

Proměnlivost a evoluce rostlin

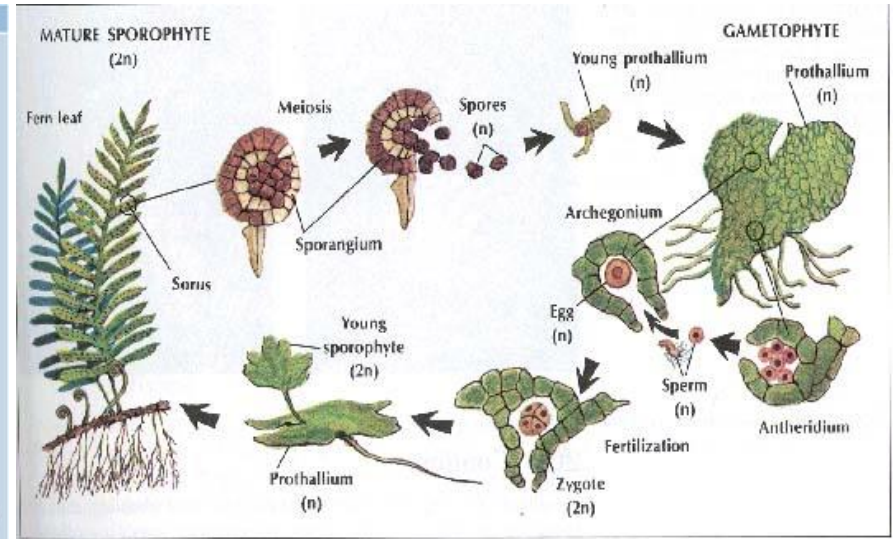
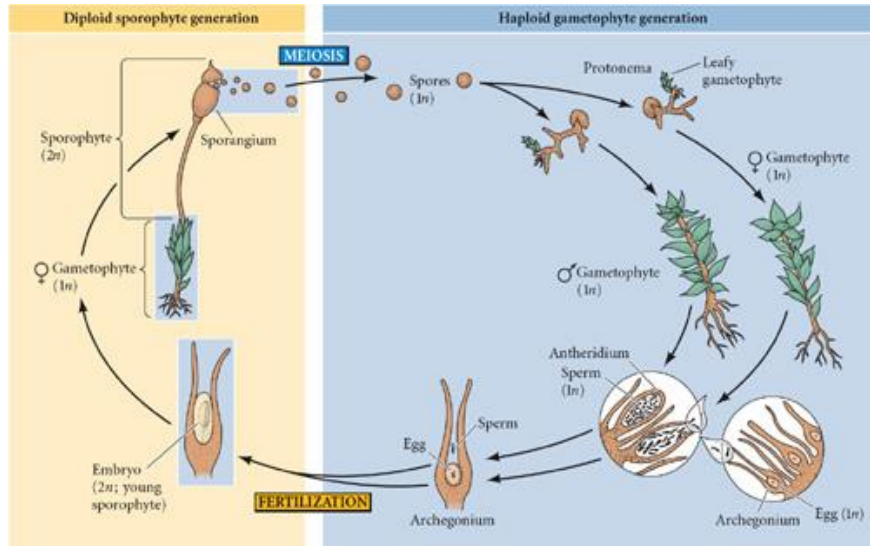
Petr Smýkal

Katedra botaniky, PřF UPOL

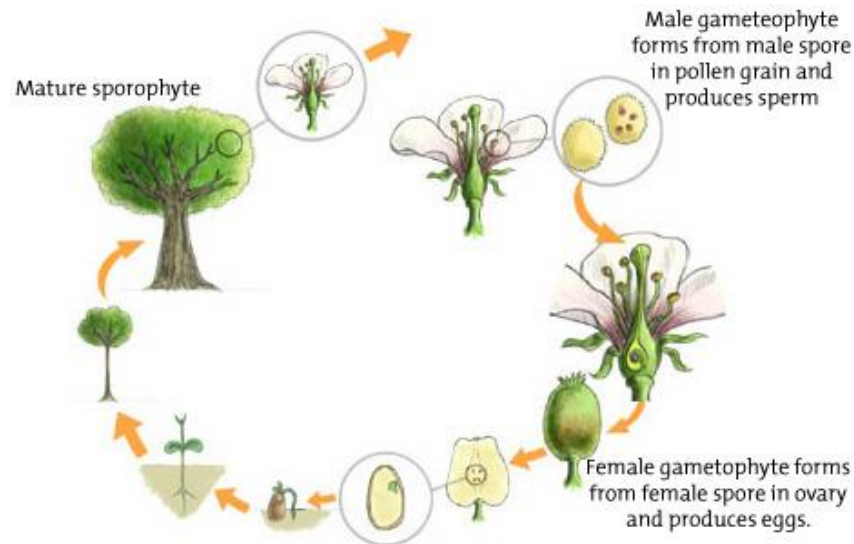
2013/14

Rozmnožovací systémy rostlin

Gametofyt x sporofyt



mechy

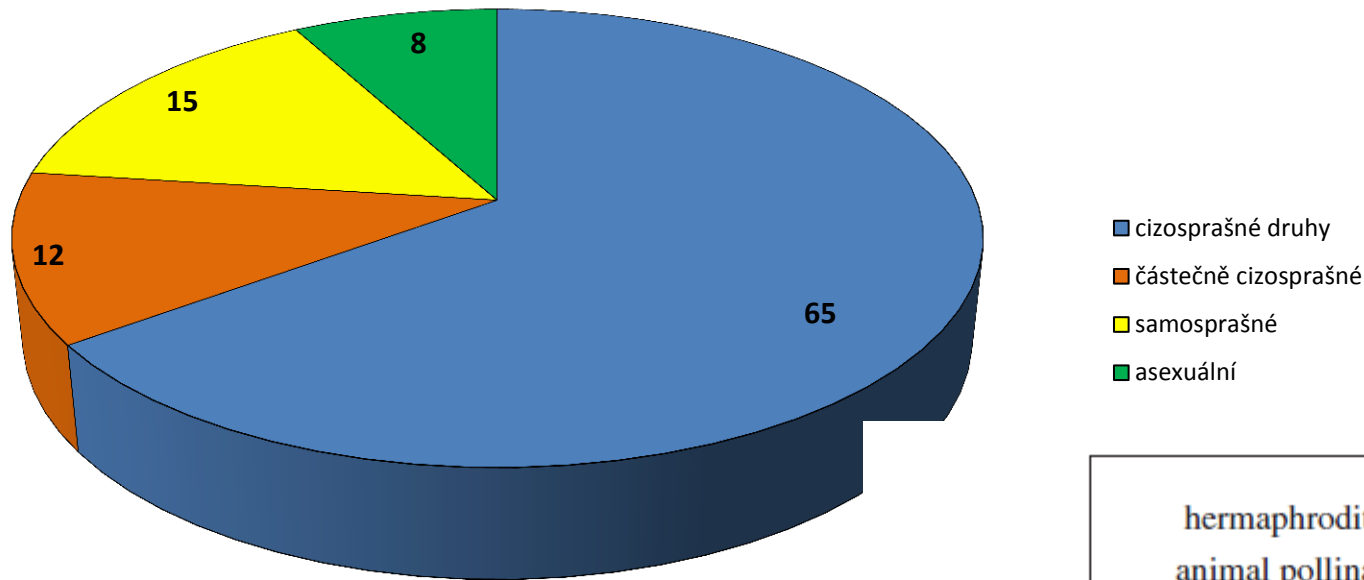


kapradiny

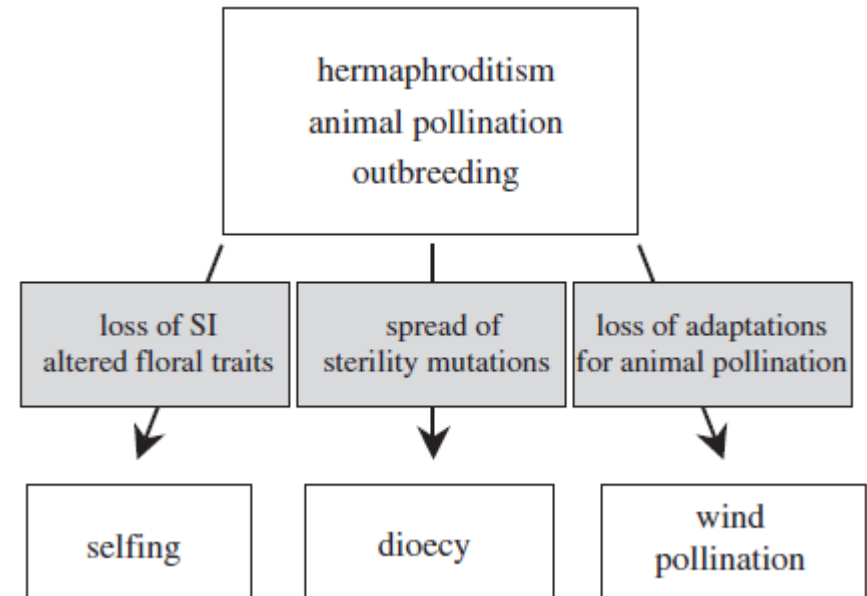
General strategies in plant mating

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

Podíl cizo- a samosprašných druhů rostlin

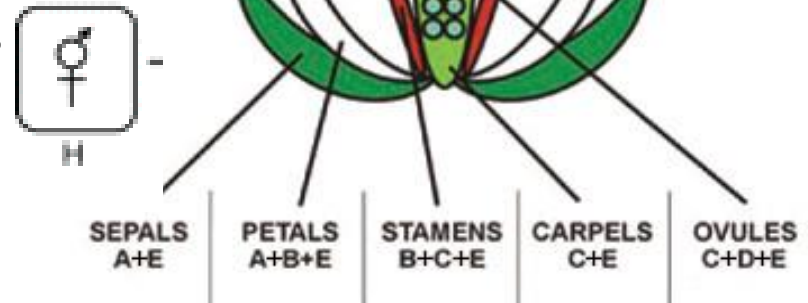


Evoluce reproduktivních systémů rostlin



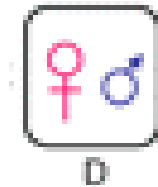
I. Typy pohlaví - květy

Oboupohlavné (= hermafroditní).
(75% krytosemenných)



Jednopohlavné - **Tyčinkové (samčí)**

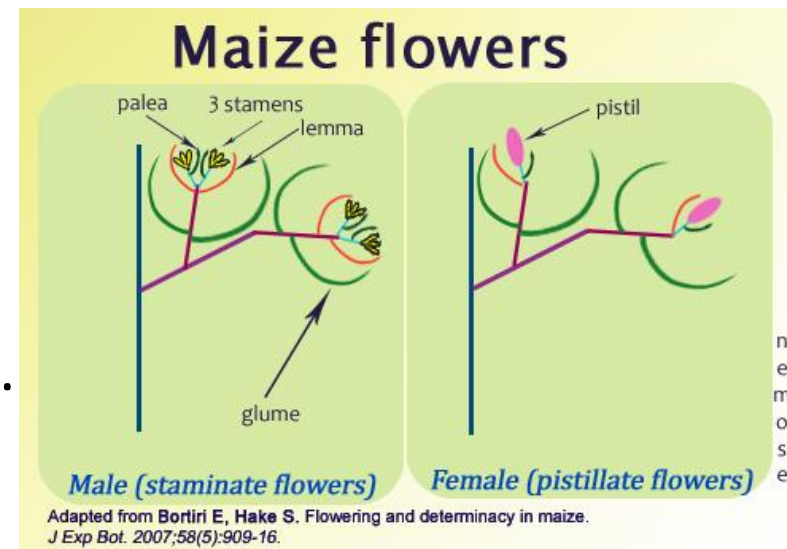
Mají funkční prašníky. Mohou obsahovat i nefunkční pestíky.



Jednopohlavné - **Pestíkové (samičí)**

Mají funkční pestíky.

Mohou obsahovat i nefunkční tyčinky.



