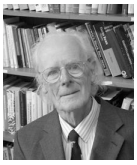
Breeding Systems

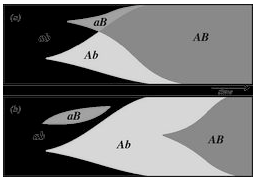
Why sexual reproduction?

Cost of males
Cost of sex (flowers, pollinator lures, loss of many gametes)
Spreads advantageous traits
Removes deleterious genes



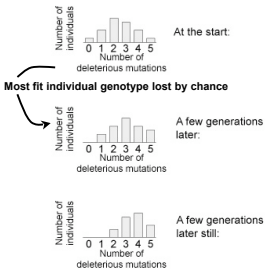
John Maynard Smith
(**Evolutionary Genetics**)

George Williams



Sexual reproduction spreads good genes through a population faster

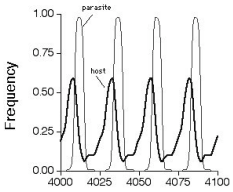
Müller's Ratchet



H J and Thea Müller

Without recombination, deleterious mutations shrink the population size, which increases the chance of fixation of deleterious mutations.
In a sexual population recombination between organisms with different deleterious mutations will regenerate the most fit genotype.

Red Queen Hypothesis



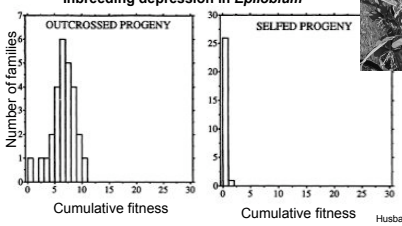
Variation in offspring to cope with arms races with predators/pests/pollinators
May hold for annual plants

Van Valen L. 1973. A new evolutionary law. Evol. Theory 1: 1-30
Matt Ridley - The Red Queen
W D (Bill) Hamilton

Variation increases fitness directly

Fitness measured by:
Number of seed per fruit,
Survival of seedlings,
Dry mass of mature plants

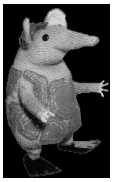
Inbreeding depression in *Epilobium*

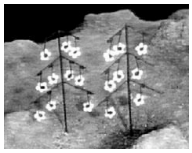


Husband and Schemsky(1997)

Suggests many recessive deleterious mutations,
Clonal spread would not be affected by this - propagation of the fit parental genotype

Plants are very different from animals





Separation of germline from soma
Mostly sexual reproduction
Often discreet generations
Overwhelmingly diploid

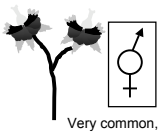
Many cells totipotent
Asexual reproduction common
Longevity/seed banks blur generations
Ploidy of various levels common

Some Vocabulary

DIOECIOUS Male and female plants
MONOECIOUS Having male and female flowers on the same plant
APOMICTIC non-sexual reproduction (vegetative and agamospermous)
DICHOGAMY: A provision in hermaphroditic flowers to ensure cross-fertilization (and prevent self-fertilization) by a difference in the time of maturity of the anthers and the stigma
DICLINOUS: Having stamens or pistils in separate flowers
DIOECIOPOLYGAMOUS: Polygamous with a tendency to dioeciousness, or to the prevalence of flowers of one sex on individual plants, such as a plant with mostly female flowers
DIOECIOUS: Bearing male and female flowers on separate plants
POLYGAMOUS: Bearing both unisexual or bisexual flowers on the same plant or on plants of the same species
UNISEXUAL flowers either male or female only
BISEXUAL flowers with anthers and stigmas
AGAMOSPERMY Seed without gametes -
Diplospory - 2n gametophyte embryosac develops as an embryo
Apospory - unreduced (2n) cell from gametophye develops as embryo
Adventitious Embryo - Embryo from maternal somatic tissue
ALLOGAMY Out breeding
AUTOGAMY In breeding - self fertile
PROTANDROUS Male parts of flower develop first
PROTGYNOUS Female parts of flower developing first
GEITONOGAMY selfing within a plant, via pollinator movement
CLEISTOGAMY obligate selfing within a flower that never opens
CHASMOGAMOUS open pollinated flowers

