NEWS & VIEWS

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ON THE NATURE OF THINGS: ESSAYS

New Ideas and Directions in Botany

Plasticity in selective embryo abortion may limit the mating costs of geitonogamy in self-compatible plants: a hypothesis

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Geitonogamy involves pollination of flowers by pollen from other flowers on the same plant. In hermaphroditic plants with multiple flowers in anthesis at the same time, this mode of pollination is likely to be near ubiquitous (de Jong et al., 1993; Harder and Barrett, 1995; Vaughton and Ramsey, 2010). In self-compatible species, geitonogamy may incur fitness costs because of inbreeding depression (i.e., the reduction in fitness of selfed seeds relative to outcrossed seeds), seed discounting (i.e., a reduction in the production of outcrossed seeds because seeds are selfed), and pollen discounting (i.e., a decrease in outcross siring success because self-pollen deposition reduces opportunities for cross pollination) (Lloyd, 1992; Busch and Delph, 2012). Because of these mating costs, geitonogamy is commonly recognized as a pervasive and non-adaptive by-product of floral display size leading to the evolution of diverse floral strategies that function to limit geitonogamy (Lloyd, 1992; de Jong et al., 1993; Barrett, 2003). However, if geitonogamy is both ubiquitous and unavoidable, it is worth considering how self-compatible plants cope with geitonogamy after ovules are selfed, but this has not been explored in the literature on plant reproductive ecology.

In this essay, we propose a novel hypothesis for how self-compatible plants may take advantage of the benefits of reproductive assurance through geitonogamy while avoiding the seed discounting cost after geitonogamous selfing has occurred. We propose that after ovules are selfed through geitonogamy, they can mature into seeds, providing reproductive assurance if cross-fertilized ovules are limiting, but that selfed ovules will be preferentially aborted if cross-fertilized ovules are abundant. Such post-fertilization mating flexibility in stochastic pollination and fertilization environments may allow geitonogamy to provide reproductive assurance with limited seed discounting costs. It is important to emphasize that according to the hypothesis we propose here geitonogamous seed discounting can be reduced but not pollen discounting, which may still be significant (Harder and Barrett, 1995).

Our hypothesis depends on the key assumption that maternal parents can selectively abort ovules fertilized by low-quality pollen (self-pollen or pollen of close relatives) when resources are limiting but not when resources are abundant; i.e., there is plasticity in selective embryo abortion. For example, in several studies fruit or ovule abortion was lower and progeny vigor higher in intact flowers or inflorescences than in those receiving hand-thinning treatment, indicating that otherwise viable embryos were aborted when resources were limiting (Stephenson and Winsor, 1986; Casper, 1988; Rocha and Stephenson, 1991; Melser and Klinkhamer, 2001). However, there is also evidence indicating that selective embryo abortion caused by inbreeding depression can be resource independent (Wiens et al., 1987). The generality of our key assumption is uncertain, but the mechanism underlying plasticity in selective abortion may be that maternal parents can distinguish between fertilized inbred and outcrossed ovules or that selfed embryos are outcompeted by outcrossed embryos when resources are limiting (Korbecka et al., 2002). We now develop a simple conceptual model to illustrate the conditions in which our new hypothesis may operate.

THE CONCEPTUAL MODEL

We model a self-compatible plant population in a stochastic pollination and fertilization environment in which selfing and outcrossing rates are unpredictable. Pollination is inherently highly stochastic, which appears to select for an overproduction of ovules in some species (Rosenheim et al., 2016). Even if a plant receives plentiful outcross pollen, the number of seeds produced may be much smaller than the number of ovules fertilized (Harder and Routley, 2006). Thus, in our model, ovule number is never limited.