II. Typy pohlaví - rostlina

Jednodomé (monoecická). Tyčinkové a pestíkové květy na jedné rostlině:
Aglaonema, Fagus, Betula, Euphorbia, Zea



Dvoudomé (dioecická) – asi 7% všech rostlin

Tyčinkové a pestíkové květy na odlišných rostlinách.

Silene latifolia, Humulus lupulus, Cannabis sativa



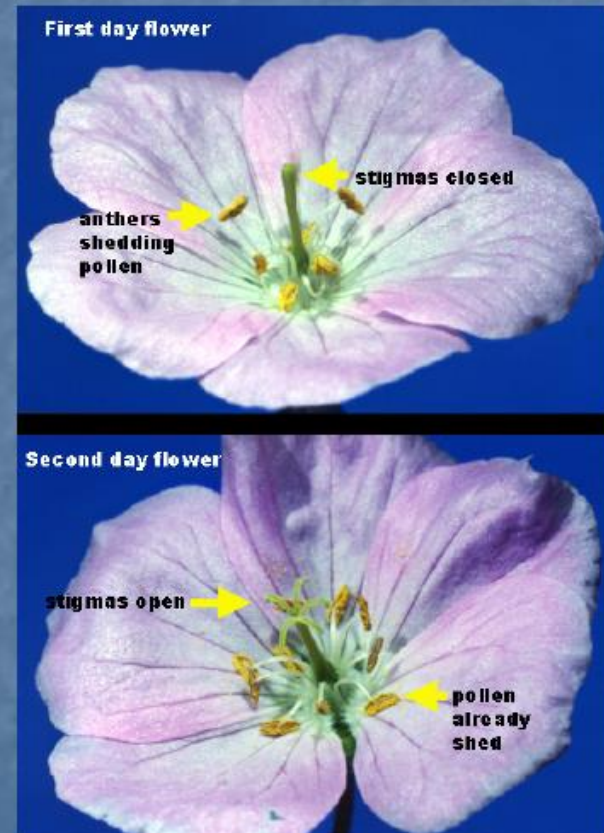
Why be an Hermaphrodite?

- Facultative selfing.
 - If pollinators are not available.
- Male/female shared investment in attractants and rewards.
 - Two for the price of one?
 - Attractants affect male and female fitness gain curves differently.
- Temporal separation of investment in male and female function.
 - Male today, female tomorrow.



Why not be an Hermaphrodite?

- Interference of sexual function.
 - Mechanical interference.
 - Favors evolution of herkogamy or dichogamy.
 - Self pollination.
 - Problematic when physiological self-incompatibility is lost and genetic load is high.
 - Evolution of dioecy on islands.
- Decreased pollination for females.
 - If pollen is a reward for pollinators.



Pohlavní chromozómy u rostlin

Samčí a samičí květy (top) a pohlavní X and Y chromozómy (bottom) u *Silene latifolia*.



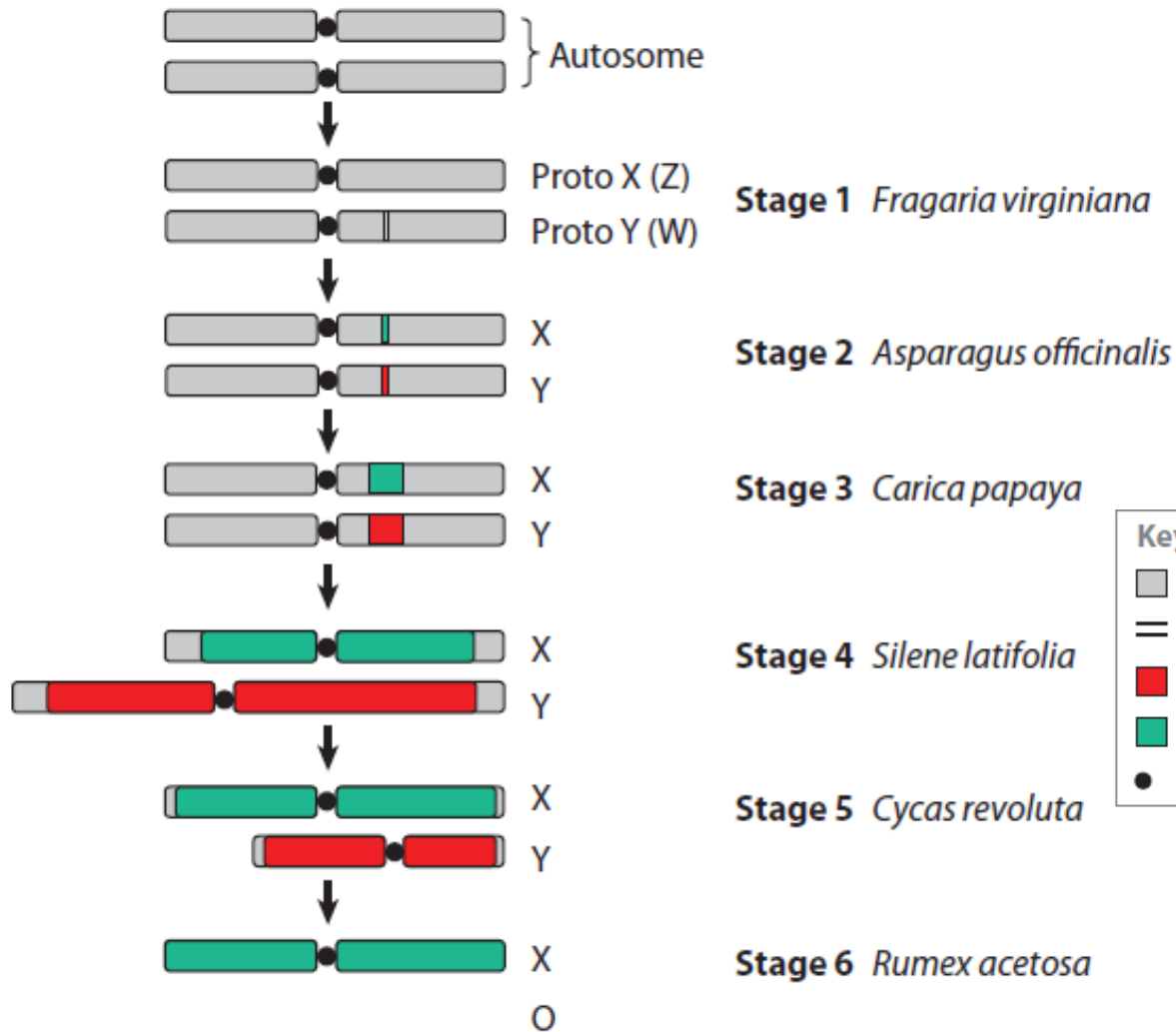
Meadows R (2012) Sex Chromosome Equality in Plants. PLoS Biol 10(4): e1001312. doi:10.1371/journal.pbio.1001312
<http://www.plosbiology.org/article/info:doi/10.1371/journal.pbio.1001312>

Sex Lability

- Many plant species change sex.
 - Plant size (larger plants are female).
 - Sugar maples.
 - Jack in the pulpit.
 - Environment (females grow in less stressful microhabitats).
 - Salt bush.
 - Salt grass.
 - Mosses.



Evolve pohlavních chromozómů



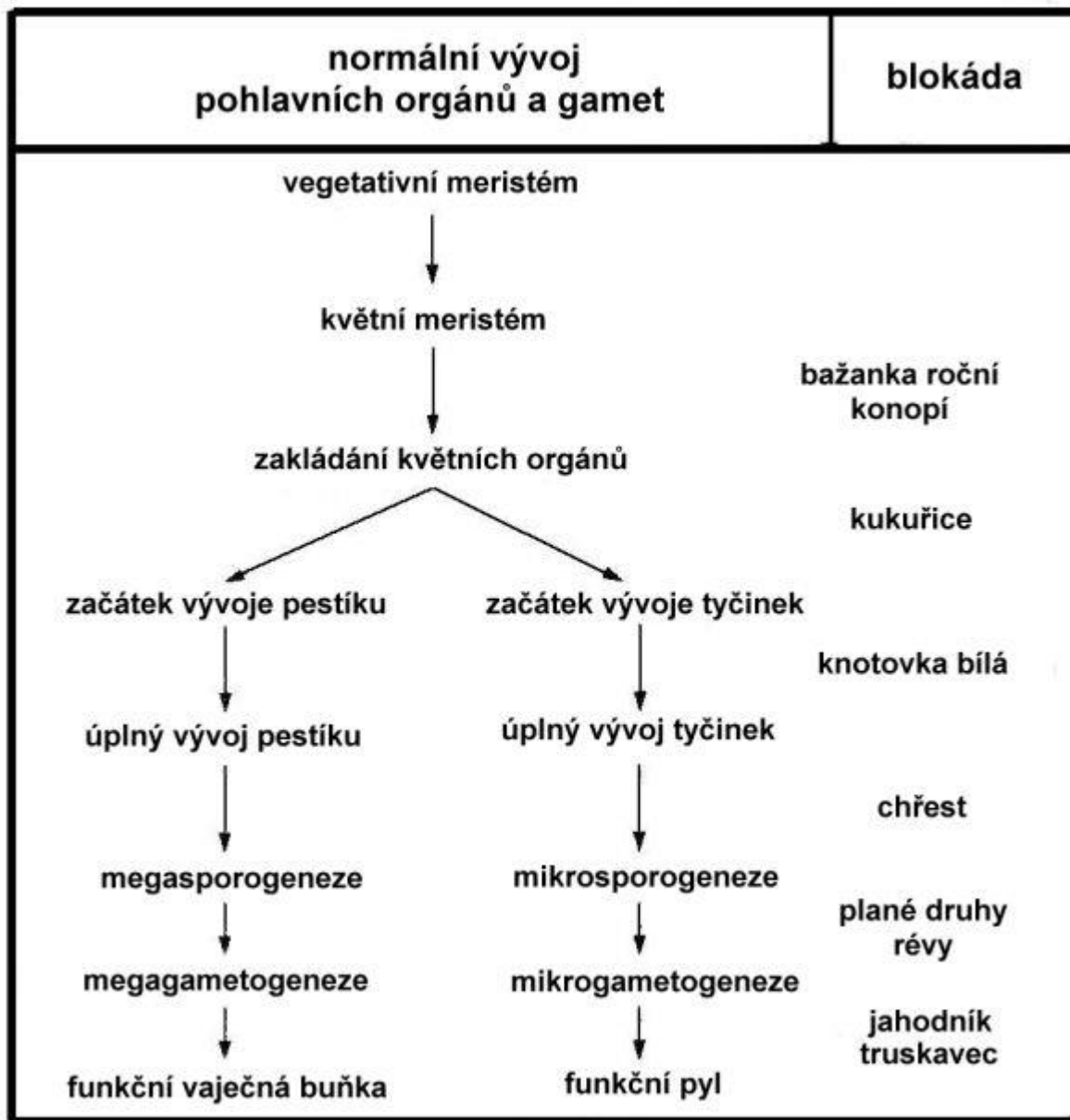
Homomorphic sex chromosomes

Actinidiaceae	<i>Actinidia deliciosa</i>	—	—	Active Y system
	<i>A. chinensis</i>	Male heterozygous	Yes	Active Y system
Amaranthaceae	<i>Acnida</i> species	Male heterozygous	—	Active Y system
Asparagaceae	<i>Asparagus officinalis</i>	Male heterozygous	Yes	Active Y system
Asteraceae	<i>Antennaria dioica</i>	Male heterozygous	No	—
Caricaceae	<i>Carica papaya</i>	Male heterozygous	No	Active Y system
	<i>Vasconcellea</i> species	Male heterozygous	No	Active Y system
Caryophyllaceae	<i>Silene otites</i>	Uncertain	—	—
Chenopodiaceae	<i>Spinacia oleracea</i>	Male heterozygous	Yes	Active Y system
Cucurbitaceae	<i>Bryonia multiflora</i>	Male heterozygous	—	—
	<i>Ecballium elaterium</i>	Male heterozygous	—	Active Y system
Dioscoreaceae	<i>Dioscorea tokoro</i>	Male heterozygous	—	Active Y system
Euphorbiaceae	<i>Mercurialis annua</i>	Male heterozygous	Yes	Active Y system
Ranunculaceae	<i>Thalictrum</i> species	Male heterozygous	Yes	—
Rosaceae	<i>Fragaria</i> species	Female heterozygous	—	—
Vitaceae	<i>Vitis</i> species	Male heterozygous	Yes	Active Y system

McCLUNG, C. E. 1901. Notes on the accessory chromosome. *Anatomischer Anzeiger* 20: 220–226.

