optima may arise due to selection caused by pollinators that vary in morphology or behaviour (Krauss *et al.*, 2017; Minnaar *et al.*, 2019). For example, *Polemonium brandegeei* is pollinated by both hummingbirds and hawkmoths (Kulbaba and Worley, 2013). The authors note that these two pollinator classes exert contrasting directional selection on herkogamy and corolla width, resulting in an intermediate phenotype in natural populations.

Several studies have explored how flower colour variation influences siring success (Stanton *et al.*, 1986, 1989; Devlin *et al.*, 1992). For example, insect pollinators preferentially visit *Raphanus raphanistrum* plants with yellow flowers (Stanton *et al.*, 1989) leading to significantly higher male fitness through increased pollen export (Stanton *et al.*, 1986). Interestingly, flower colour does not influence seed production.

Variation in floral display size is also thought to influence male reproductive success because plants with larger displays may attract more pollinator visits (Schmid-Hempel and Speiser, 1988; Klinkhamer and de Jong, 1990; Eckhart, 1991; Mitchell, 1994; Galloway *et al.*, 2002). In *Asclepias exaltata*, siring success increases linearly with floral display size (Broyles and Wyatt, 1990). However, pollinators tend to visit more flowers sequentially on large displays (Dudash, 1991; Harder and Barrett, 1995; Snow *et al.*, 1996; Mitchell *et al.*, 2004), which may increase geitonogamous self-pollen receipt and reduce outcross siring success on a per-flower basis (Karron *et al.*, 2009; Karron and Mitchell, 2012).

Pollination intensity

The influence of floral traits on reproductive success can vary with the pollination environment. When pollinators are rare, and thus pollinators are not competing for floral resources, trait preferences should be strong because the pollinator will preferentially visit the most rewarding phenotypes (Goulson, 1999). Under these circumstances seed production (and pollen dispersal) will be greatest for plants that receive more, or more effective, visits. Variance among individuals in relative fitness through both male and female pollination success may increase in pollen-limited environments, enhancing the opportunity for selection (Richards *et al.*, 2009; Sletvold and Agren, 2016).

An increased opportunity for selection with severe pollen limitation has been demonstrated for female fitness (Ashman and Morgan, 2004). For example, Trunschke *et al.* (2017) found a positive relationship between pollen limitation and net selection across 12 species of orchids. Importantly, this relationship can occur within a single population, where variation in pollinator composition and trait expression is minimized. Sletvold and Agren (2016) experimentally manipulated the degree of pollen limitation in a natural population of the orchid *Gymnadenia conopsea* and found that pollinator-mediated selection on floral traits increased significantly in treatments with high pollen limitation.

When pollen limitation occurs, pollinator preference for certain trait values may cause strong directional selection through both sexual functions (Willson and Burley, 1983). By contrast, when pollen is not limiting there will be little variation in female reproductive success (all plants are at capacity), and male reproductive success should largely reflect pollen abundance. In this case there may not be a consistent relationship between floral traits and male fertility if most pollen has been removed from each pollen donor. However, donors might still differ in male reproductive success if they differ in post-pollination success.

Research that quantifies variation in siring success following both natural pollination and artificial mixed pollination can potentially disentangle pollination and post-pollination processes. An elegant study by Krauss (2000) measured siring success in a small, isolated population of *Persoonia mollis.* Control flowers received open pollination, and experimental flowers received an equal quantity of pollen from all 15 plants in the population. Variance in siring success was much greater following application of pollen mixtures, and differed markedly from variation in siring success associated with natural pollination. In the following section, we highlight the mechanisms of post-pollination sorting, and discuss how the quantity of pollen deposited on stigmas may influence variation in siring success.

INFLUENCE OF POST-POLLINATION PROCESSES ON VARIANCE IN SIRING SUCCESS

When pollen arrives on a flower, its germination and growth provide considerable opportunity for variance in siring success (Lyons *et al.*, 1989; Marshall and Folsom, 1991; Swanson *et al.*, 2016). This variation can be strongly affected by both genetic and environmental factors (Delph *et al.*, 1997; Herrera, 2002, 2004).