We assume that after fertilization, the selfed and outcrossed ovules in a plant are f_s and f_o, respectively. Selfing occurs through geitonogamy, and in this simple model, we do not consider intraflower selfing, which could be restricted by various floral mechanisms (e.g., unisexual flowers, strong protandry). The resource cost of maturing a seed is S, and thus, if all fertilized ovules are matured into seeds, the total resource cost of seed production is $(f_s + f_o)S$. The total resources available for seed production is R. We focus on the conditions in which inbreeding depression is >0.5 (Winn et al., 2011). If inbreeding depression is <0.5, complete selfing should evolve (Huang and Burd, 2019).

For simplicity, we assume selective embryo abortion occurs soon after fertilization, and thus, aborted embryos do not consume significant resources for seed production. If there is no plasticity in selective embryo abortion, following Harder et al. (2008), we assume that selfed and outcrossed ovules have proportions k_s and k_o surviving to become seeds, respectively [$k_s \le k_o$ because of inbreeding depression, and $(k_s f_s + k_o f_o)S \le R$].

Stochastic pollination may lead to three outcomes in relation to ovule fertilization. First, under favorable pollination conditions, enough ovules are cross-fertilized (i.e., $f_o S \ge R$). If there is selective embryo abortion, all selfed ovules and $f_o - R/S$ outcrossed ovules are aborted, and plants produce R/S outcrossed seeds (Fig. 1A). Therefore, there is no seed discounting cost to geitonogamy. If there is no selective embryo abortion, each plant produces $f_s k_s$ selfed seeds and $f_o k_o$ (equal to $R/S - f_s k_s$) outcrossed seeds (Fig. 1A). Thus, through selective abortion, $f_s k_s$ more outcrossed seeds can be produced (i.e., seed discounting is reduced by $f_s k_s$).

Second, under moderate pollen limitation enough ovules are fertilized, but cross-fertilized ovules are limited, i.e., $(f_o + f_s)S \ge R > f_o S$. If there is selective embryo abortion, each plant produces f_o outcrossed seeds and $R/S - f_o$ selfed seeds, meaning that $f_s - (R/S - f_o)$ selfed ovules are aborted (Fig. 1B). The production of $R/S - f_o$ selfed seeds provides reproductive assurance with no seed discounting cost. If there is no selective embryo abortion, each plant produces $f_s k_s$ selfed seeds and $f_o k_o$ (equal to $R/S - f_s k_s$) outcrossed seeds (Fig. 1B). Thus, through selective abortion, $f_o - f_o k_o$ more outcrossed seeds can be produced, i.e., seed discounting is reduced by $f_o - f_o k_o$.

Finally, under severe pollen limitation, too few ovules are fertilized, i.e., $(f_o + f_s)S < R$. There should be no abortion of fertilized ovules, and each plant produces f_s selfed seeds and f_o outcrossed seeds (Fig. 1C). The production of f_s selfed seeds provides reproductive assurance and results in no seed discounting cost. The unused resources, $R - (f_o + f_s)S$, may be used for increasing seed size or seed production through delayed self-fertilization (Goodwillie and Weber, 2018).

We have proposed a new hypothesis describing how after ovule fertilization, plasticity in selective embryo abortion may enable geitonogamy to provide reproductive assurance without incurring seed discounting costs. This process is more likely to occur in unpredictable pollination and fertilization environments. However, if we consider the entire pollination and fertilization process, geitonogamy may still cause some seed discounting because ovules selfed through geitonogamy could be otherwise outcrossed. There are two issues that need to be clarified here.

