

Notes: Evolution of Self-Incompatibility

Investigating the Role of Self-Incompatibility Systems in the Prevention of Bi-Parental Inbreeding

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Abstract

The majority of angiosperm species are hermaphroditic, with flowers harboring both male and female reproductive organs. This opens up the possibility of self-fertilization, an extreme form of inbreeding. Plants are also highly susceptible to bi-parental inbreeding due to local dispersal of pollen and seeds. Angiosperms have evolved many systems to avoid inbreeding depression by preventing self-fertilization. The most wide-spread mechanism is genetic self-incompatibility (SI) by which genetically similar pollen is rejected based on alleles at the S-locus. Due to this genetic component, SI also reduces mating between related individuals. Using a spatially explicit, individual-based simulation, this study seeks to investigate if self-incompatible taxa benefit from reduced bi-parental inbreeding in addition to the prevention of self-fertilization. If so, this additional benefit may explain the success of SI systems in angiosperms.

1 Model Description

1.1 Population Structure

In this model, the population lives on a geographically continuous $X \times Y$ rectangular lattice, where each cell may be occupied by a single, hermaphroditic, diploid individual. Generations are non-overlapping.

1.2 Genetics

Each individual is a diploid organism with two chromosomes per haploid set ($2n = 4$). Chromosome 1 contains the S locus followed by m neutral markers. Each marker has a recombination rate with S of 2^{n-m-1} where n is the marker number and m is the total number of markers. The marker furthest from the S locus will have a recombination rate of 50% with S and is thus unlinked. One cross-over event will occur each time a gamete is produced, hitting the marker region 50% of the time. Mutations will occur at the S -locus and markers via the infinite alleles model at rate μ_s and μ_m respectively.

Chromosome 2 contains a single A locus which is diallelic and only experiences forward mutations at rate μ_a . A mutation at the A locus will result in a recessive, deleterious, lethal allele. Chromosomes will be passed to gametes through Mendelian inheritance.

1.3 Dispersal

There are two different dispersal mechanisms in this model: dispersal of male gametes in pollen and dispersal of embryos in seed. Both pollen and seed dispersal will have a uniform direction and exponential distance. The probability density of dispersal in polar coordinates is

$$f(r, \theta | \sigma) = \frac{1}{2\pi} \frac{e^{-\frac{r}{\sigma}}}{\sigma}$$

where θ is the angle of dispersal from the positive x-axis and r is the dispersal distance. Pollen and seed may have different parameters of dispersal, σ_p and σ_s , respectively.

1.4 Mating Systems

The model implements five different mating scenarios.

1.4.1 No Self-Incompatibility (NSI)

Under NSI, all individuals are compatible with themselves and all other individuals. Self-fertilization occurs when pollen does not disperse out of its own cell.

1.4.2 Physical Self-Incompatibility (PSI)

Under PSI, individuals are obligate outcrossers, but there are no genetic mating-types preventing biparental inbreeding. Self-fertilization is prevented, but biparental inbreeding is always allowed. Pollen is compatible with any plant that does not occupy the same cell as the pollen donor.

1.4.3 Gametophytic Self-Incompatibility (GSI)

Under GSI, the S phenotype of the pollen is determined by its own gametophytic, haploid genotype. Pollen will be compatible if its single S allele does not match either S allele in the pollen recipient.

1.4.4 Codominant Sporophytic Self-Incompatibility (SSI)

Under SSI, the S phenotype of the pollen is determined by the diploid genotype of the sporophyte (pollen donor). All S alleles are codominant and therefore will be expressed by the pollen. Pollen will be compatible with any plant that does not share either of its S alleles.

1.4.5 Dominant Sporophytic Self-Incompatibility (BSI)

Under BSI, the S phenotype of the pollen is again determined by the diploid genotype of the sporophyte. However, dominance relationships exist between S alleles so the pollen will only express the dominant S allele. The S alleles in the population (S_1, S_2, \dots, S_n) are randomly assigned into a dominance hierarchy for determination of the phenotype. A new allele arising by mutation is assigned a random value between 0 and 1, where higher values are considered dominant over lower values. Pollen will be compatible with any plant that does not share the pollen's dominant allele.

1.5 Events

1.5.1 Initialization

The simulation begins by populating the lattice by uniformly distributing N individuals ($N \leq X \times Y$) such that there is at most a single individual per cell. In the initial generation, genotypes are assigned to individuals such that each individual possesses a distinct allele at each S locus and at each marker for a total of $2N$ unique alleles per locus in the population. The genotype for the A locus will initially be set to *wild-type*. A burn-in period will allow the population to reach equilibrium.

1.5.2 Pollen Dispersal

The plant in the first occupied cell generates p pollen grains. A new location is determined for each pollen grain based on dispersal centered on the pollen donor. If the pollen lands outside of the lattice or on an unoccupied cell it is discarded. If a pollen grain lands on an occupied cell, it is checked for compatibility with the pollen recipient. The compatibility is determined by the mating system scenario of the simulation. For each simulation, compatibility will be determined based on one of the mating system types: NSI, PSI, GSI, SSI or BSI. If the pollen is not compatible it is discarded; otherwise, it is randomly assigned to one of o ovules in the pollen recipient.

Once all of the pollen grains from the first plant have been processed, the same procedure will be repeated in the next occupied cell. This will continue until all of the plants have an opportunity to disperse pollen. A reservoir sampling strategy is used to uniformly sample the pollen received by each ovule. Once pollen dispersal is completed, ovules will either remain empty or contain a single uniformly sampled pollen grain.

1.5.3 Seed Dispersal

The plant in the first occupied cell will produce a seed for every fertilized ovule. Ovules will abort if they contain two mutated copies of the A allele. A new cell location is determined for each viable seed based on dispersal centered on the maternal plant. If the seed lands outside of the lattice it is discarded; otherwise, the seed is assigned to that cell.

Once all of the seeds from the first plant have been processed, the same procedure will be repeated in the next occupied cell. This will continue until

all of the plants have an opportunity to disperse their seeds. A reservoir sampling strategy is used to uniformly sample the seeds that land on each cell. Cells will either be empty or contain a single, uniformly sampled seed. These seeds will make up the next generation.