Family	Species	Female sex chromosome	Male sex chromosome	Viability of YY genotype	Sex determination
Heteromorphic sex chromosomes					
Cannabidaceae	<i>Cannabis sativa</i>	XX	XY	Yes	X to autosome ratio
	<i>Humulus lupulus</i>	XX	XY	Yes	X to autosome ratio
	<i>H. lupulus</i> subsp. <i>cordifolius</i>	X ₁ X ₁ X ₂ X ₂	X ₁ Y ₁ X ₂ Y ₂	—	X to autosome ratio
	<i>H. japonicus</i>	XX	XY ₁ Y ₂	No	X to autosome ratio
Caryophyllaceae	<i>Silene latifolia</i> , <i>S. dioica</i> , <i>S. diclinis</i>	XX	XY	No	Active Y system
Cucurbitaceae	<i>Coccinia indica</i>	XX	XY	—	Active Y system
Polygonaceae	<i>Rumex angiocarpus</i>	XX	XY	—	—
	<i>R. tenuifolius</i>	(XX)XX	(XX)XY	—	—
	<i>R. acetosella</i>	(XXXX)XX	(XXXX)XY	—	Active Y system
	<i>R. graminifolius</i>	(XXXXXX)XX	(XXXXXX)XY	—	—
	<i>R. hastatulus</i>	XX	XY or + XY ₁ Y ₂	—	X to autosome ratio
	<i>R. acetosa</i>	XX	XY ₁ Y ₂	—	X to autosome ratio
	<i>R. paucifolius</i>	(XX)XX	(XX)XY	—	—

Sex chromosomes of plants were first described in white campion and hop (Blackburn, 1923; Winge, 1923), sorrel (Kihara and Ono, 1923), and *Elodea* (Santos, 1923).



Jednotlivé fáze potlačení vývoje orgánů určitého pohlaví
u dvoudomých rostlin (Zdroj: Janoušek, 1996)

Polygamní

Andromonoecická. Druhy kde všichni jedinci mají jak oboupohlavné tak jen samčí květy. Vyskytuje se u přibližně 1.7% krytosemenných rostlin.

Filipendula (Rosaceae), *Veratrum album* (Liliaceae).

Androdiecická. Druhy kde někteří jedinci mají samčí a jiní oboupohlavné květy.

Polygonum bistorta (Polygonaceae), *Datisca* (Datiscaceae). Vzácný případ.

Gynomonoecická. Druhy kde všichni jedinci mají samičí a oboupohlavné květy.

Asteraceae, *Silphium perfoliatum*, *Parietaria officinalis*

Gynodiecická. Druhy kde někteří jedinci mají samičí a jiní oboupohlavné květy.

Geranium sylvaticum (Geraniaceae),
Valeriana (Valerianaceae), *Thymus vulgaris*

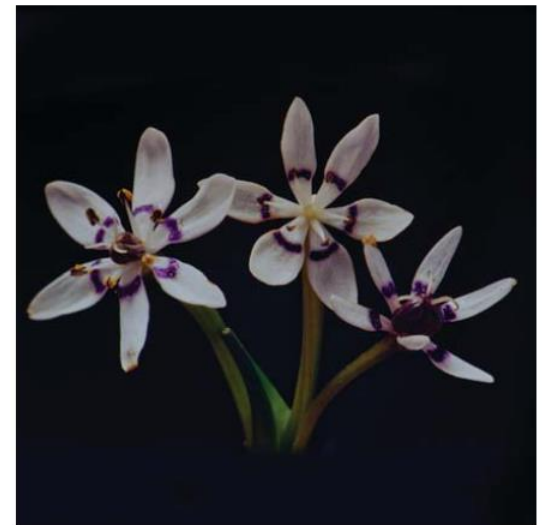


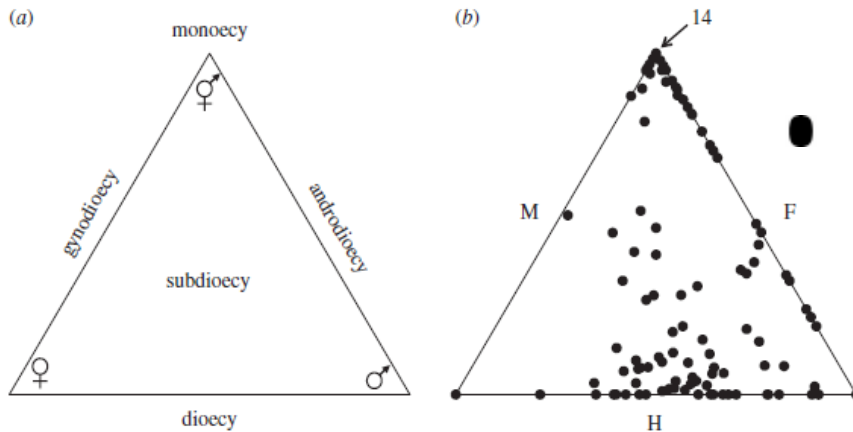
FIG. 6 Subdioecy in *Wurmbea dioica*. Populations contain three sex morphs (left-to-right): hermaphrodite, male and female. See Vaughton and Ramsey (2012). Photograph by Glenda Vaughton and Mike Ramsey.

III. Typy pohlaví – populace

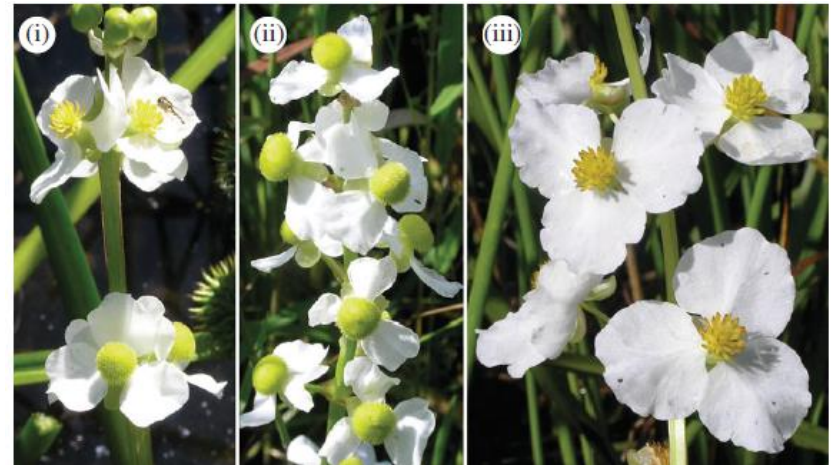
Polygamonoecie (= trimonoecická)

Druhy s jedinci se samčími, samičími i oboupohlavnými květy.

Aesculus hippocastanum, *Gunnera*, *Saponaria ocimoides*



Sagittaria latifolia



Polygamodioecie

Druhy s jedinci se samčími a samičími květy, ale kde se také vyskytují oboupohlavné květy.

Cleome spinosa (Capparaceae)

Trioecie

Druhy, kde odlišní jedinci mají buď samičí, samčí nebo oboupohlavné květy.

Fraxinus (Oleaceae), *Atriplex canescens* (Chenopodiaceae), *Silene acaulis* (Caryophyllaceae), *Asparagus officinalis* (Liliaceae)

Reprodukční systémy rostlin

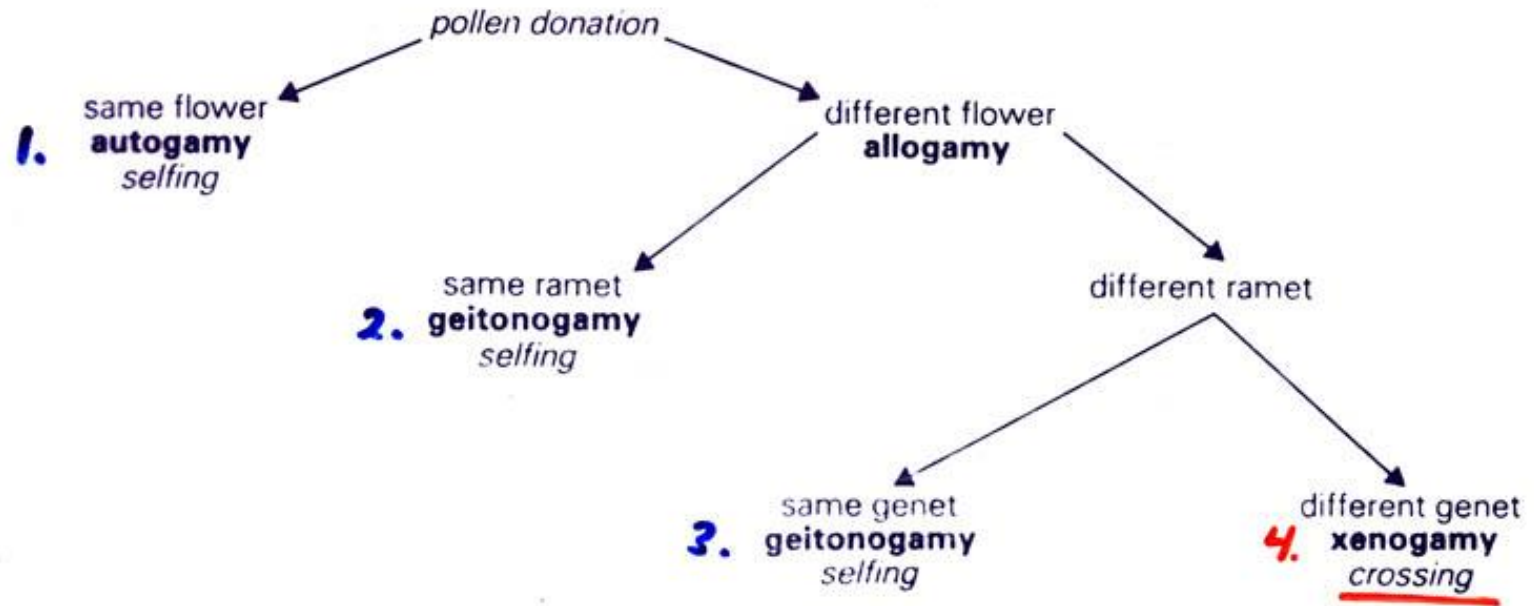
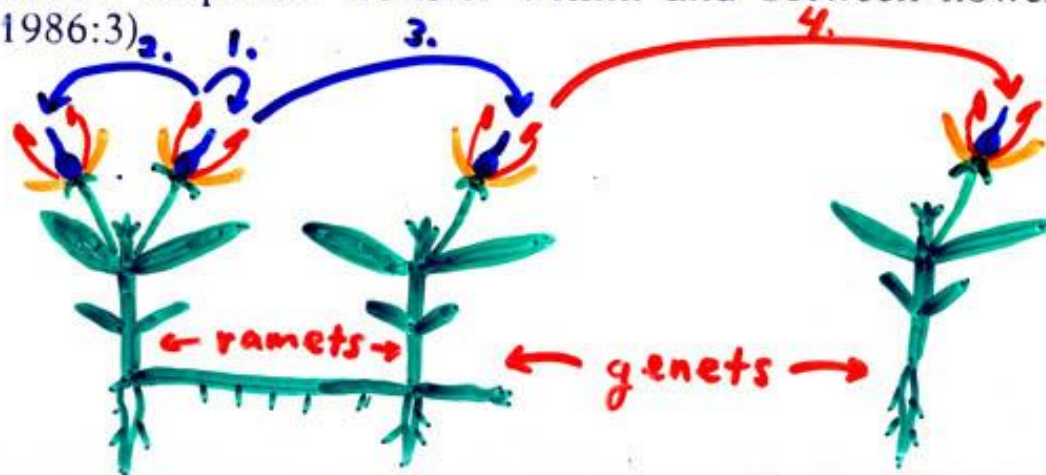