Pollen germination is the first step of this process – hydration of pollen and success in producing a pollen tube may differ greatly among pollen donors (Fig. 2; Snow and Spira, 1991; Sari-Gorla *et al.*, 1992; Jolivet and Bernasconi, 2007). Germination can also be affected by pollination events (e.g. pollen directly contacting the stigma may have an advantage over pollen separated from the stigma by several layers of pollen), and maternal plants can also delay pollen germination in some circumstances (Galen *et al.*, 1986; Lankinen *et al.*, 2007; Bochenek and Eriksen, 2011; see also Lankinen *et al.*, 2016). Pollen germination may be influenced by the presence of heterospecific pollen on a stigma as well (Arceo-Gómez and Ashman, 2014; Briggs *et al.*, 2015). Furthermore, flower age may influence pollen germination, especially in self-incompatible species (Marshall *et al.*, 2010). In self-incompatible *Leptosiphon jepsonii*, self pollen cannot sire seeds on the first day of stigma receptivity, but can on the second day (Goodwillie *et al.*, 2004).

Once pollen grains have germinated, pollen tubes must enter the stigma, and then grow down the style toward the ovary (Figs 2 and 3). Pollen tubes are generally not able to reach the ovules without drawing resources from the style (Stephenson *et al.*, 2003), and crowded pollen grains can compete for access to resources (Cruzan, 1986), while maternal plants may choose to provision some pollen tubes over others (Malti and Shivanna, 1985). For these and other reasons pollen tube growth rates often vary greatly among donors (Jones, 1920; Mazer, 1987; Cruzan, 1990; Snow and Spira, 1991; Delph *et al.*, 1997; Marshall, 1998; Lankinen *et al.*, 2009). McCallum and Chang (2016) found that a 10% difference in the diameter of *Ipomoea purpurea* pollen strongly influenced the likelihood of fertilization. There also is evidence in *Viola tricolor* that pollen or pollen tubes can experience interference competition, inhibiting the germination or growth rate of adjacent gametophytes (Lankinen and Skogsmyr, 2002). Perhaps reflecting this, studies of *Lesquerella fendleri* and *Raphanus sativus* have shown that siring success in single donor pollinations is generally a poor predictor of siring success in mixed pollinations (Mitchell and Marshall, 1995; Marshall and Diggle, 2001).

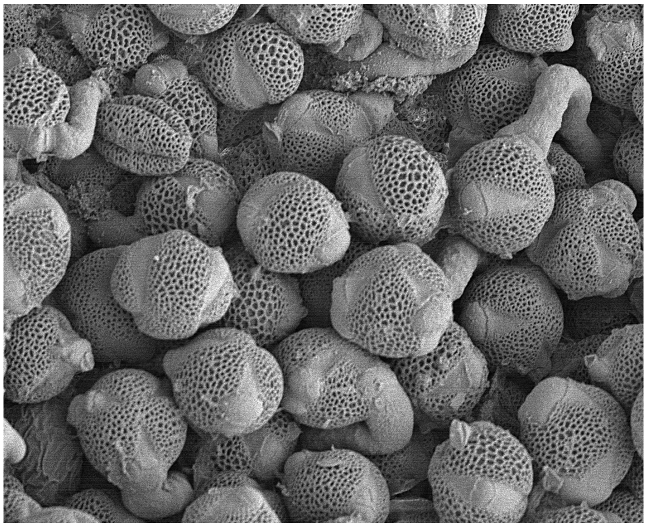

Fig. 2. Pollen germinating on a *Mimulus ringens* stigma. Note that a few grains are not hydrated, and only some of the grains have formed pollen tubes. Pollen grains are 15–25 µm in diameter. Image: Wendy Semski.

Navigation to the ovule is an important but often overlooked aspect of post-pollination success (Higashiyama and Takeuchi, 2015). For example, in *Raphanus sativus* the tendency for donors to target basal vs. distal ovules within the ovary is heritable, suggesting that this and other aspects of navigation may differ among pollen donors (Marshall and Evans, 2016). Although guidance clearly involves attractants produced by female tissue (Higashiyama *et al.*, 2003), the extent to which males differ in pollen tube navigational abilities is not yet known.

Once ovules are fertilized, the maternal plant can have enormous latitude for preferentially provisioning or aborting individual ovules, or whole fruits. There is abundant evidence that these decisions are often non-random with respect to donor identity, and that they may or may not be strictly based on the vigour of the resulting zygote (Stephenson, 1981; Willson and Burley, 1983; Casper, 1984; Bertin, 1985; Cruzan, 1986; Marshall and Folsom, 1991; Montalvo, 1992; Rigney *et al.*, 1993; Marshall and Evans, 2016).

