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Selection During Reproduction in Mimulus guttatus

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ABSTRACT

A lack of genomic studies examining gametophytic selection and selective embryo abortion—which occur during the reproduction of angiosperms—leaves questions regarding the adaptive and evolutionary effects of these processes. Analyzing deviations from Mendelian segregation offers an avenue for identifying loci targeted by GS and SEA, and their contributions to purging of genetic load. However, other selective processes such as meiotic drive and cytonuclear interactions, as well as pollen and ovule abortion, can cause distortion. To distinguish the effects of GS and SEA from other causes of distortion, we will perform reciprocal crosses between highly homozygous and highly heterozygous individuals of *Mimulus guttatus* and conduct pooled sequencing of pollen and seeds. Given that a large fraction of the genome is expressed in pollen and seeds, we expect a large proportion of the genome to exhibit segregation distortion due to GS and SEA.

BACKGROUND

Pre-Pollination Pollen Selection

Since pollen grain development is dependent on the expression of the haploid genotype[4], we expect that genetic load may cause the failed development of a subset of pollen grains, resulting in an unequal distribution of paternal alleles among pollen grains available for pollination.

Gametophytic selection (GS)

Fig. 1

When more pollen grains are deposited on a stigma than there are ovules available to fertilize, the reproductive success of genetically distinct pollen will depend on their germination time and pollen tube elongation rate.[1]
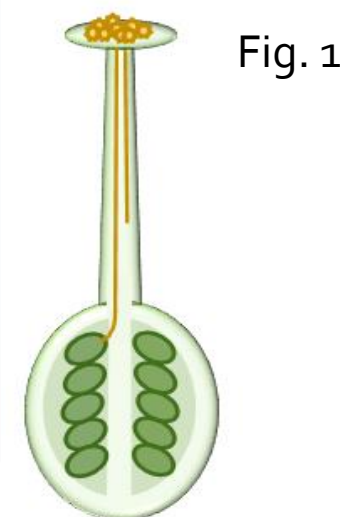
Meiotic Drive

Fig. 2

Structural variation between homologous chromosomes can lead to the biased segregation of one chromosome to the egg cell, resulting in the preferential transmission of the favored chromosome to the next generation[3]
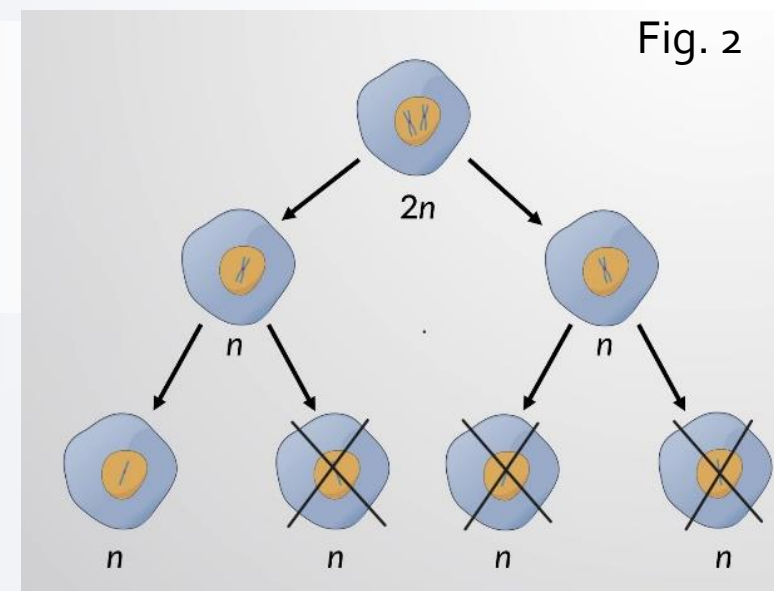
Ovule Abortion

Since ovules are resource sinks, a maternal plant in a stressful environment may not have the resources needed to adequately supply resources to all ovules produced, and thus default to reducing the number of sinks requiring resources prior to ovule fertilization.