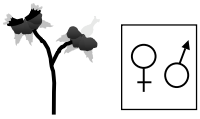
Co-sexual - plant male and female

All hermaphodite



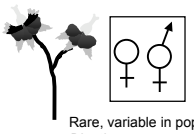
Very common, *Arabidopsis*

Monoecious



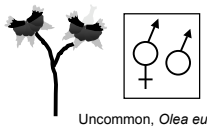
Common, *Begonia, maize*

Gynomonoecious



Rare, variable in pops. *Dianthus*

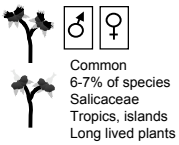
Andromonecious



Uncommon, *Olea europaea*

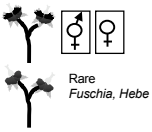
Dicliny - at least some individuals unisexual

Dioecious



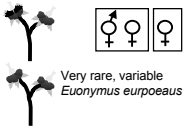
Common
6-7% of species
Salicaceae
Tropics, islands
Long lived plants

Gynodiecious



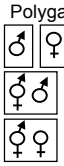
Rare
Fuschia, Hebe

Subgynoecious



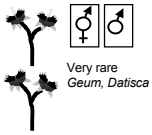
Very rare, variable
Euonymus eurpoeaus

Polygamous



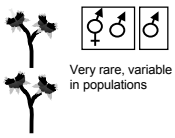
Very rare.
Usually due to environmental effects

Androdioecious



Very rare
Geum, Datisca

Subandroecious



Very rare, variable in populations

Promoting Diversity

Sexual segregation - unisexual flowers (Prevents geitogamy)

Separation in space encourages outcrossing

Promoting Diversity

Plants with sex chromosomes - enforces outcrossing

Male Tree **American Holly *(Ilex opaca)*** Female Tree

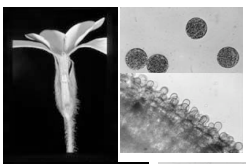
See work on Silene by Deborah Charlesworth

Promoting Diversity

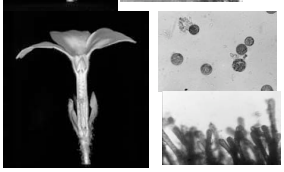
Separation in space by floral forms
Enforces outcrossing

Primulus Pin and Thrum Forms

Pin
Stigma high



Thrum
Stamens high



Promoting Diversity

Separation in time I Protogyny

Promoting Diversity

Separation in time II Protoandry

Anthers first

A few hours later

stigma arms open

Later stigma arms curl back to allow self pollination

Plants often combine sexual and asexual which makes it easier for them to use the advantages of sex, without suffering all the costs

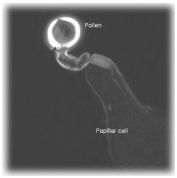
Sporophytic self incompatiblity

Known in Brassicaceae, Asteraceae and the Convolvulaceae

A transmembrane receptor, S-receptor kinases (SRK) in the stigma recognises a S-locus cystein rich protein (SCR) in the exine (sporophytic) coat of the pollen grains.

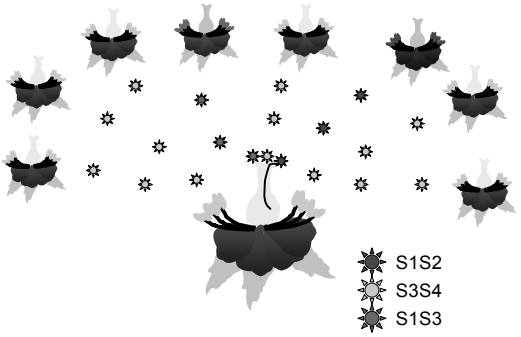
Both loci are highly polymorphic

A match results in no hydration or germination of the pollen



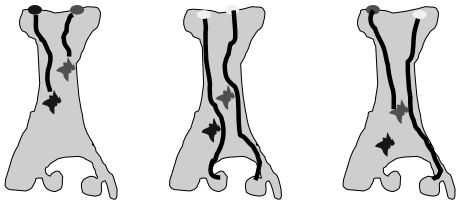
Self incompatability systems

A signaling system to recognise and reject self/similar



Gametophytic self incompatiblity

Characterised in *Oenothera* sp.,
Solanaceae
Papaveraceae
Poaceae
Ranunculaceae
Rosaceae

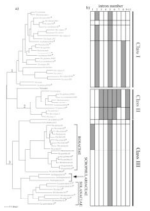


RNAse in style stops pollen tube growth if genotype of pollen matches

SI mechanisms have evolved multiple times in Angiosperms

Three self-incompatibility systems characterized at molecular level among Brasicaceae, Papveraceae and Solanaceae are unrelated.