Whether pollen is self or cross is another important contributor to variation in donor success. Indeed, Darwin (1876) was the first to notice that self pollen grew more slowly than cross pollen, even in otherwise self-compatible species. Some studies assessing paternity following application of mixed pollen loads have found higher siring success for outcross pollen (Rigney *et al.*, 1993; Kruszewski and Galloway, 2006; Figueroa-Castro and Holtsford, 2009), but other studies have found that self and outcross pollen are equally successful at siring seeds (Sorin *et al.*, 2016).

Variance in male reproductive success can be affected by all of the processes mentioned above, and those effects can be context-dependent. Consider an environment where pollination intensity is low, so that seed production is pollen-limited, in that adding more pollen will increase seed production (Fig. 3, 'Low'). Here, a large fraction of pollen grains successfully fertilizes ovules, and attrition of pollen tubes will usually be

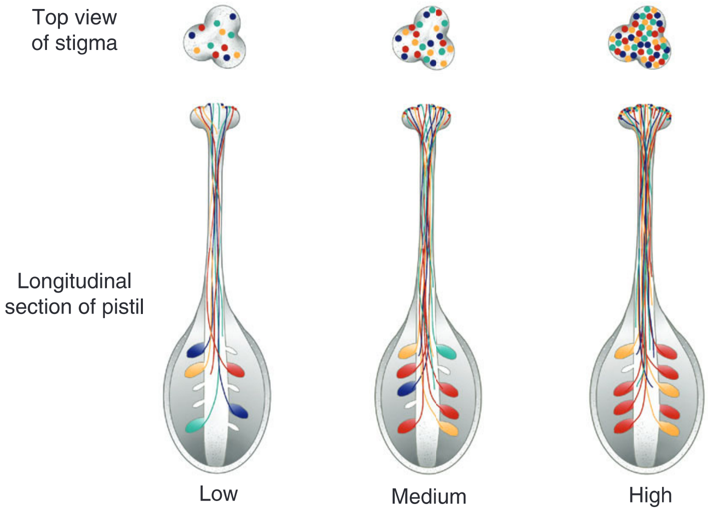

Fig. 3. Pollen sorting as a function of the intensity of pollination. The three pistils in the diagram represent low, medium or high pollen loads. The coloured dots on each stigma represent equal numbers of pollen grains from four different pollen donors. These donors differ in speed of pollen tube growth, with red fastest, followed by yellow, light blue and purple (slowest). Unfertilized ovules are small and white; fertilized ovules are larger and coded by the colour of the pollen donor. Illustration: Allysa Hallett.

density-independent (Harder *et al.*, 2016*a*, *b*). In this circumstance there will be little sorting among pollen grains or pollen tubes based on donor identity; even slow-growing pollen tubes may eventually fertilize an ovule (Bertin, 1990; Mitchell, 1997). Thus, when there is pollen limitation, only pollen that germinates poorly or does not produce vigorous pollen tubes, whether because of environmental damage or genetic identity (including self-incompatibility genotypes), will be sorted out. This will generate relatively little variation in male fertility. In this situation, the success of each pollen donor will probably be most affected by proportional representation of its pollen on the stigma.

However, when the number of pollen tubes reaching the ovary exceeds the number of ovules, seed production is not limited (adding more pollen will not increase seed production). In this situation density-dependent competition can occur (Fig. 3, 'High'; Haldane, 1932; Cruzan, 1986; Winsor *et al.*, 1987; Bochenek and Eriksen, 2011; Harder *et al.*, 2016*a*, *b*), and there will be abundant opportunity for sorting among pollen grains based on their ability to speedily and effectively fertilize ovules (Cruzan and Barrett, 1996; Shaner and Marshall, 2003; Ruane, 2009). Variation in male reproductive success should then increase with the size of the pollen load. This is because an increasingly large number of pollen grains will be unsuccessful as the pollen load increases beyond that required to fertilize all ovules (Fig. 3). The distinction between density-dependent and density-independent growth of pollen tubes is one reason that the extent of pollen limitation (and therefore the abundance and effectiveness of pollinators) is a key ecological context for understanding variance in male reproductive success.