FIGURE 22.4 Patterns of pollen transfer within and between flowers and plants. (From Richards 1986:3)



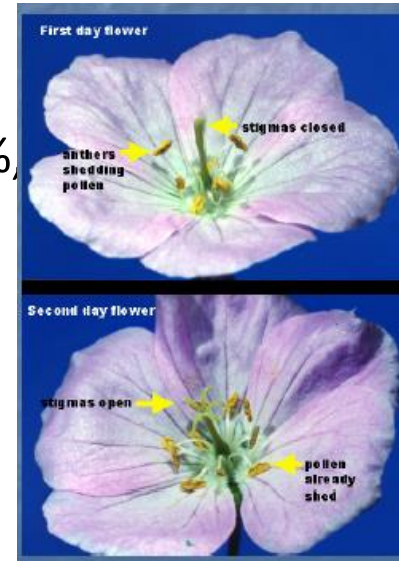
Reprodukční systémy rostlin

Cizosprašnost (= outcrossing, = xenogamie, = allogamie)

Vajíčko a pyl pocházejí z geneticky odlišných jedinců

u živočichů běžně zajištěna odděleným pohlavím,

u rostlin oddělené pohlaví je výjimka (flóra Evropy 3%, Hawaj 25%,
Nová Kaledonie, NZ, Kostarika 23%)



Mechanismy bránící samoopylení :

1. **Dichogamie.** Prašníky a blizna v květu dozrávají v odlišný čas

A) **Proterandrie, protandrie (prvoprašnost)** – pyl dozrává dříve než vajíčka –
častější případ, např. hořec, chrastavec, kakost, netýkavka, sléz, vrbovka, čeledě
hvězdnicovité, miříkovité, zvonkovité

B) **Proterogynie, protogynie (prvobliznost)** – vajíčka dozrávají dříve než pyl, např.
bika, čemeřice, drnavec, jitrocel, plamének, pryšec, psárka, tomka, zimolez.

Herkogamie

- je prostorové oddělení samčích a samičích pohlavních orgánů v jednom květu.
- Je to jeden ze způsobů, kterými se některé rostliny brání samoopylení.

Knautia arvensis

Květ v samičí etapě,
z květu vystupují
čnělky s bliznami



Květ v samčí etapě, z
květu vystupují
tyčinky s prašníky

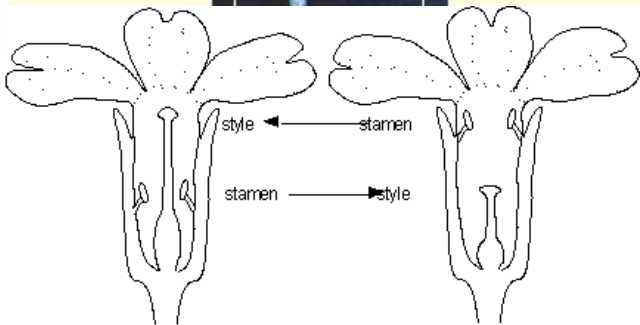
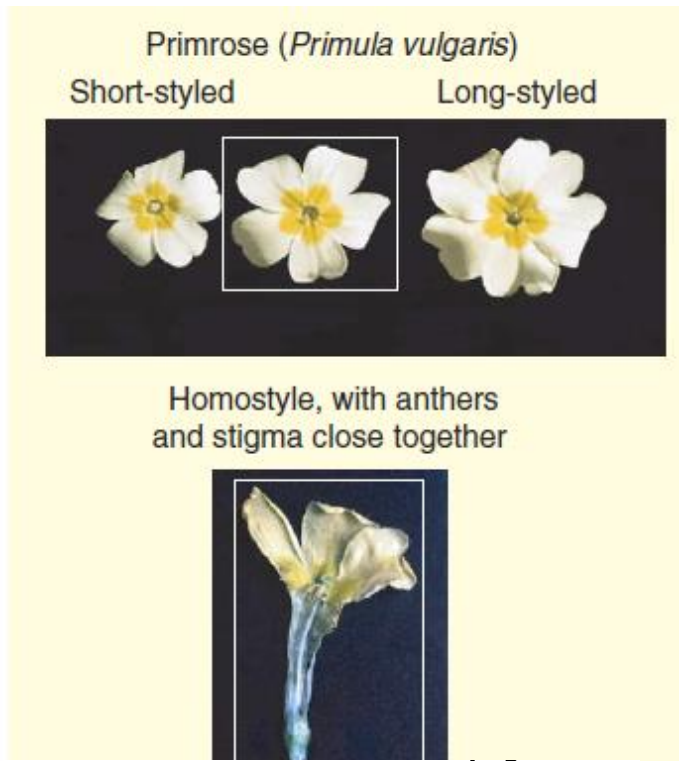
Dichogamie

- je vzájemné časové posunutí dozrávání vajíček a pylu v oboupohlavném květu.

2. Self-Inkompatibilita

a. Heteromorfní systémy - odlišná květní morfologie.

Heterostylie - odlišná délka a uložení prašníků



Primula scotica
a homostyle species

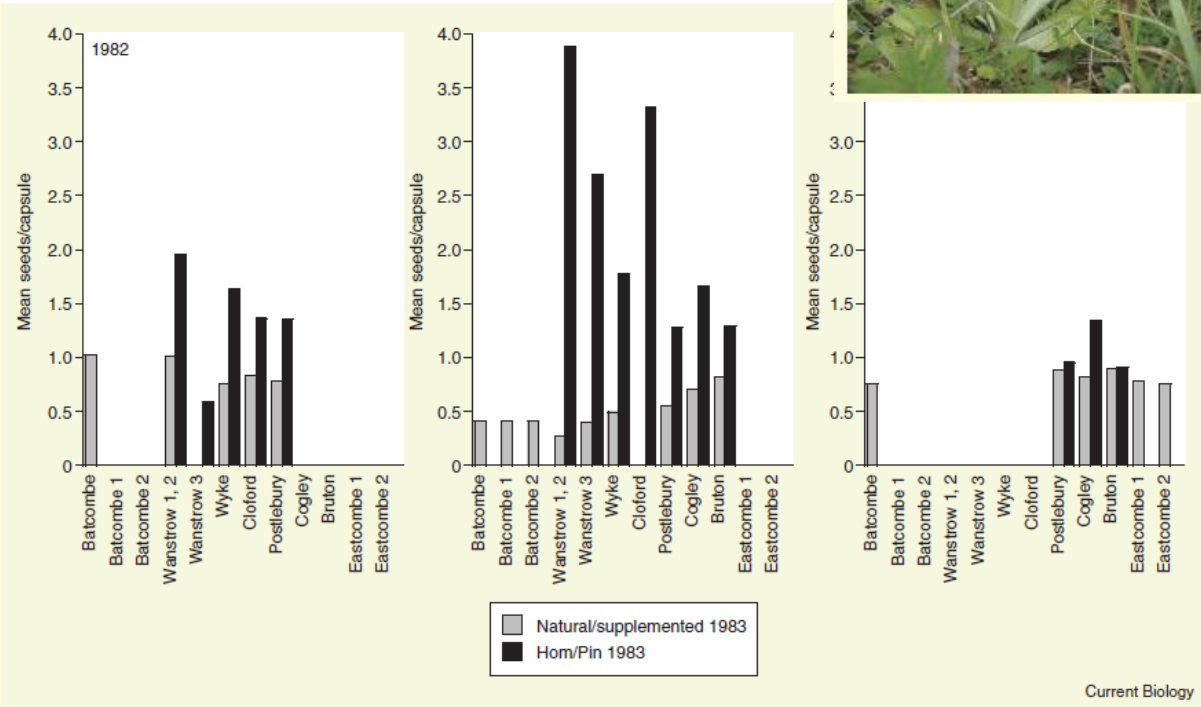


Figure 4. Reproductive assurance in several English natural populations of *Primula vulgaris* in which homostyle plants occur (data from [81]). The figure compares the results for 1982 to 1984 from naturally pollinated flowers of the 'pin' (long styled, self-incompatible) morph with flowers of the same morph experimentally pollinated to ensure excess pollen receipt (supplemented), and with naturally pollinated flowers of homostyle plants. Only the long-styled morph supplementation results are shown, because supplementation of flowers of the short-styled morph is difficult, but the few results were very similar to those shown. In 1982 and 1984, seed numbers per fruit under natural pollination were slightly below those achieved by supplemented flowers (the grey bars are only slightly below 1), indicating good pollination levels. Homostyles nevertheless often had somewhat higher seed set per fruit (and per plant) than the self-incompatible long-styled morph (black bars often higher than 1). In 1983, the flowering season was unusually rainy. Pollination was evidently poor, as pin plants' seed numbers under natural pollination were low, relative to flowers with pollen added (grey bars often less than 1). In that year, homostyle plants' seed output greatly exceeded that of pin plants (black bars much higher than 1). Thus the homostyle flowers benefited from reproductive assurance in 1983.

Darwin's legacy: the forms, function and sexual diversity of flowers

Spencer C. H. Barrett*



Figure 1. Examples of species that exhibit the six reported stilar polymorphisms in flowering plants: (a) distyly—*Primula beesiana* (Primulaceae); (b) tristily—*Eichhornia azurea* (Pontederiaceae); (c) stigma-height dimorphism—*Narcissus gaditanus* (Amaryllidaceae); (d) enantiostyly—*Wachendorfia paniculata* (Haemodoraceae); (e) flexistily—*Alpinia mutica* (Zingiberaceae); (f) inversostyly—*Hemimeris racemosa* (Scrophulariaceae), image courtesy of Anton Pauw. General features of these

Distylie

Dva odlišné květní morfotypy :

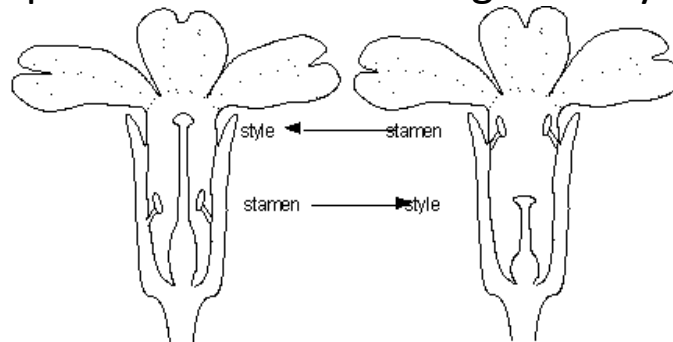
pin (dlouhá čnělka, krátké prašníky) a **thrum** (krátká čnělka, dlouhé prašníky).

Určeno jedním lokusem (S) se dvěmi alelami (S and s). Produkují také odlišný pyl.

Primula (Primulaceae). Poprvé popsáno Darwinem (1877).

Pin=špendlík (samičí) X thrum=kartáč (samčí) méně fertilní než thrum (samičí) X pin (samčí), což je dáno velikostí vodivých pletiv čnělky jimiž musí pylová láčka prorůst.

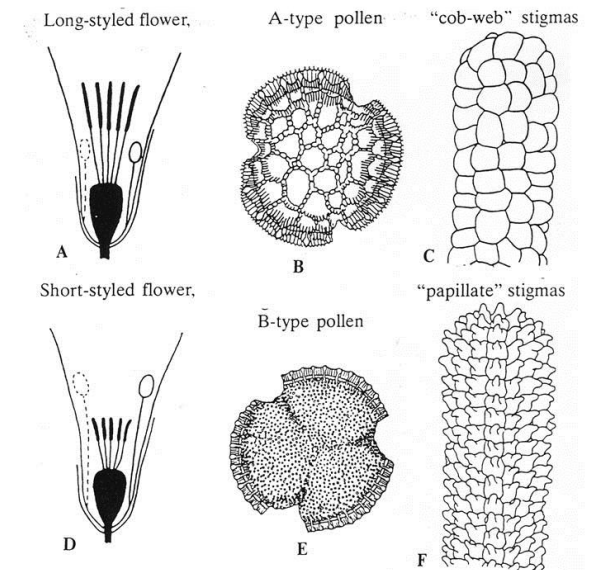
Thrum určující geny jsou dominantní a heterozygotní (Ss), pin jsou homozygotní recesivní (ss). Genotyp SS genotype neexistuje, protože by musel vzniknout jen k kombinace thrum X thrum, což je nekompatibilní. Následně tak genetický systém garantuje 1:1 mix pin a thrum rostlin.



