VARIATION IN PLANT MATING SYSTEMS

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General strategies in plant mating

Selfing

Perfect Flowers (hermaphroditic)	Self-pollination	autogamy, cleistogamy
	Cross-pollination	chasmogamy
	Heterostyly -- physical separation of style and stamen	distyly, tristyly
	Dichogamy -- temporal separation of anther/stigma maturation	protandry, protogyny
	Self-incompatibility	sporophytic SI, gametophytic SI
Imperfect Flowers	Monoecy Dioecy	androdioecy/monoecy, gynodioecy/monoecy, polygamodioecy...

Outcrossing

Predictions from plant architecture

Asexual

- Flowers can be self-compatible or self-incompatible
- Exhibit obvious traits (bulbils, bulblets, stolons, rhizomes)
- Apomicts: may not exhibit obvious features

‘Inbred’

- Small flowers (typically few)
- Unscented flowers
- Nectaries, nectar guides absent
- Synchronous maturation of anthers, ovules
- Anthers adjacent stigma
- Stigmatic region poorly-defined

‘Outbred’

- Showy flowers (typically many)
- Scented flowers
- Nectaries, nectar guides present
- Asynchronous maturation of anthers, ovules (dichogamy)
- Anthers and stigma separated (heterostyly)
- Stigmatic region well-defined

Asexual reproduction

ADVANTAGES

- Adapted genotypes preserved
- Reproductive effort minimized; assurance in limited cross-pollination.
- In agronomic settings, *genotypic frequencies cannot be changed*
- Apomixis: seed production without ovule fertilization. Seeds derive from 2N cells in embryo sac or adjacent tissue; meiosis circumvented.
  - Widespread: 35+ families, 400+ species
    - Asteraceae (*Achillea millefolium*)
    - Rosaceae (*Potentilla gracilis*)
    - Poaceae (many: *Poa, Bromus*)
- Most frequent in polyploid species

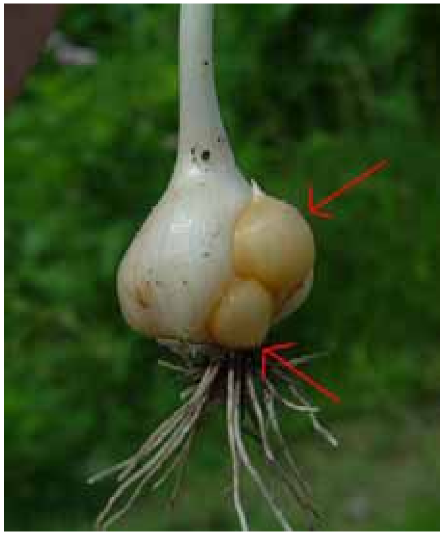


Photo: K.R. Robinson
Illinois Natural History Survey

Why not be asexual?

DISADVANTAGES

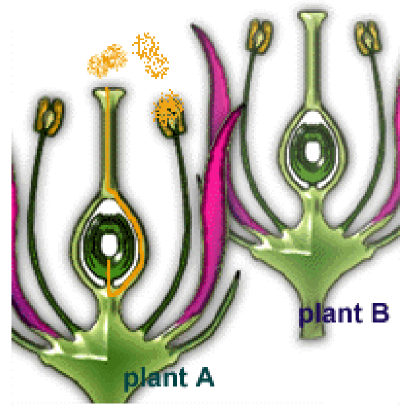
- Genotypic frequencies cannot be changed; can only change via mutation or mitotic recombination
- Within-population genetic variability may be limited if populated by few genets

Sexual Reproduction

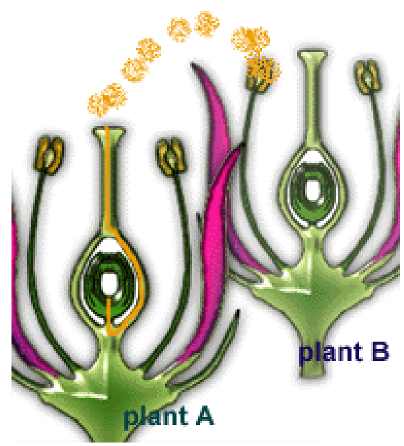
- Offspring produced through meiosis, fertilization
  - Offspring genetically different from parents due to recombination
- Diversity of floral and plant forms…
  - 'Perfect': **hermaphroditic** flowers with androecium (stamens) and gynoecium (pistil); ~70% of angiosperms
  - 'Imperfect': flowers either staminate, pistillate

‘Perfect’… but different

- Self-compatible (SC)
  - Capable of self-pollination or cross-pollination



- Self-incompatible (SI)
  - Only capable of cross-pollination due to sporophytic or gametophytic incompatibility
  - Genetic control: “S-allele” system
  - Inability of hermaphroditic plant to produce zygotes w/ self pollen



Why self?