It is useful to recognize two patterns of mating that contribute to variation in male fertility (Waser *et al.*, 1987). First is a concordant mating pattern. This occurs when the rank order of performance for different donors is shared across maternal plants – there are some males that sire more offspring on all maternal plants. This might occur through higher pollen vigour of particular males, or through female choice. This is also referred to as 'general combining ability' (Lyons *et al.*, 1989). Second is a discordant mating pattern (male–female complementarity). This occurs when the rank order is not consistent across mothers, and might reflect female choice, genes with complementary effects between the pollen and style, or self-incompatibility (Charlesworth *et al.*, 1987). This is often referred to as 'specific combining ability' (Lyons *et al.*, 1989). Complementarity can be detected as a statistical interaction between donor identity and recipient identity (Lyons *et al.*, 1989). Self-incompatibility is a common example of complementarity (Vekemans *et al.*, 1998). Higher mating success of unrelated individuals is also a form of complementarity as this can lower the incidence of biparental inbreeding (Waser and Price, 1989; Ayre *et al.*, 2019). Non-random mating that is concordant encourages selection for whatever male attributes provide an advantage, while complementarity may generate frequency-dependent selection for specific combinations. Both of these patterns of non-random mating can increase variance in male fertility, and tend to be more common in contexts where pollen is not limiting.

Beyond variation in the amount of pollen present, there may be variation in the timing of pollen arrival (Mulcahy, 1983; Spira *et al.*, 1996; Karron *et al.*, 2006). If pollen all arrives in one visit, proportional representation in the pollen load is probably a key factor determining paternity. However, if pollen arrives in several separate and widely spaced visits, the timing of arrival may become more important. In between are situations in which separate pollen deliveries arrive in short enough succession that slow-growing pollen from an early visit can be overtaken by fast-growing pollen from a later visit, decoupling pollen performance from timing of arrival (Sorin *et al.* 2016).

INTEGRATING RESEARCH ON POLLINATOR BEHAVIOUR, FLORAL TRAITS, SIRING SUCCESS AND POST-POLLINATION PROCESSES

Realized male fertility in the wild depends on both pollen delivery and success in post-pollination growth and fertilization. These processes may potentially interact to magnify or lessen the variance in siring success. Here we explore the interplay between pollination and post-pollination events, and how these processes may respond to ecological factors such as pollination intensity (Fig. 4). We also highlight some of the most pressing questions about variance in male reproductive success and identify critical data needed to address these questions.

When pollination intensity is low, pollinator discrimination amongst pollen donors may lead to high variance in donor pollination success (see *Pollination intensity*; Fig. 4A). However, an increase in the rate of pollinator visitation may lessen the variance amongst donors, especially when nearly

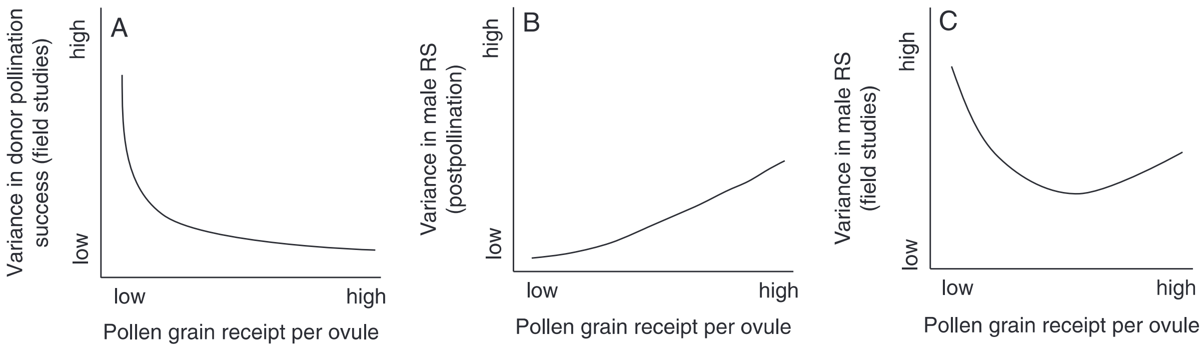

Fig. 4. Predicted relationships between pollination intensity and (A) variance in pollination success, (B) variance in male reproductive success (RS) during the post-pollination phase, and (C) overall variance in male siring success including both pollination and post-pollination influences.

all pollen has been dispersed from flowers. Quantification of the relationship between pollination intensity and the success of individual donors in exporting pollen to receptive stigmas is difficult to achieve, as it requires the ability to distinguish the donor composition of pollen grains on stigmas throughout the population. The most promising approach for distinguishing pollen grains of different donors involves microsatellite genotyping of individual pollen grains (Hasegawa *et al.* 2015). Although this technique is costly, it can potentially distinguish pollen grains of each donor in a study population. For example, Hasegawa *et al.* (2015) successfully determined the pollen parent for 824 pollen grains from 60 *Castanea crenata* donors. Another promising technique involves labelling pollen grains of each donor with quantum dots, semiconductor nanocrystals that glow under UV excitation (Minnaar and Anderson, 2019). Currently only four colours can be used, limiting the number of pollen donors that can be compared in a study population. However, in the future it may become possible to distinguish additional quantum dot colours, or perhaps they could be combined to allow a larger sample of pollen donors to be distinguished (Minnaar and Anderson, 2019).