Limonium vulgare (Plumbaginaceae).

Květy s dlouhou čnělkou (pins) produkují A-typ pylových zrn a mají "cob-web" typ blizny.

Květy s krátkou čnělkou (thrum) produkují B-typ pylových zrn a mají papilózní typ blizny.



Limonium vulgare (Baker 1966)

2) Tristylie.

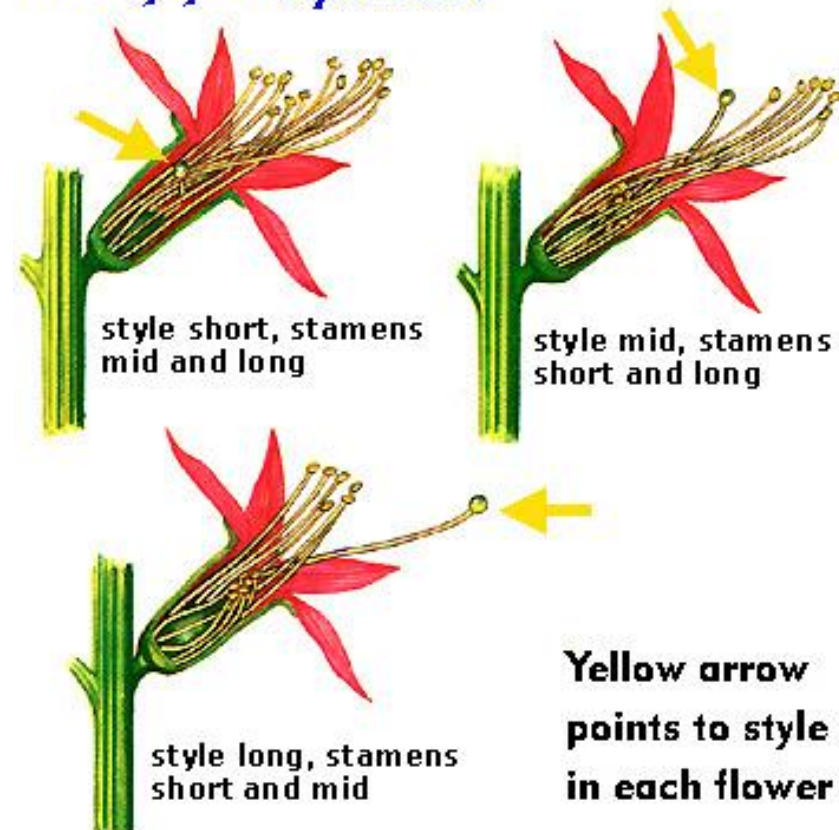
Tři květní morfotypy, každý se dvěmi odlišnými délkami čnělky.
Určeno dvěmi lokusy (S and M), každý se dvěmi alelami

Lythrum salicaria (Lythraceae). Studováno již Darwinem (1877)

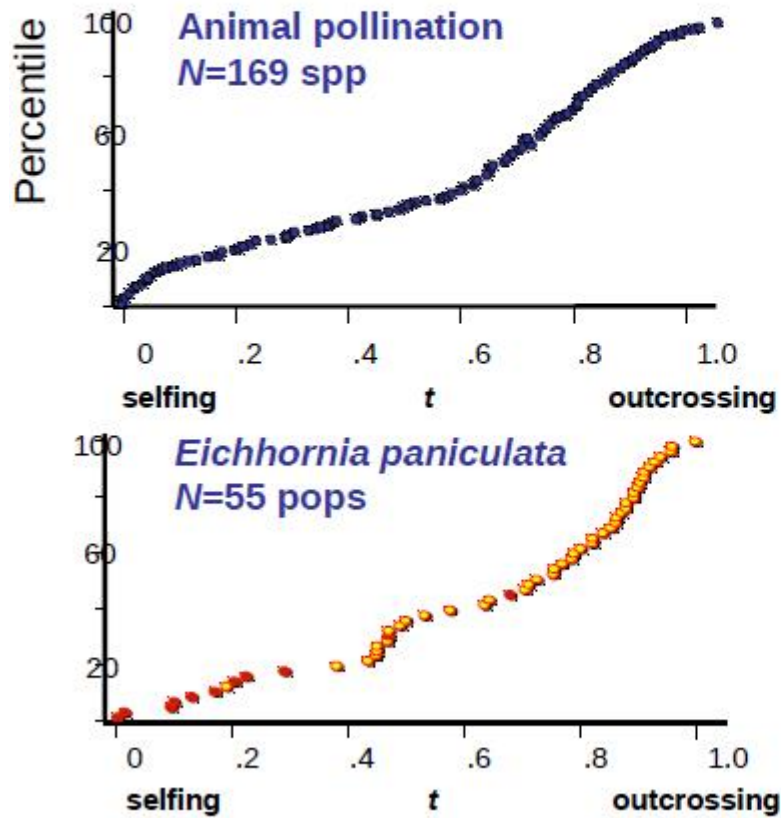
Eichhornia crassipes (Pontederiaceae)



Tristylie in *Lythrum*



Eichhornia crassipes (Pontederiaceae)

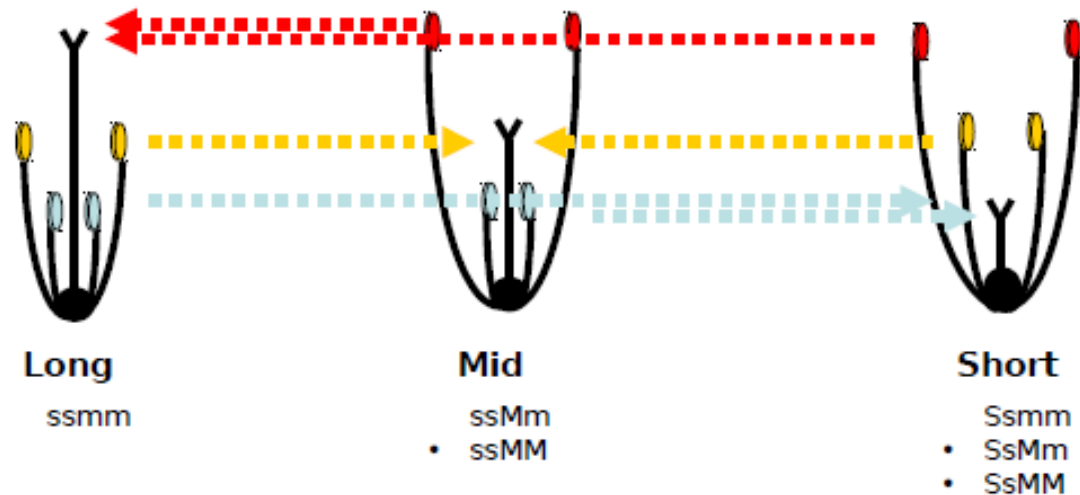


Evolution. 2001 51: 202
Phil. Trans. R. Soc. Lond. B. 2003 358:
991

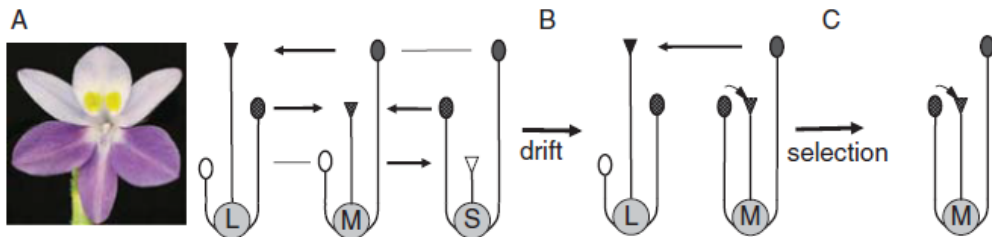
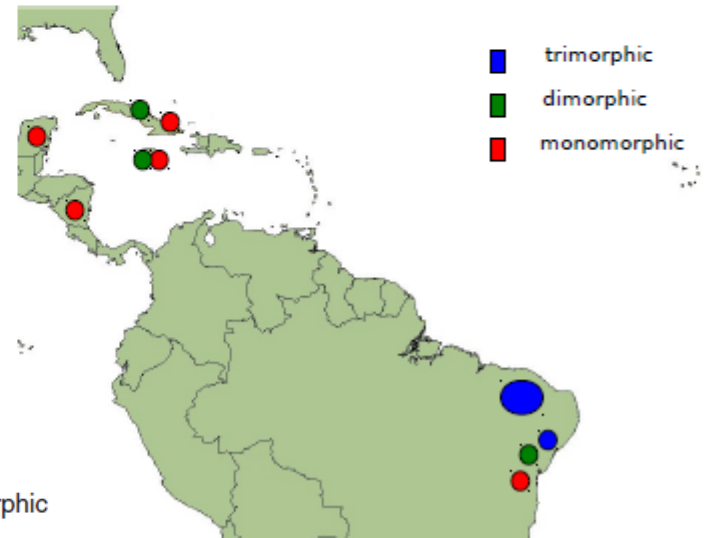
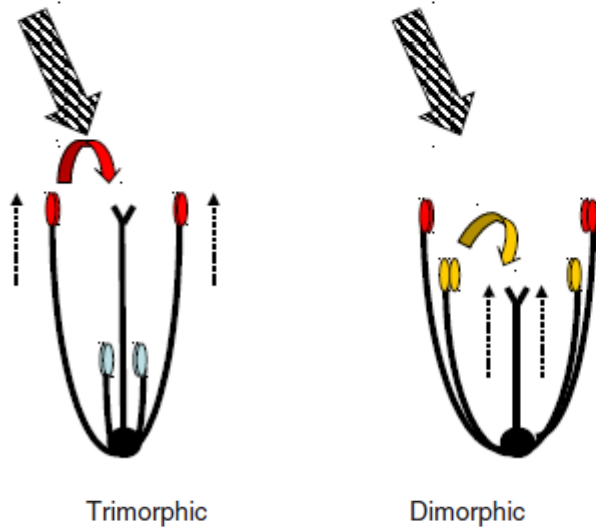
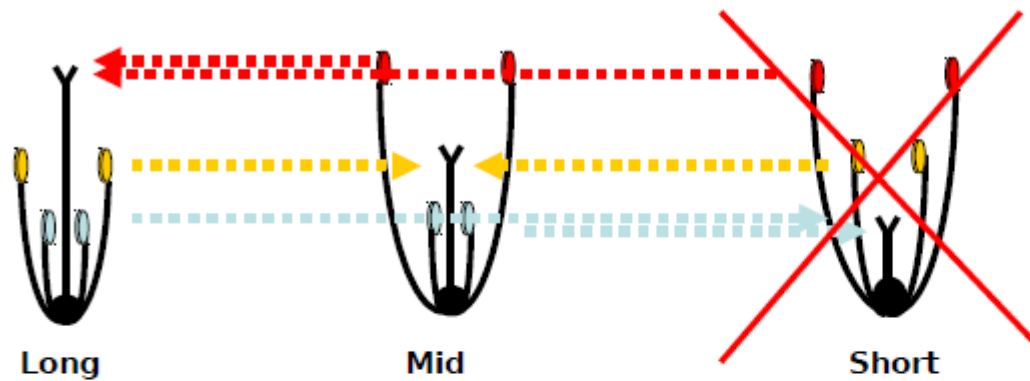
Eichhornia paniculata (Pontederiaceae)