Selective Embryo Abortion (SEA)

Genetically distinct embryos of varying fitness may compete for resources from the maternal plant, with more fit embryos becoming stronger resource sinks and surviving to become seeds, while less fit embryos fail to acquire adequate resources and are aborted.[2]
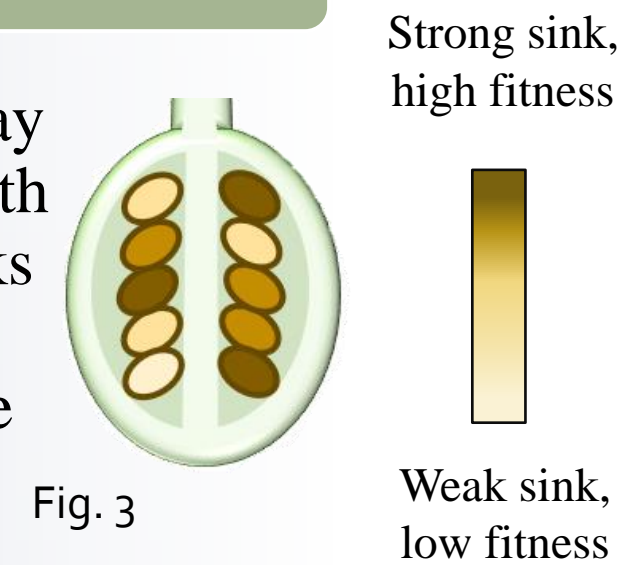
Strong sink, high fitness

Fig. 3

Weak sink, low fitness

References

[1]Winsor, J.A., Peretz, S. and Stephenson, A.G. (2000). *Am. J. Bot.*
[2]Korbecka, G., Klinkhamer, P.G.L. and Vrieling, K. (2002). *Plant Biology.*
[3]Fishman, L., Willis, J. (2004). *Genetics.*
[4]Losdat, Sylvian, et al. (2014). *J Evo Bio.*
[5]Kelian Sun, Kimberly Hunt, Bernard A. Hauser, (2004). *Plant Physiology.*

Acknowledgments

AIMS & SIGNIFICANCE

We have developed models of expected segregation patterns for GS and SEA but other selective processes, including selection on developing pollen grains prior to pollination, female meiotic drive, ovule abortion, and cytonuclear interactions, can mimic these expected patterns. The number of loci targeted by GS and SEA as well as their selective strength are unknown. **The goal of this work is thus to distinguish the effects of GS and SEA from other selective processes. We aim to identify loci targeted by GS and SEA and to estimate the strength of selection to better understand the evolutionary significance of these processes.**

MATERIALS AND METHODS

Collection Location: Columbia River Gorge

- One population from each of the following locations:
  - Latourell Falls
  - Lower Wahkeena Falls

Fig 5

Fig. 4

Study Species: *M. guttatus*

- Clonal growth
- Sexual reproduction, self-compatible
- Short generation time
- Amenable to hydroponics