In contrast to the decelerating relationship between pollen donation success and pollination intensity (Fig. 4A), the variance in post-pollination reproductive success among donors is likely to increase with pollination intensity (Fig. 4B). When seed production is pollen-limited there is little sorting based on pollen donor identity. However, as the number of pollen grains per ovule increases, there is likely to be more sorting, leading to greater variance in siring success (Figs 3 and 4B).

To facilitate comparisons with natural populations, post-pollination experiments should be as realistic as possible. For example, the number of pollen donors in a mixture should closely match mate diversity within fruits in the focal population. Because fruits of many flowering plants are multiply sired by three to six donors (Mitchell *et al.*, 2005, 2013; Pannell and Labouche, 2013; Krauss *et al.*, 2017; Christopher *et al.*, 2019) this will often mean preparing realistic mixtures of pollen. Likewise, the intensity of pollination should match that in the field [e.g. if a population is pollen-limited because pollen delivery is typically low, hand pollinations to investigate post-pollination events should also use small pollen loads (compare Fig. 4A with 4B)].

The contrasting effects of pollination intensity on donor success in the field (Fig. 4A) vs. post-pollination siring success (Fig. 4B) yield two interesting implications. First, the relative contribution of pollination and post-pollination processes to variation in male reproductive success may not be constant, but rather may vary with pollination intensity. Second, variation in male reproductive success in the wild may in some circumstances exhibit a U-shape, with higher variance when pollination intensity is very low or very high (Fig. 4C).

The relative magnitude of variance caused by pollination and post-pollination processes depends on the pollination environment (Fig. 4A, B). Several studies have shown high variance in male success in low pollination environments (Kulbaba and Worley, 2013; Briscoe Runquist *et al.*, 2017). This may correspond to the left-hand side of Fig. 4C. Although these studies did not measure post-pollination processes, it is possible that pollination events are most important in affecting variance (Fig. 4A). However, if pollen delivery increases, variance may decrease because most donors would successfully export pollen. If pollen were even more abundant, the magnitude of post-pollination processes might increase because of pollen competition, subsequently increasing variance in male success.

There is little empirical evidence concerning the relationship between post-pollination success and pollen receipt. Some researchers have suggested that the effects of post-pollination events on siring success (and, by inference, variance) should be smaller than those for pollination events (Charlesworth *et al.*, 1987; Wilson *et al.*, 1994). If that were the case, one would expect that post-pollination events would not offset pollination events in affecting variation in overall siring.

CONCLUSION

There are no studies that have varied the intensity of pollen delivery and have measured the variance in male success in both the pollination and post-pollination phases. Such studies would provide insight concerning the ecological conditions that favour selection on floral traits such as nectar production and flower size, and on physiological traits such as pollen tube growth rate. It is important that both phases are studied in concert; this will allow researchers to infer the strength of and opportunity for selection on floral traits and physiological traits (pollen tube growth rate) at the same time. These studies would also allow researchers to understand how pollination intensity can affect selection at any stage of the reproductive process.

GLOSSARY

Female reproductive success: the seed production of an individual plant, summed across all fruits on that individual.

Male reproductive success/siring success: the success of a plant's pollen at fertilizing ovules across all seed-producing individuals in the populations.

Pollen competition: a situation in which gametophytes from more than one male are present in excess of the number required to fertilize the available ovules. These competitive interactions can occur at any point in the siring process, including on the stigma during pollen grain germination, growth of pollen tubes down the style, or fertilizing ovules in the ovary.

Pollen limitation: a reduction in seed or fruit production because there is not sufficient pollen to fertilize all ovules.

Pollen sorting: the process that occurs when pollen competition occurs, and results in only a subset of the pollen on the stigma successfully fertilizing ovules.

Pollination intensity: the amount of pollen arriving on stigmas relative to the amount necessary for full seed set.

Pollination phase: the interactions and processes that occur from pollen production on the sire, to pollen removal, transport and arrival on recipient stigmas.

Post-pollination phase: the interactions and processes that occur once pollen has reached the stigma, including pollen germination, pollen tube growth and fertilization.

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