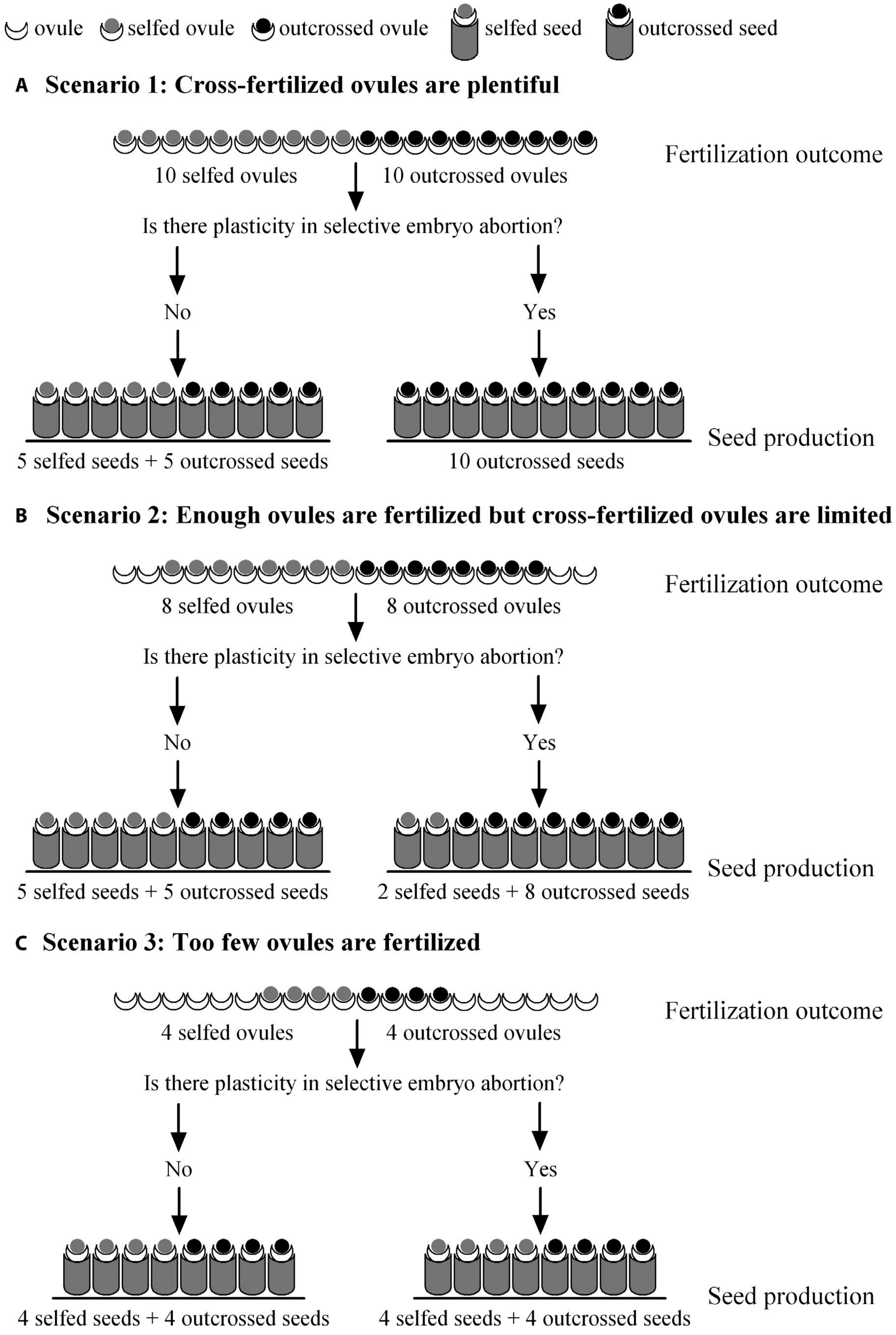
First, if geitonogamy is unavoidable, seed discounting due to fewer cross fertilizations is also unavoidable. But seed discounting due to resource competition between selfed and outcrossed ovules can be restricted if there is selective embryo abortion. Thus, we suggest in the future it may be more fruitful to investigate seed discounting that is avoidable than to study cases where it is not.

Second, if geitonogamy can be avoided it is possible that it could be adaptively maintained. If so, the cost of geitonogamy may be outweighed by its benefit in providing reproductive assurance, as appears to occur in some wind-pollinated species (Friedman and Barrett, 2008; Hesse and Pannell, 2011). However, we note that demonstrating that geitonogamy is adaptive under particular conditions is likely to be experimentally challenging, as it requires estimates of seed discounting, pollen discounting, and reproductive assurance (see Busch and Delph, 2012), which to our knowledge has not been possible in any empirical study to date.