I

Latourell Falls Population

Wahkeena Falls Population

selfed / selfed

II

L3S   L3LW4   LW4L3   LW4S

III

L3S   L3   L3LW4   LW4L3   L3LW4   LW4L3   LW4S
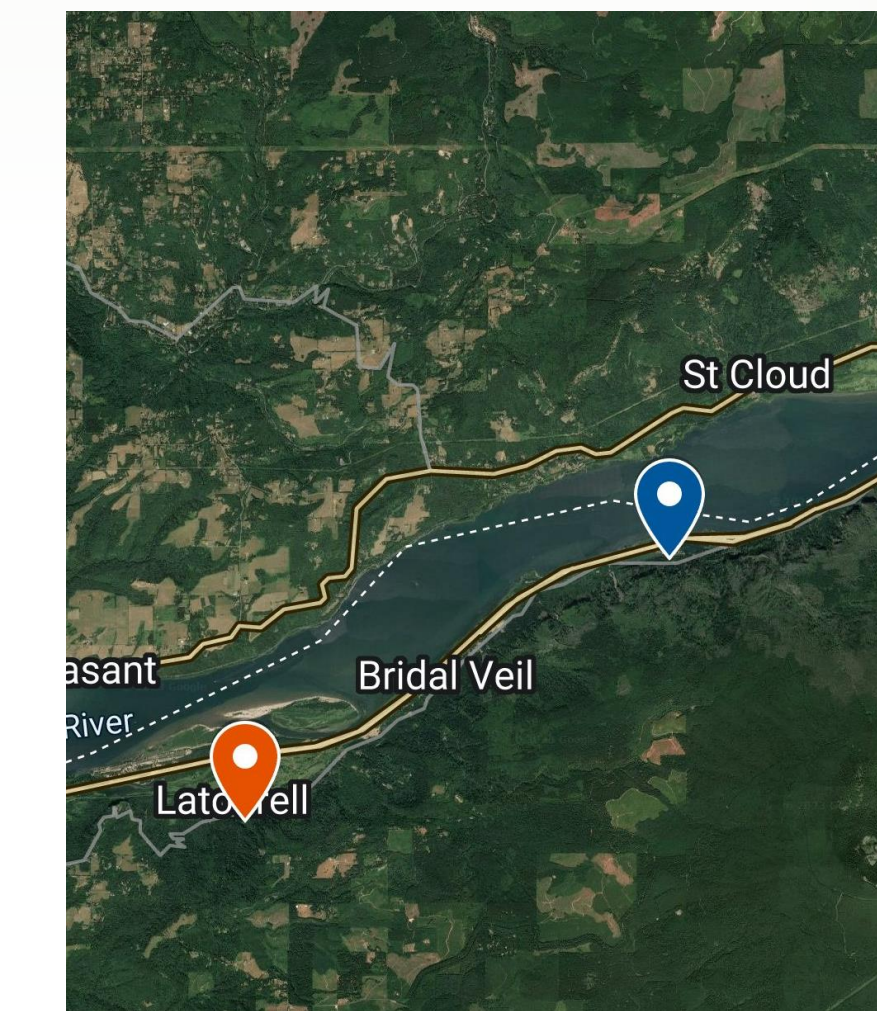LW4L3   L3LW4   L3   L3   LW4S   LW4S   LW4L3

Fig 6

1. Produce Homozygous and Heterozygous Genets (Fig 6)

I. One genet each from two populations in the Columbia River Gorge will be used to conduct the first generation of crosses (Generation I).

II. **Homozygotes:** An autogamous (within-flower) cross will be conducted for each genet to generate progeny with increased homozygosity across the genome.

III. **Heterozygotes:** Reciprocal crosses between each genet will be conducted to produce progeny with increase heterozygosity across the genome.

2. Perform Reciprocal Crosses between Generation II (Fig 6)

I. Each of the two genets of selfed offspring (L3S and LW4S) will be crossed reciprocally with the heterozygotes produced from interpopulation crosses that included the selfed offspring's parent (L3LW4 and LW4L3).

II. Each crossing is reciprocal (where each parent is both a pollen donor and an ovule donor in two individual pollination events) to account for cytoplasmic (mitochondrial and chloroplast) and nuclear genome interactions.