Diploid ($2n = 16$) annual, aquatic species

Tristylous (3 morphs) { Long
Mid
Short



Transition to monomorphic selfing populations

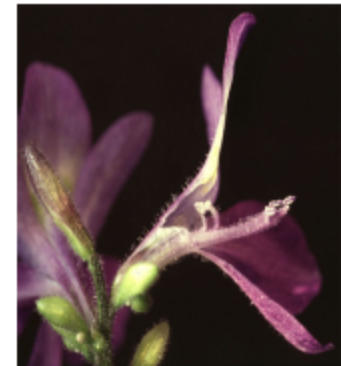
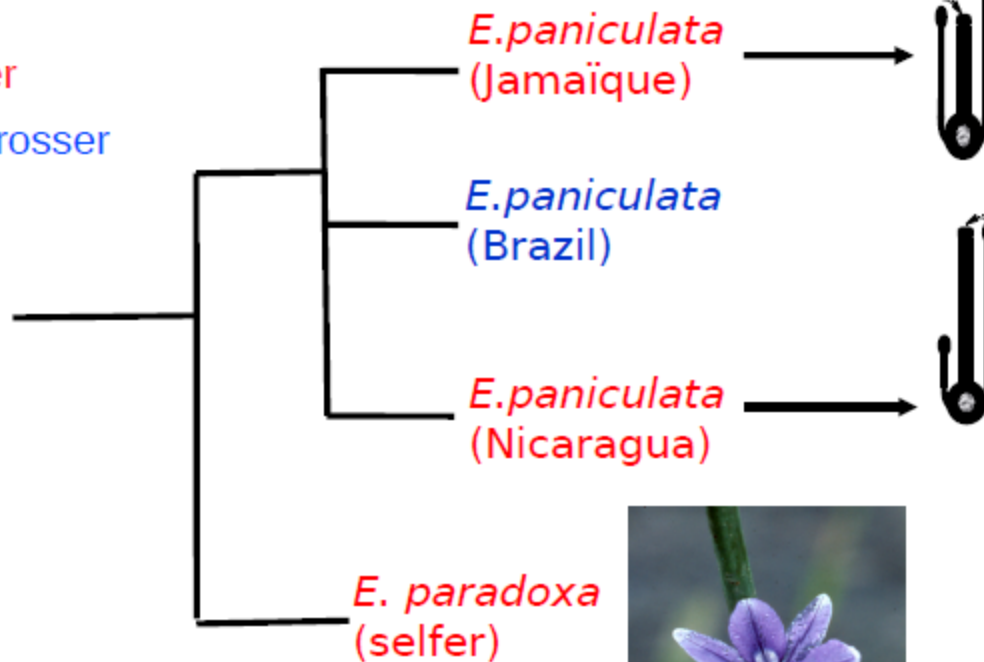


□ Reduced selection efficacy in selfers ?

Population genomics approach

■ selfer

■ outcrosser



Results: Tests of selection were consistent with purifying selection constraining evolution of the transcriptome. However, we found an elevation in the proportion of non-synonymous sites that were potentially deleterious in the *E. paniculata* selfers relative to the outcrosser. Measurements of codon usage in high versus low expression genes demonstrated reduced bias in both *E. paniculata* selfers.

Conclusions: Our findings are consistent with a small reduction in the efficacy of selection on protein sequences associated with transitions to selfing, and reduced selection in selfers on synonymous changes that influence codon usage.

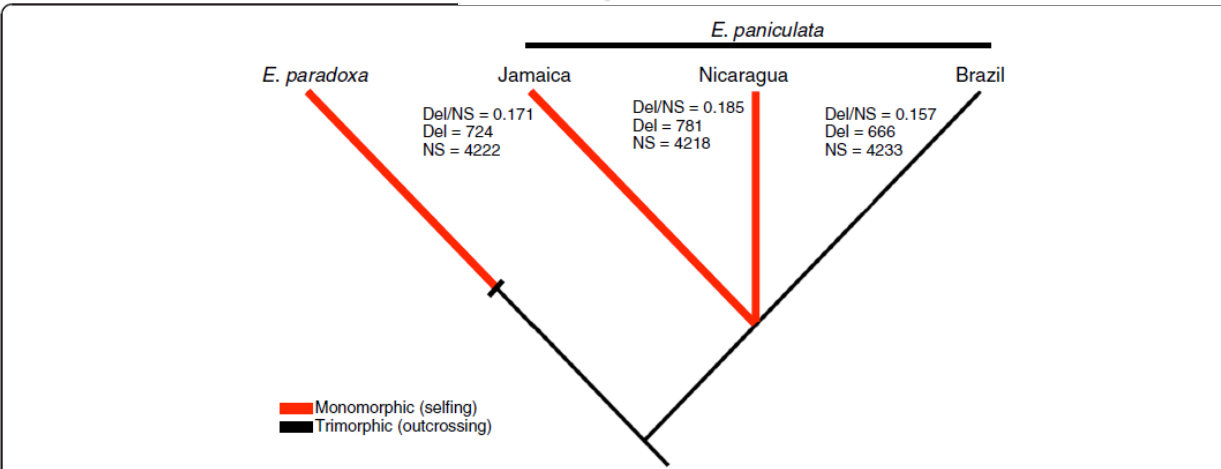


Figure 1 Counts of the number of deleterious (Del) non-synonymous sites and the total number of non-synonymous (NS) sites in selfing and outcrossing genotypes of *Eichhornia paniculata*. Deleterious mutations were identified using the program MAPP, which uses evolutionary constraint in homologous proteins to infer the potential fitness impact of non-synonymous changes. The colours along the branch reflect the putative model of changes in mating system although the exact timing of the transition along each branch is not known. The branch lengths are not to scale.

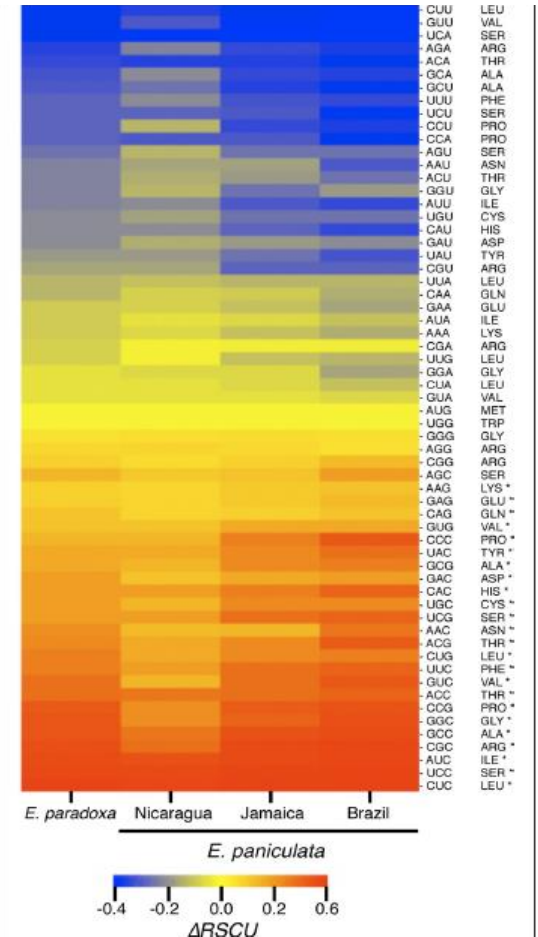
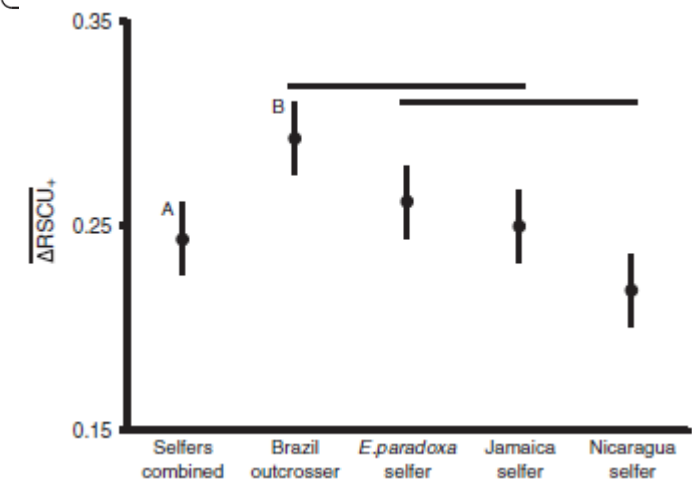


Figure 2 Heat map of $\Delta RSCU$ values for four genotypes of *Eichhornia* included in this study. Each column represents a single genotype. Each row corresponds to one of the 61 codons (excluding stop codons), where the value of $\Delta RSCU$ for each genotype is indicated. Codons are ordered by the mean value of $\Delta RSCU$ across all genotypes. Optimal codons identified as part of the consensus set of codons are marked with an asterisk. The figure was generated with the software CIMMiner (<http://discover.nci.nih.gov/cimminer>).

Heteroantherie (= různoprašníkuvost)

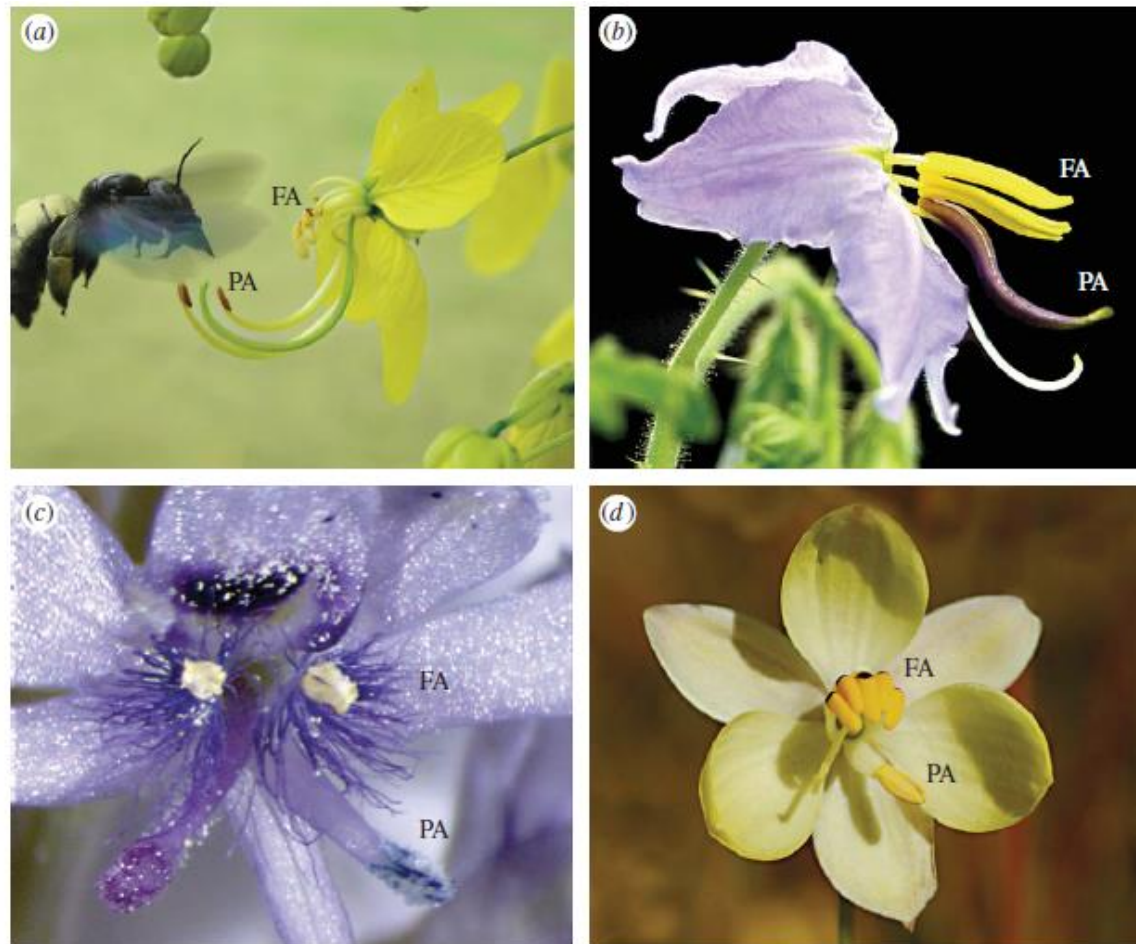


Figure 3. Examples of species that exhibit heteranthery: (a) *Cassia fistula* (Caesalpinioideae) being visited by a Carpenter bee (*Xylocopa* spp.). FA indicates the feeding anthers and PA the pollinating anthers; (b) *Solanum citrullifolium* (Solanaceae), image courtesy of Mario Vallejo-Marin; (c) *Heteranthera multiflora* (Pontederiaceae) exhibits dimorphic enantiostyly, a left-handed flower is illustrated (see §3c); (d) *Cyanella alba* (Tecophilaeaceae) is reported to be dimorphically enantiostylous, a left-handed flower is illustrated. Image courtesy of Lawrence Harder.