- Reproductive assurance
  - Unpredictable pollinators
- Purging genetic load may occur when selfing rate is high
  - ‘genetic load’: reduction in fitness from the maximum possible because of segregation
  - Load can be purged to the degree that it arises from deleterious recessive alleles (Barrett and Charlesworth, Nature, 1991)

Why avoid selfing?

- Why *not* self?
  - Increasing homozygosity results in expression of deleterious recessive alleles
  - Heterozygous genotypes may have high fitness because 'normal' alleles are dominant
- Overdominance for fitness
  - 'Heterosis': heterozygous genotype is most fit
- Importance of segregation, recombination for variation
  - Selfing populations less able to respond to environmental change(?)

Why be a hermaphrodite?

- Interference of sexual function
  - Mechanical interference
- Self pollination
  - Problematic if physiological self-incompatibility is lost and genetic load is high
- Decreased pollination for females
  - If pollen is the reward for pollinators

The cost of selfing: inbreeding depression

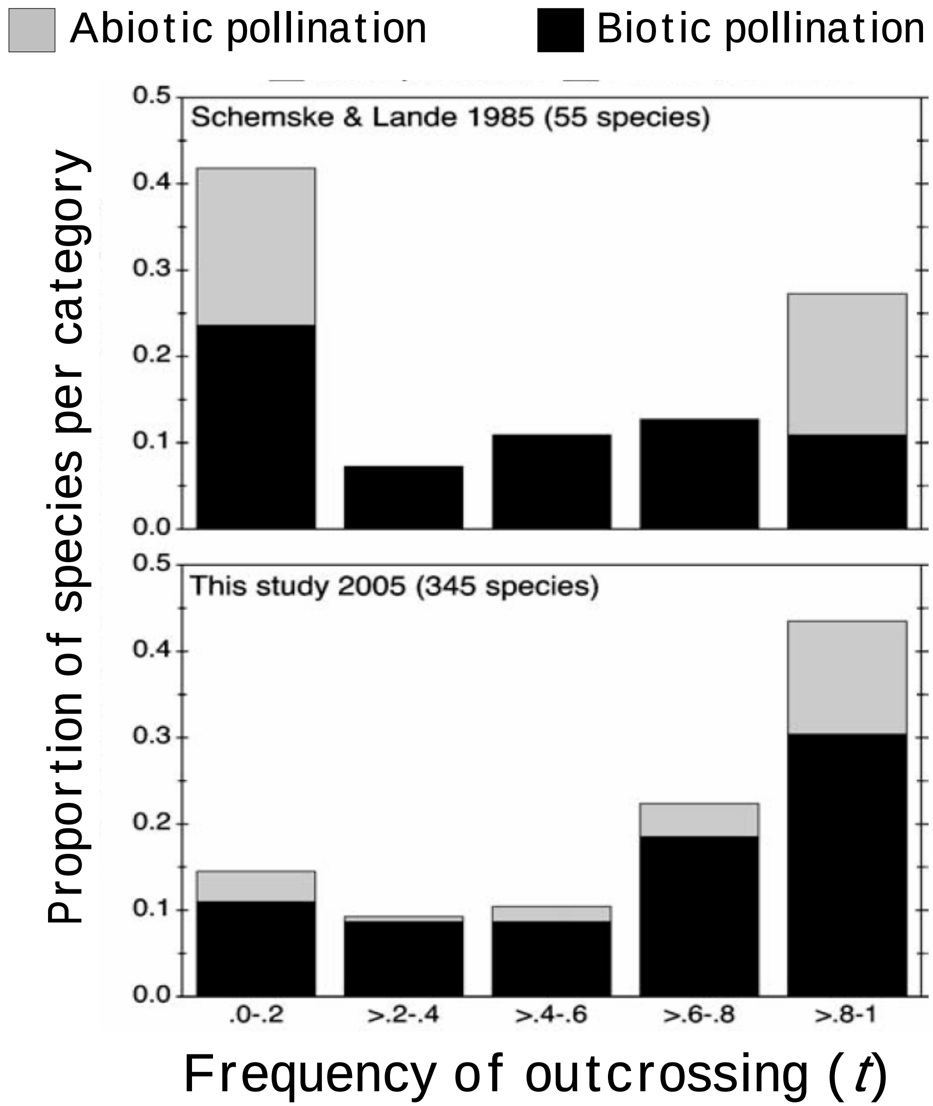
- Lande and Schemske:
  - Inbreeding depression is not a constant; evolves jointly with degree of selfing
  - As populations inbreed, deleterious recessive alleles are expressed and purged by selection
  - Positive feedback: spread of alleles that lead to increased selfing
  - *Prediction*: *"two stable states"*
    1. Inbreeding, with weak inbreeding depression
    2. Outcrossing, with strong inbreeding depression.