III. The crossing design using each of the two selfed genets in Generation II will produce eight distinct cross types (Generation III).
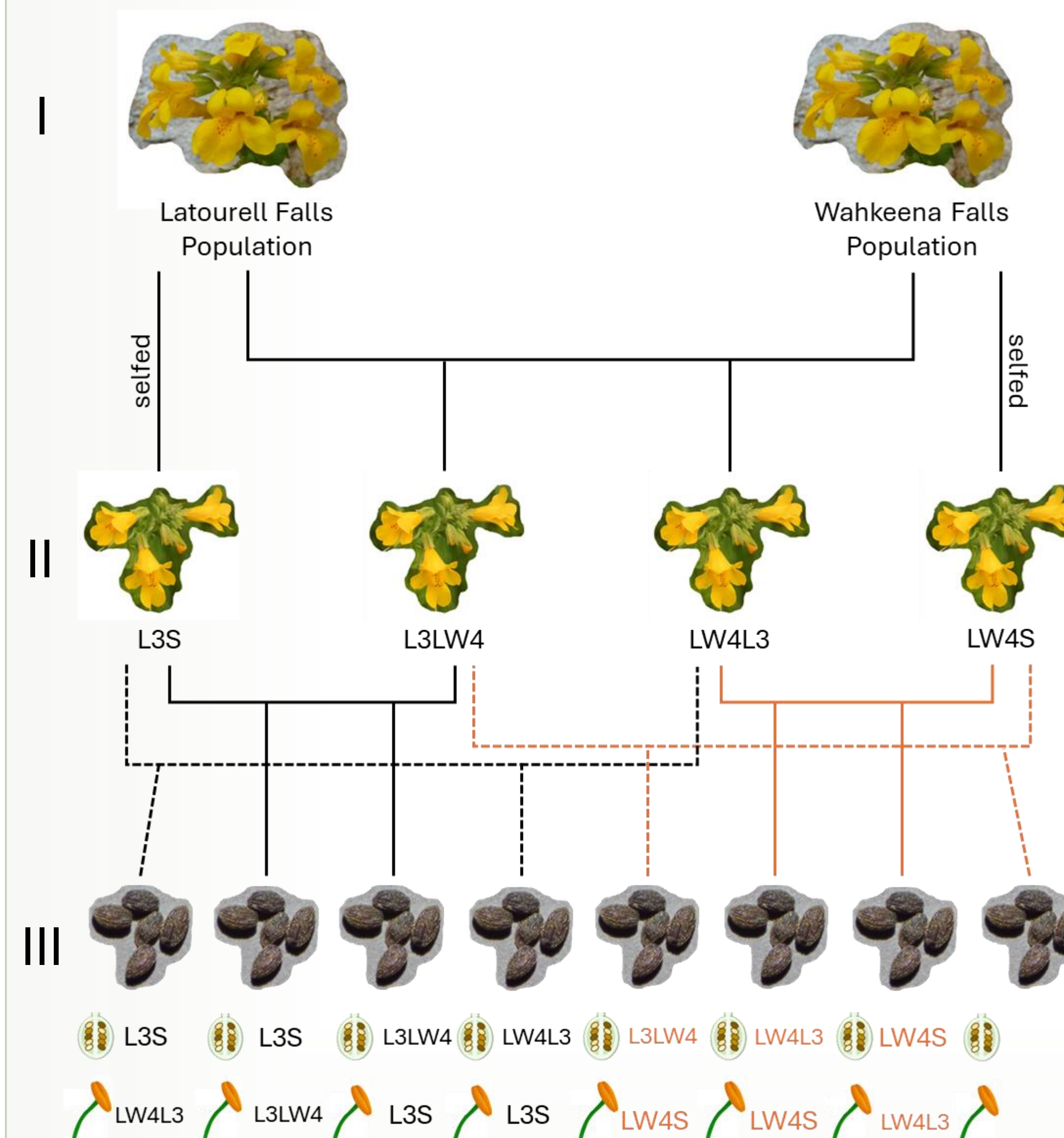
DATA ANALYSIS

I. Allele Frequency Analysis
   I. Chi-square tests will be used to identify and analyze allele frequency distortions from the expected ratio of 1:3 (Figure 8).
   II. The strength of selection on distorted loci will be estimated using the following equation:

$$\frac{(observed - expected)}{expected}$$

Fig. 8

Parent Genotype

	a	A
A	a A	A A
A	a A	A A

Expected Offspring Genotypes
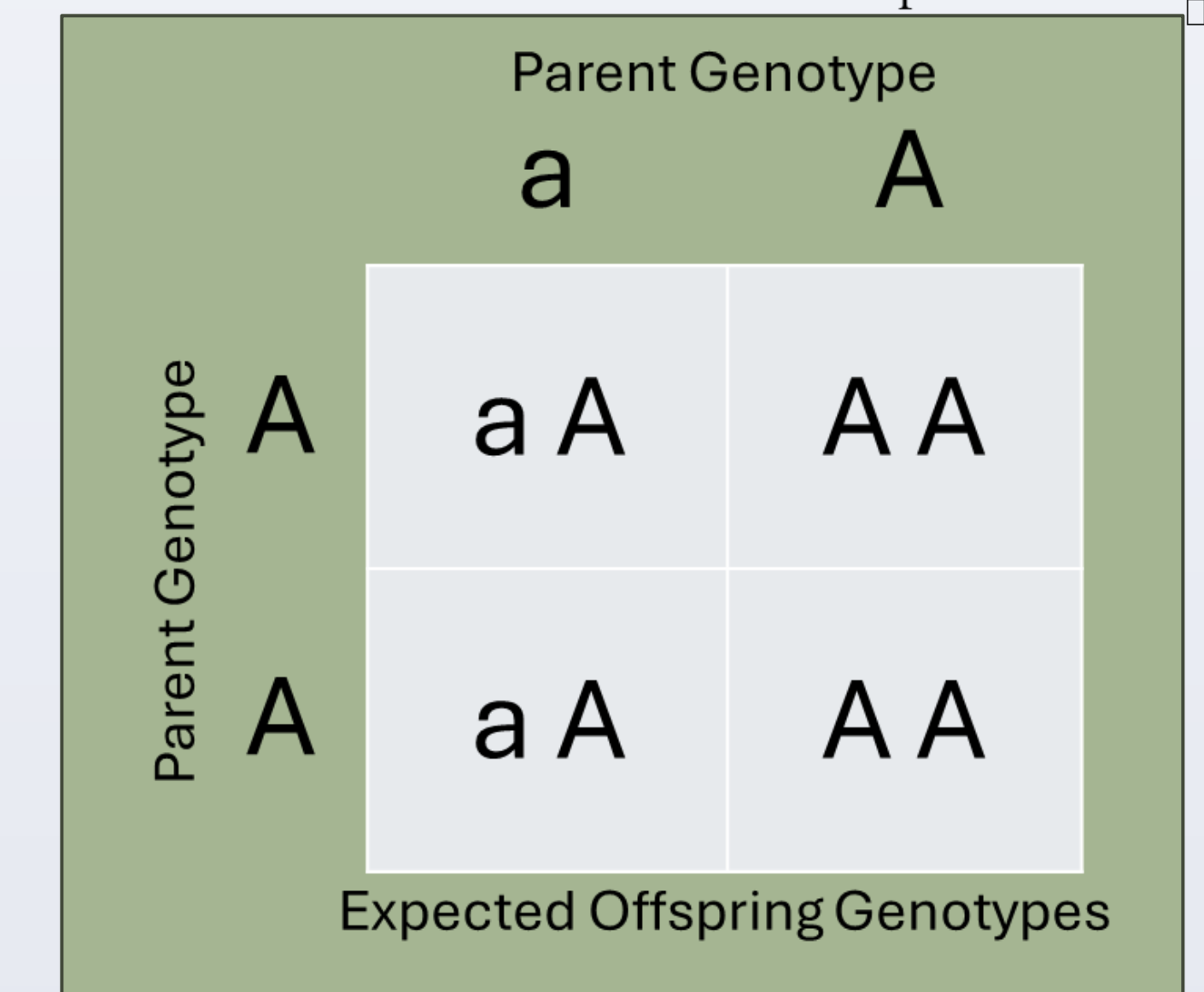
I. Interpreting Distortion in Sequenced Pollen Grains
   I. Distortion observed in F1 pollen samples suggests selection occurring during pollen development and potential pollen abortion.
II. Interpreting Distortion in Generation III Seeds (Figure 9)
   I. When the maternal plant is heterozygous, and the paternal plant is homozygous, female meiotic drive—but not GS—may occur.