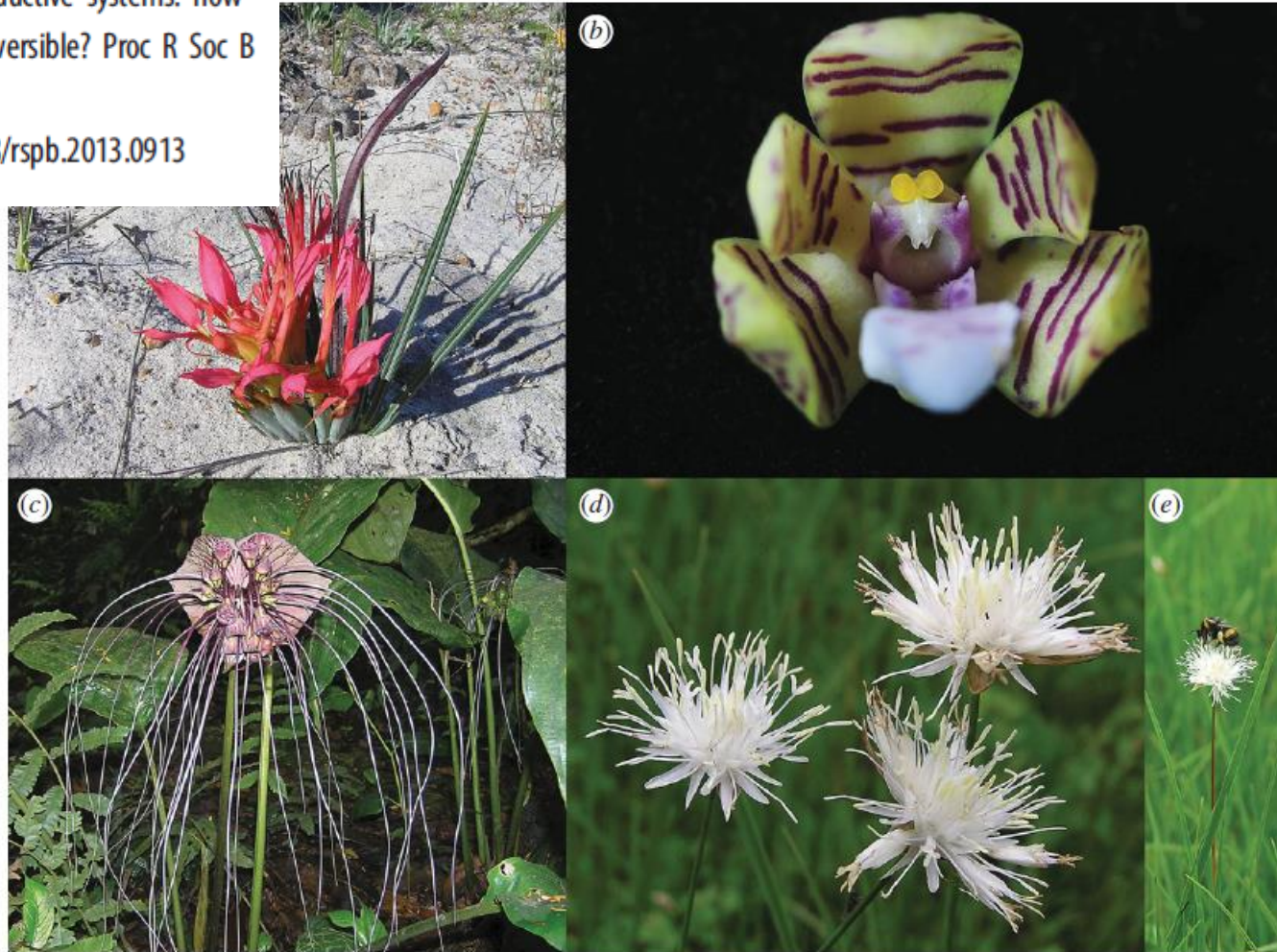


Figure 1. Examples of specialized pollination systems discussed in this article: (a) *Babiana ringens* (Iridaceae) endemic to the Cape region of South Africa is pollinated exclusively by malachite sunbirds, which use the naked inflorescence axis as a perch when feeding on nectar; (b) *Acampe rigida* (Orchidaceae), a nectarless species from southern Yunnan Province, China, exhibits structural adaptations to the flower facilitating self-pollination by rain drops (ombrophily). Image courtesy of Jiang-Yun Gao; (c) *Tacca chantrieri* (Dioscoreaceae) possesses several traits assumed to function in attracting carrion flies (sapromyophily); however, populations in southern Yunnan Province are highly self-pollinating; (d) unlike most members of the Juncaceae, which are predominantly wind pollinated, *Juncus allioides* (Juncaceae), a common species of wet grasslands of the Tibetan plateau, China, possesses showy floral displays and is visited by a wide range of generalist pollinators; (e) *Bombus lucorum* visiting *J. allioides*. Image courtesy of Shuang-Quan Huang.

Rostliny a atraktivita pro opylovače – generalizace/specializace



Plant reproductive systems and evolution during biological invasion

SPENCER C. H. BARRETT,* ROBERT I. COLAUTTI* and CHRISTOPHER G. ECKERT†

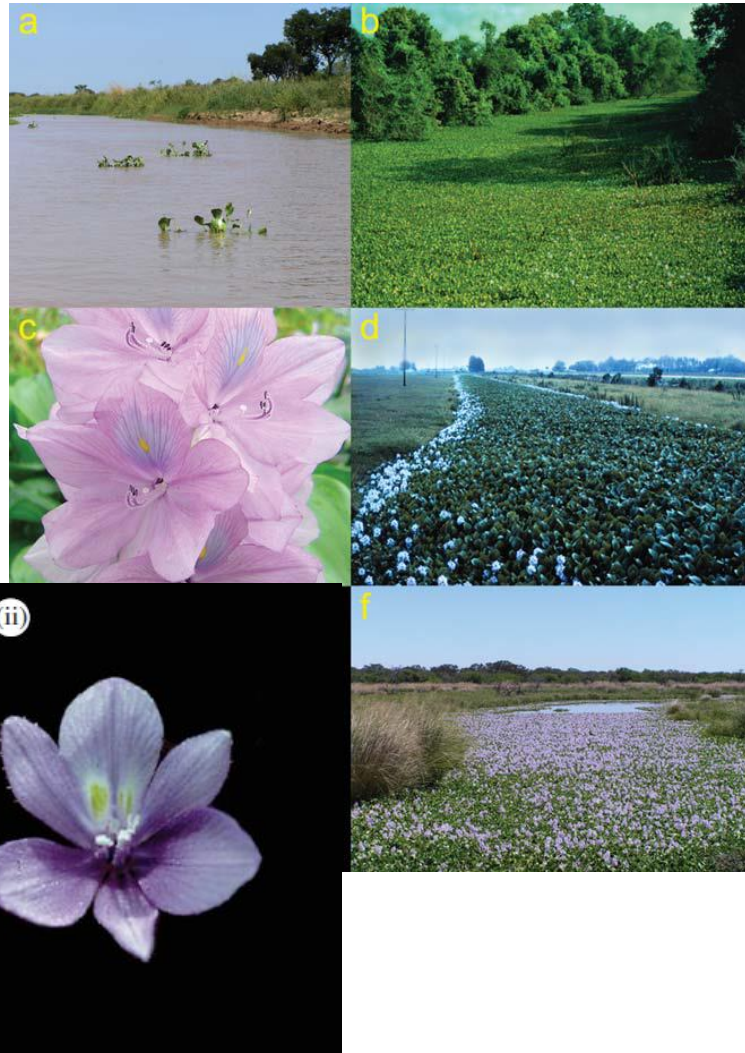


Fig. 2 Biological invasion by water hyacinth (*Eichhornia crassipes*). (a) water-dispersed floating plants along tributaries of the Rio Parana, Rosario, Argentina. In the introduced range, these initiate new invasions and also function in 'mate-finding', particularly in the native range where all three floral morphs occur; (b) severe river infestation resulting from prolific clonal propagation near Louisiana, USA. Flowering can be infrequent in these primarily clonal populations; (c) the mid-styled morph illustrating the physical separation between female and male sexual organs, which limits the autonomous self-pollination of flowers. This morph dominates throughout the introduced range; (d) blockage of a canal in Florida, USA by clonal propagation. Note the band of flowering at the colony edge, which is probably stimulated by contact with the substrate. Although seed is often produced in these circumstances it rarely germinates owing to an absence of safe sites; (e) selfing variant of the mid-styled morph from Palo Verde Marsh, Guanacaste Province, Costa Rica. Stigmas and long-level anthers are adjacent resulting in autonomous self-pollination of flowers; (f) mass flowering in Argentina stimulated by receding water levels. Under these circumstances sexual reproduction is common, especially if clones are destroyed by desiccation. Sexual populations in the native range often contain mixtures of floral morphs.

(i) Outcrossing and (ii) selfing flowers of tristyloid *Eichhornia paniculata* (Pontederiaceae)

Homomorfní systémy.

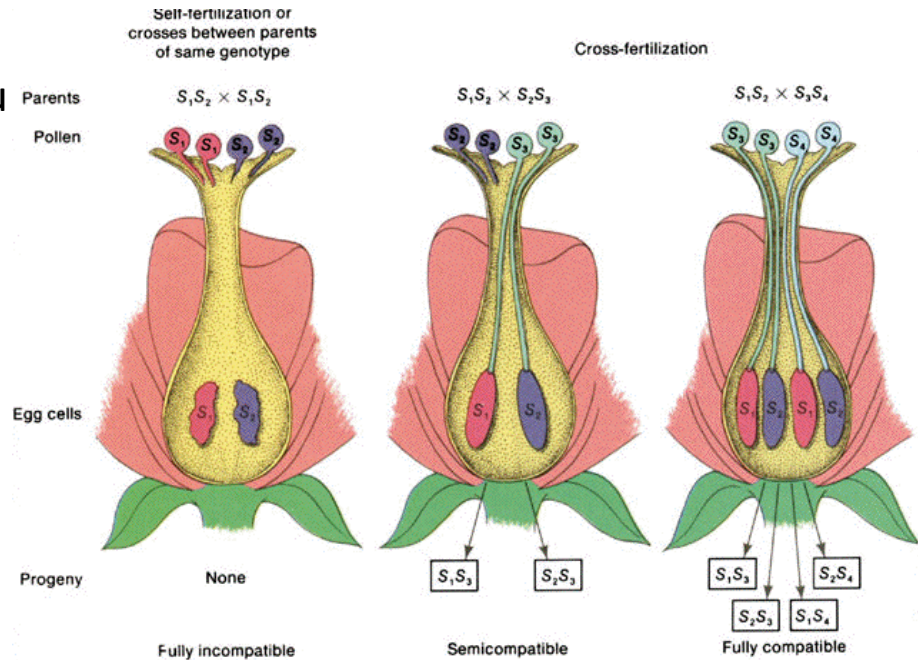
Morfologicky neodlišitelní jedinci. Odlišné rozmnožovací typy geneticky kontrolované "S" alelami. Kontrolované jedním lokusem s mnoha alelami. Rodičovské S alely musí být odlišné pro úspěšnou reprodukci.