Showy, self-pollinating flowers (*Gossypium*)

Lande and Schemske, Evolution [1985a]

Does the hypothesis hold?

- Survey outcrossing rates: 345 species
- Sample bias: Aster, Legume, Myrtle, Grass, and Pine families
- 'Highly outcrossing' (t>0.8) most common
- 'Mixed mating' (0.2<t<0.8) represents 42% of all species
- Animal pollinated species *twice as likely to exhibit a mixed mating system*



Goodwillie et al., Ann. Rev. Ecol. Evol. Syst. [2005]

How is mixed mating maintained?

1. Heteromorphic flower systems. (e.g., cleistogamous and chasmogamous flowers)
2. Single flower type produced, but fruit contains selfed, outcrossed, or mixed progeny (proportion determined by timing of pollination and post-pollination processes)

- *Evidence*: Autonomous (same flower) and geitonogamous (same plant) selfing tolerated by the majority of species from all outcrossing classes in Goodwillie et al. (even $t > 0.8$)

How is mixed mating maintained?

3. Genetically based selfing rate polymorphisms may be common, e.g., populations with SC and SI individuals

- *Evidence*: Demonstrated self-incompatibility is common in "highly outcrossing" species (*approximately 50% of all species show SI*) but is exceedingly rare in 'mixed mating' species
- Population-level SC/SI polymorphism is not a primary contributor to mixed mating patterns

Complications: polyploidy

- Polyploidy may have a pronounced impact on breakdown of self-incompatibility.
  - Miller and Venable (2000): 37 closely related diploid-polyploid species pairs from *Lycium* (Solanaceae)
  - In 26 cases: diploids SI, polyploids SC
  - May not be universal, since many polyploid species show SI in the Asteraceae, Onagraceae and Plantaginaceae (Mable , 2004)
- Polyploidy: also associated with apomixis

Complications: polyploidy

Species	Ploidy	Chromosomes
Achillea millefolium	2X, 4X (3X, 5X, 6X)	2n = 18, 36 (27, 45, 54)
Bromus carinatus	8X (to 12-ploid?)	2n = 56 (84)
Danthonia californica	2X, 4X (6X)	2n = 18, 36 (48)
Deschampsia cespitosa	2X, 4X (3X)	2n = 14, 28 (21)
Elymus glaucus	4X	2n = 28
Eriophyllum lanatum	2X, 4X,5X,6X	2n = 16,32,40,48
Koeleria macrantha	2X, 4X	2n = 14, 28
Leymus cinereus	4X, 3X, 4X	2n = 28, 42, 56
Lupinus latifolius	2X, 4X	2n = 24, 48
Poa ampla	very high	2n = 63 (147)
Potentilla gracills	very high	2n = 52-109
Pseudoroegneria spicata	2X (4X)	2n = 14 (28)
Stipa comata	4X (?)	2n = 44

Discussion points: General

What are the most pressing issues for addressing seed increase for WV natives?

1. **Definition of breeding system (self/outcross)**
2. **Identification of animal pollinators**
3. **Estimating inbreeding depression (1 gen captivity)**
4. **Estimating outbreeding depression**
5. **Intraspecific ploidy variation in common gardens**
6. **Seed zone delimitation (using what criteria?)**
7. **Agronomic practices**
8. **Other**

Discussion points: Mating

With specific regard to seed increase for WV restoration natives…

- **1a. What is the importance of breeding system in an agronomic setting?**
- **1b. Does mixed mating offset reductions due to absence of specific pollinators?**
- **2. What is the best approach to determine whether a plant is primarily outcrossing (e.g., *Eriophyllum lanatum*), selfing or apomictic?**
- **3. Does it matter if mating system changes for one generation in an agronomic setting (e.g., increase/decrease in cleistogamy, selfing)?**