   II. When the maternal plant is homozygous and the paternal plant is heterozygous, GS—but not meiotic drive—may occur.
   III. If a similar magnitude of distortion occurs in both directions of the cross, this is indicative of SEA.
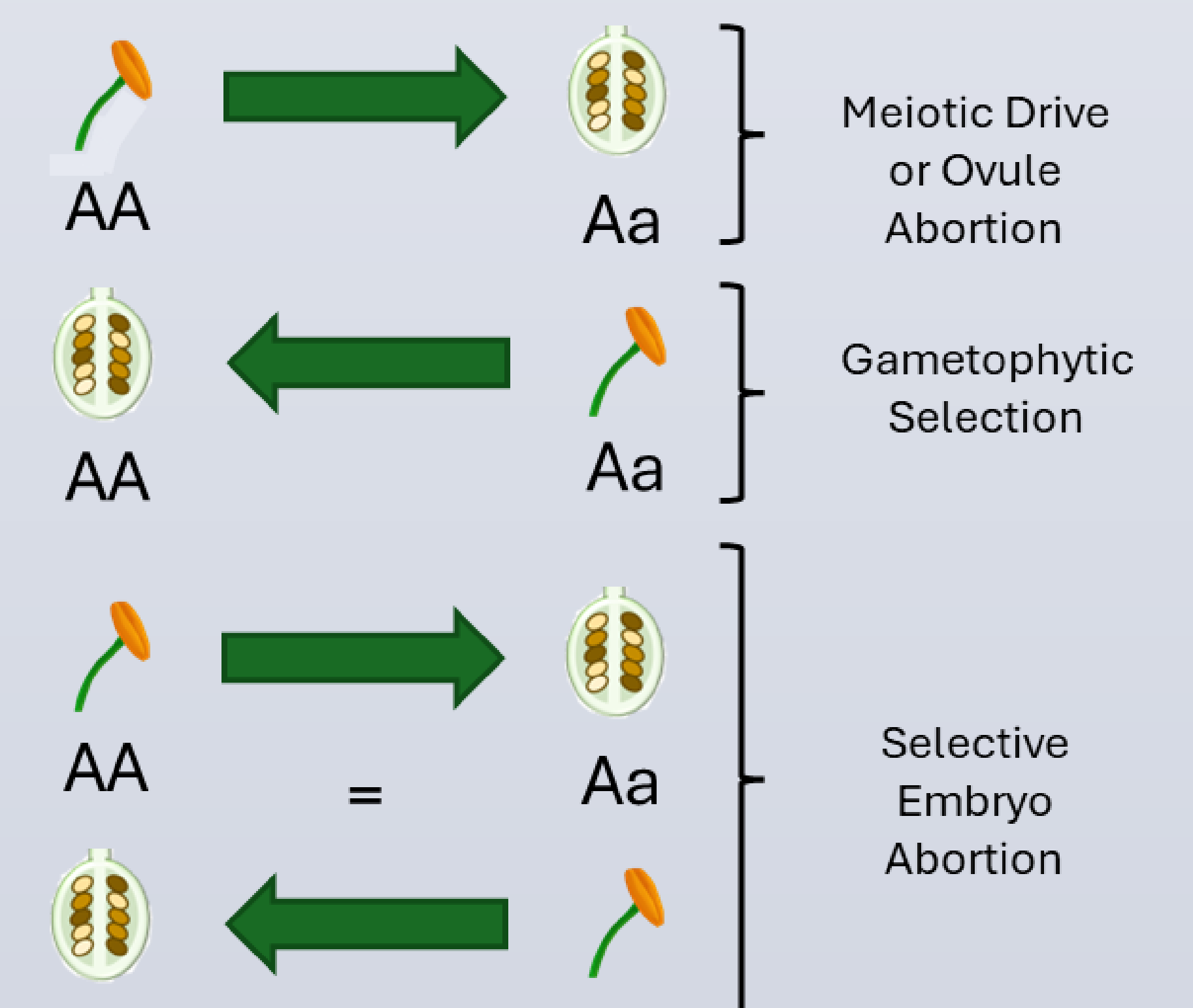
Distortion Indicates:

AA → Aa   Meiotic Drive or Ovule Abortion

AA ← Aa   Gametophytic Selection

AA → Aa
           Selective Embryo Abortion
AA = Aa ←

Fig. 9