ML phylogeny of plant T2-type RNases



From the possible monophyletic origin of Class III enzymes and that ~ 75% of dicots were evolved from families with S-RNAse type GSI, Igic and Kohn(2001) concluded that Rnase based self-incompatibility was the ancestral type self-incompatibility of eudicot species.

Avoiding sex

JBS Haldane
Coined the word 'clone' from the greek for twig

Vegetative reproduction - Breaking off

Elodea canadensis - exclusively veg rep in Europe
Fallopia japonica - exclusively veg rep in Europe

Introduced to UK in 1840
Found throughout Europe by 1880

Introduced early 1800s
Proscribed under Wildlife and Countryside Act 1981

Advantages of staying the same

Proven formula

Very fast

Single plant can colonise

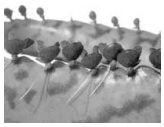
If also sexual then has a 3:2 advantage over outcrossers in next generation (Fisher)

No cost of males

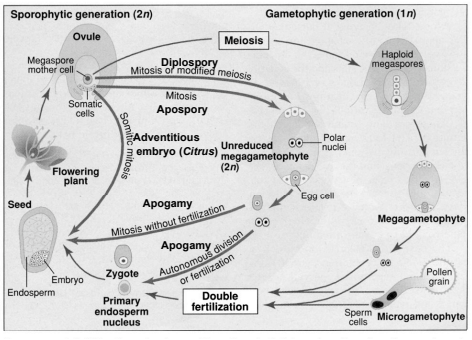
No cost of pollination

Vegetative reproduction - Second chances

Many perennial plants use vegetative and sexual reproduction at different times - garners both benefits



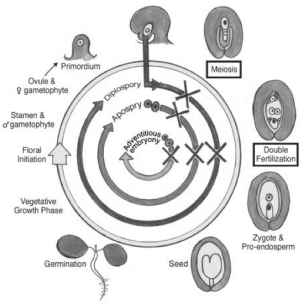
Clover - stolons
Convulous - roots, stems
Willow - suckers
Grasses - tillering
Kalanchoe - vivipery



Apomixis combines the benefits of seeds with the benefits of asexual reproduction

Vielle Calzada et al., (1996) Apomixis: The Asexual Revolution *Science*, 274 1322-1323.

Apomixis combines the benefits of seeds with the benefits of asexual reproduction



From maternal tissues

From somatic gametophyte cells

From the megaspore mother cell

Found in >400 species, >40 families

Probably more as it needs genetic data to prove

Biased distribution:

Commonest in Asteraceae, Roasaceae, Poaceae

Not in gymnosperms, uncommon in Orchidaceae

Associated with: Physiological self incompatability

Dioecy

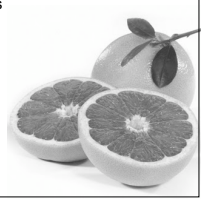
Heterostyly

Almost always perennials

Vegetative reproduction

Dehiscent fruits

Very rarely obligate



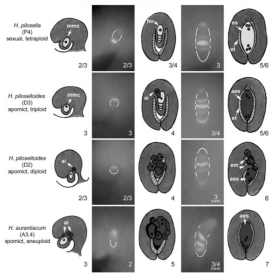
Hawkweeds are facultative apomicts

All bases covered

Viable pollen

Apomictic

Vegetative repro



Sexual repro, **apospory**

Apomixis genes

Mostly a small number of loci are involved.
Single dominant gene in:
Pennisetum, Brachiaria, Ranunculus, Heiracium

Taraxacum:
Two loci, one regulating diplospory, the other parthenogenisis

A key goal is producing apomictic F1 hybrid strains for agriculture

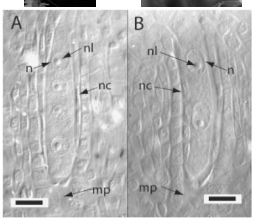
Vijverberg K, Milanovic-Ivanovic S, Bakx-Schotman T, van Dijk PJ. (2010)
Genetic fine-mapping of DIPLOSPOROUS in Taraxacum (dandelion; Asteraceae)
indicates a duplicated DIP-gene. BMC Plant Biol. ;10:154

Used AFLPs to define the DIP-locus to 0.6 cM, which is estimated to cover ~200-300 Kb. Recombination in this region supressed so very difficult to clone

Loss of Meiosis 1 function underlies some apomictics

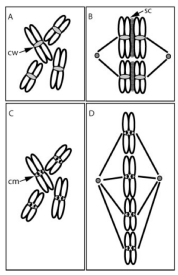
Eringium strigosus

Eringium annuus



4 haploid nuclei

Failure of Meiosis 1
2 unreduced nuclei



wt

dyad

DYAD is required for chromatid cohensin and the synaptonemal complex (sc). Linked to Apomixy loci in *Tripsacum*

How do apomixis genes spread?