Our model is clearly overly simplistic because it ignores several biologically realistic features of plant reproduction. For example, when resources limit seed production, selective embryo abortion may not be complete (i.e., more selfed ovules are matured than indicated in our model, Fig. 1A, B), and selective embryo abortion may incur a fitness cost if maternal resources are required to distinguish between selfed and outcrossed embryos. Also, selective embryo abortion can occur well after ovule fertilization, which may decrease its benefit.

Despite these limitations, our hypothesis is novel because it links research on plasticity in selective embryo abortion with geitonogamy. By doing so, it suggests that the effects of geitonogamy on plant reproduction may not always be unconditionally detrimental as commonly viewed. Given the widespread occurrence of geitonogamous

FIGURE 1. An illustration of how maternal parents might take advantage of the reproductive assurance benefits of geitonogamy while avoiding its seed discounting costs in a stochastic pollination and fertilization environment after fertilization has occurred. In each of the three scenarios, ovules are selfed through geitonogamy, and resources available can mature a total of 10 selfed and outcrossed seeds. We assume that if there is no plasticity in selective embryo abortion, selfed and outcrossed ovules compete equally for resources to maturation (i.e., the proportions of selfed and outcrossed ovules surviving to become seeds are equal, $k_s = k_o$). In A and B, by selectively aborting selfed ovules, more outcrossed seeds are produced. In C, where there is plasticity in selective embryo abortion it has no effect on the outcome of seed production.


ovule
selfed ovule
outcrossed ovule
selfed seed
outcrossed seed
A Scenario 1: Cross-fertilized ovules are plentiful
Fertilization outcome
10 selfed ovules
10 outcrossed ovules
Is there plasticity in selective embryo abortion?
No
Yes
Seed production
5 selfed seeds + 5 outcrossed seeds
10 outcrossed seeds
B Scenario 2: Enough ovules are fertilized but cross-fertilized ovules are limited
Fertilization outcome
8 selfed ovules
8 outcrossed ovules
Is there plasticity in selective embryo abortion?
No
Yes
Seed production
5 selfed seeds + 5 outcrossed seeds
2 selfed seeds + 8 outcrossed seeds
C Scenario 3: Too few ovules are fertilized
Fertilization outcome
4 selfed ovules
4 outcrossed ovules
Is there plasticity in selective embryo abortion?
No
Yes
Seed production
4 selfed seeds + 4 outcrossed seeds
4 selfed seeds + 4 outcrossed seeds

self-fertilization in plants with large daily floral displays it is worth exploring in the future whether geitonogamy may play a significant role in providing reproductive assurance, particularly in self-compatible species with unisexual flowers that cannot engage in intrafloral self-fertilization. If reproductive assurance through geitonogamy does not deplete resources for seed production as illustrated in Fig. 1C, delayed selfing (Goodwillie and Weber, 2018) may additionally increase fertility in unpredictable pollination environments.

Much attention in plant reproductive ecology has been devoted to exploring how self-compatible plants might reduce mating costs associated with geitonogamy (reviewed by de Jong et al., 1993; Barrett, 2003). However, because geitonogamy is unavoidable in many situations, we recommend that future studies ask if self-compatible plants can take advantage of the reproductive assurance benefits of geitonogamy while avoiding its seed discounting cost after geitonogamous selfing has occurred (Fig. 1). In addition, we recognize that our simple model represents only a first step in linking geitonogamy with selective embryo abortion and reproductive assurance. In the future, more sophisticated quantitative models with additional parameters, including a full range of gamete discounting costs and the treatment of self and outcrossed embryo discrimination as a quantitative trait, should provide additional insights into the costs and benefits of geitonogamy.

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AUTHOR CONTRIBUTIONS

Q.H. and M.R. designed the research. Q.H. wrote the first version of the manuscript that was later revised by all authors.

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