An evolutionary dead end?

Clonal diversity is generated by rare hybridisation with sexual species, as well as by somatic mutations.

Occasionally the apomictic genes are transferred to a sexual species and can start to spread a new line without the genetic load of accumulated deleterious mutations

Currently loci conferring apomixis have been identified in several species

However, recombination around these loci is suppressed, making map based cloning difficult.

Why haven't apomictic/selfing species taken over the world?

Inbreeding depression

Homozgosity of deleterious mutations

Niche disappears - Vicar of Bray

Mutational meltdown - Müller's ratchet

Effective population size is small, deleterious mutations go to fixation quicker, shrinking the population and so on

Out raced by sexual species in red queen games

Nothing ever stays the same

Consequences of breeding systems

Arabidopsis thalia - populations treated as total homozygotes (8% polymorphic microsatelite)

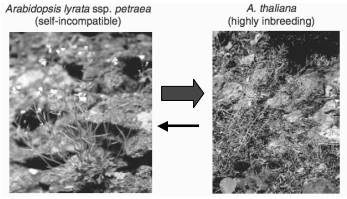
Arabidopsis lyrata - populations heterozygous at at least 85% of microsatellite loci examined

General loss of diversity

Deleterious and advantageous mutations can be homozygosied more easier

Lowers effective population size - more drift effects. Easier to fix good and lose bad.

Advantages of selfing over outcrossing



Reproductive assurance

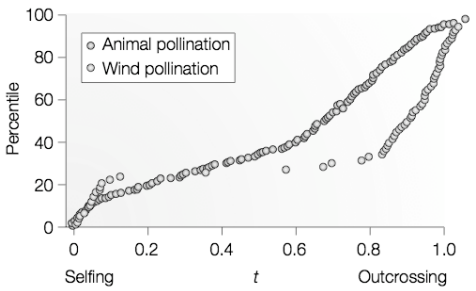
Mate finding can be unreliable

Automatic selection

Transmission advantage of being paternal and maternal parent of seed

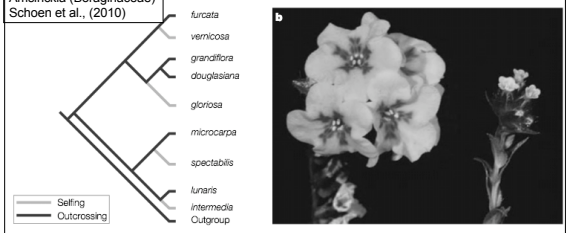
Ease of loss of SI
vs
Difficulty of evolving it

More outcrossing in Animal pollinated species
More mixed mating strategies in Animal pollinated species



What happens on the switch to selfing?

Amsinckia (Boraginaceae)
Schoen et al., (2010)

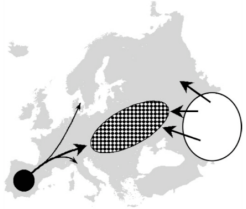


Immediate increase in inbreeding depression
later loss of inbreeding depression
Shift in allocation of resources away from pollinator attraction
Better colonising ability

How does selfing evolve from self incompatibile?

Dating the switch in *Arabidopsis* by molecular evolutionary analysis suggests it occurred 413,000 years ago.

During the expansion from refugia following the ice age.



Theory suggests changes to the ligand are likely to spread quicker

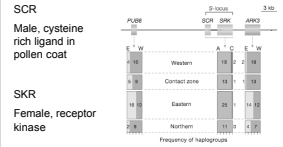
How does selfing evolve from self incompatibile?

SCR

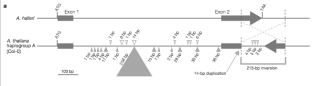
Male, cysteine rich ligand in pollen coat

SKR

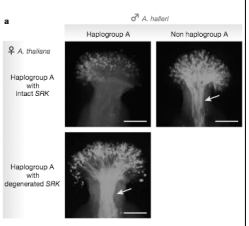
Female, receptor kinase



S-locus is much less polymorphic than flanking regions
Recent sweep



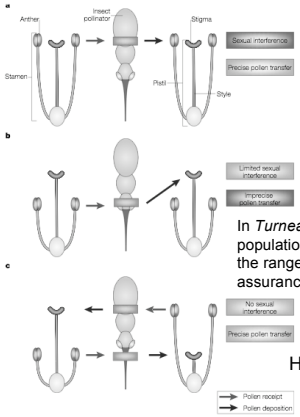
SCR-A of *A. thaliana* has lost 3/8 cysteines due to an inversion and has many indels



SRK-A alleles in *A. thaliana* can be fully functional.

(The A allele of the S-incompatability system is shared between *A. thaliana* and *A. halleri*)

Takashi Tsuchimatsu et al., (2010) Evolution of self-compatibility in *Arabidopsis* by a mutation in the male specificity gene *Nature* **464**, 1342-1346



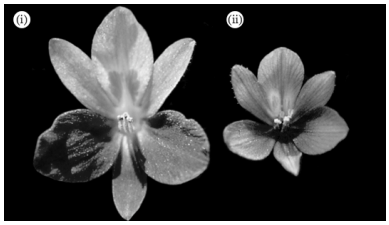
In *Primula* linked loci govern anther and style height.

Recombination between these loci gives homostyly

In *Turnea* and *Eichhornia* homostylous populations are found at the edges of the range and on islands - reproductive assurance

Heterostyly

Is selfing a path of no return?



Outcrosser (heterostyly) Selfer (homostyly)

Populations of homostylous *Eichhornia paniculata* from Jamaica Have smaller flowers than heterostylous populations from Brazil. If they became heterostylous again they may not be able to compete for pollinators

Cleistogamy and bet-hedging

Gymnarrhena micrantha
Annual composite from the Middle East

Dry years - only below ground seeds are produced
Wet years -many above ground flowers are produced

Cleistogamous Flowers

2-3 produced per plant
Below ground flower
Self pollinated
Lots of food reserves in seeds

Chasmogamous Flowers

Many small, seeds produced
Above ground flowers
Pappus on seed for enhanced wind dispersal
Outcrossed
Fewer food reserves in seeds

Also see work on Violets

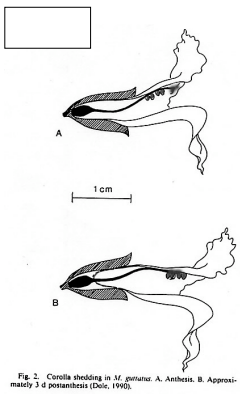


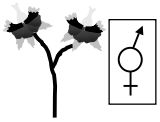
Fig. 2. Corolla shedding in *M. guttatus*. A. Anthesis. B. Approximately 3 d postanthesis (Dole, 1990).

When outbreeding fails

Fading flower brings anther down onto stigma, ensuring some seed at least is formed

Dole 1992. AJB 79:650-659

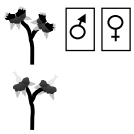
Hermaphodite

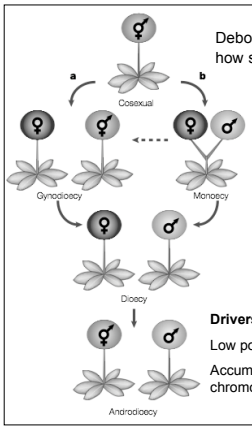


How does Dioecy evolve?

Transmission reduced by up to 50%
Loss of reproductive assurance
Requires the spread of mutations which cause sterility

Dioecious





Deborah Charlesworth - theoretical models of how such transistions could be selected for

Drivers of Dioecy

Female fertility of hermaphrodites low
(high female investment)

High inbreeding depression
Selects for outbreeding

'Easy' mutation to confer sex on individuals

Drivers back to cosexual

Low pollen availablity - Androdioecy

Accumulation of deleterious mutations on Y chromosomes, reduced male survival - Gynodioecy

Which traits correlate with dioecy?

6-7% of species
Salicaceae
Tropics, islands
Long lived plants
Fleshy fruited species
Abiotic pollination
Inconspicuous flowers

Sagittaria latifolia varies between populations

Avoiding inbreeding depression
(Avoiding geitogamy)
High female costs
Time to wait for a better pollinating year

Vamosi et al., (2003) J. Evol. Biol

What determines breeding system?

Outcrossing rates - Plant density,
Pollinator behavoir

Inbreeding depression

Ease of evolving self compatability versus difficulty of evolving incompatability systems and dioecy

Accumulation of deleterious mutations on the Y chromosome