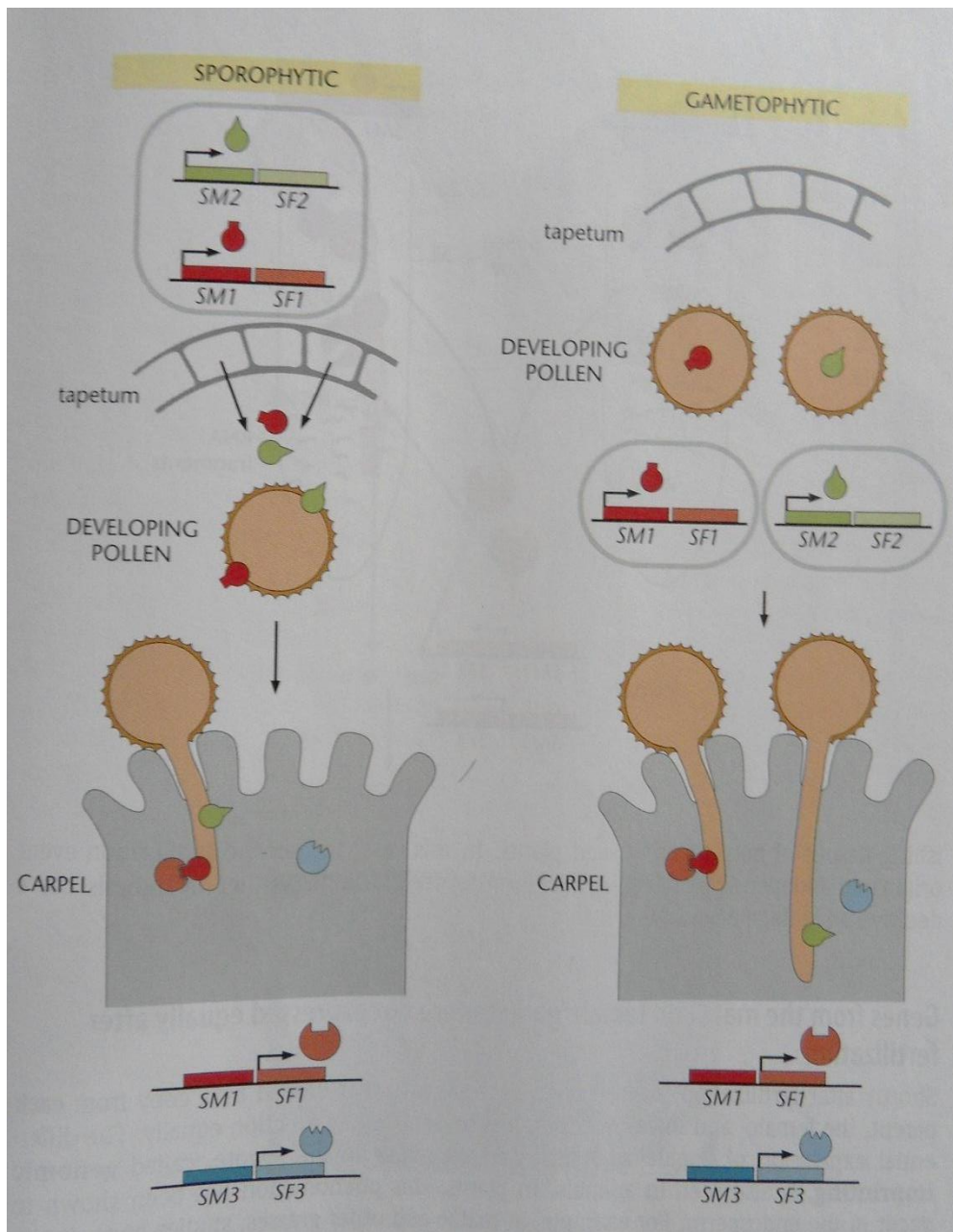
1) Gametofytická Self-Inkompatibilita (GSI).

Pylová láčka samčího gametofytu interaguje s pletivou čnělky a blizny. Určeno genotypem pylu a blizny.

2) Sporofytická Self-Inkompatibilita (SSI).

Na povrchu pylu (exiny) je uložen materiál mateřského sporofytu (tapeta). Proteiny kódované S alelami přítomnými v obou sporofytických pletivech rodičovských rostlin, vzájemně interagují.





Gametofytická SI

Solanaceae

zprostředkovaná RNázou

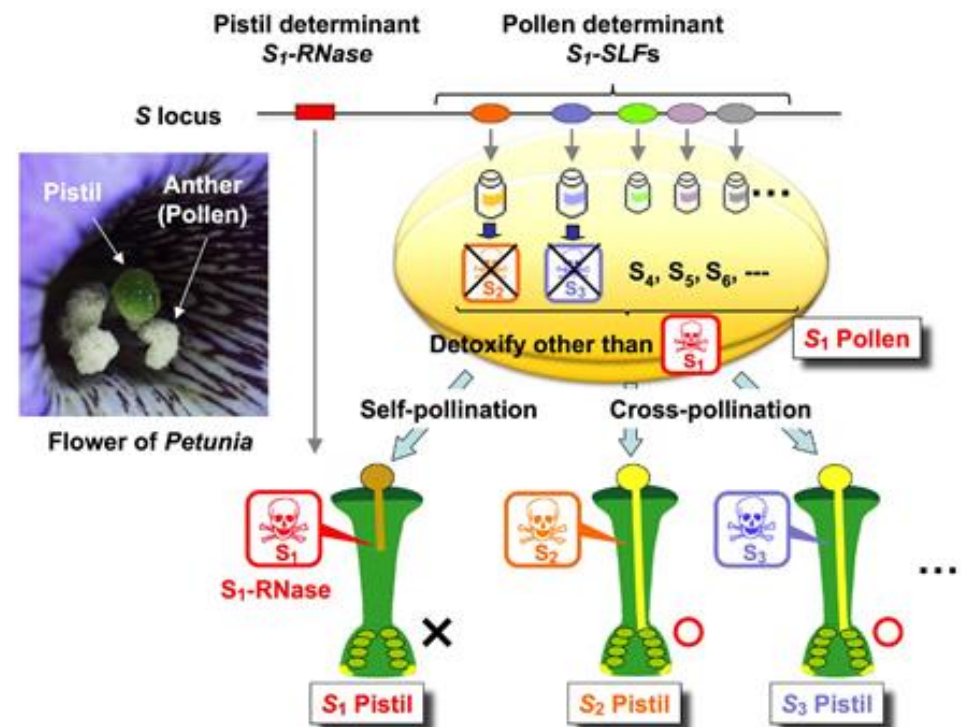
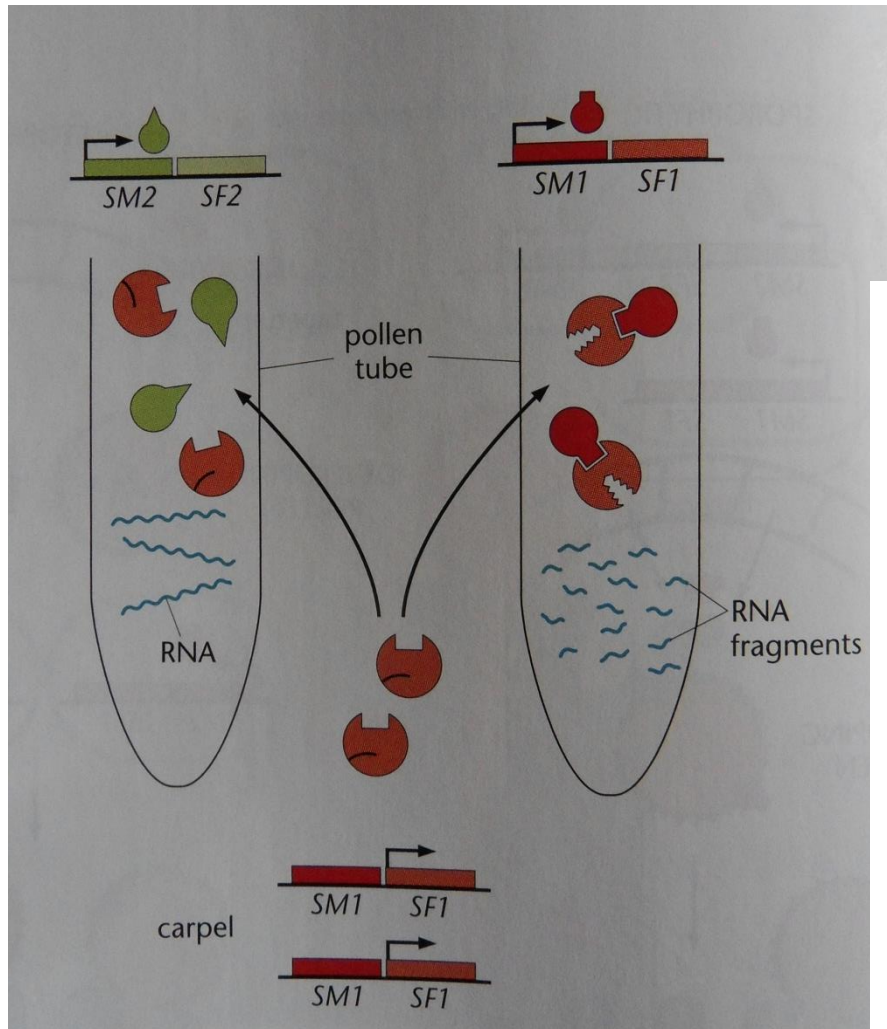
Sporofytická SI

Brassicaceae

Zprostředkovaná

S-receptor kinázou blizny

Gametofytická SI *Solanaceae* Zprostředkovaná S-RNázou



Samosprašnost - Autogamie (self-pollination, inbreeding)

Pyl i vaječná buňka pocházejí ze stejného jedince.

A. **Autogamie.** Pyl i vaječná buňka pocházejí ze stejného květu. Květ se může, nebo nemusí otevřít.

B. **Kleistogamie.** Pyl i vaječná buňka pocházejí ze stejného květu, který se neotvírá. Úplná forma autogamie. Mnoho druhů má jak kleistogamické tak chasmogamické (= otevírací se) květy na stejné rostlině.

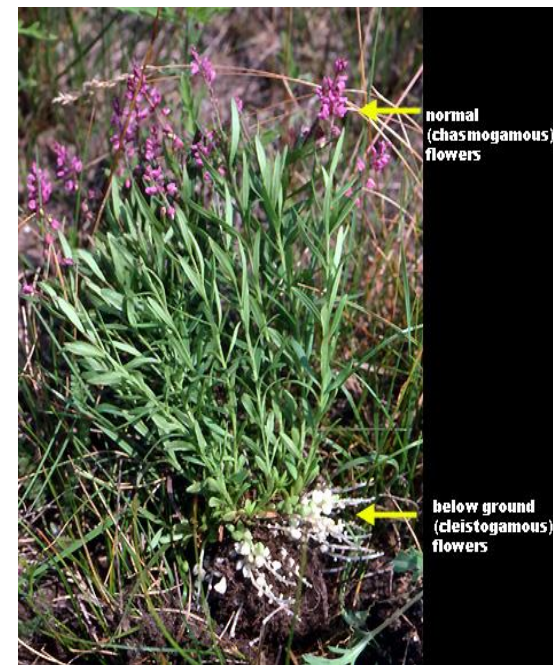
Viola sp. (Violaceae)

Polygala polygama (Polygalaceae)

Lamium amplexicaule (Lamiaceae)

Hordeum vulgare (Poaceae)

C. **Geitonogamie.** Pyl i vaječná buňka pocházejí z různých květů, ale stejného jedince.



Arabidopsis lyrata ssp. *petraea*
(self-incompatible)

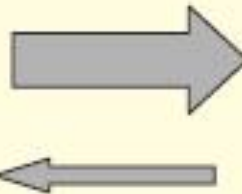


A. thaliana
(highly inbreeding)



Advantages: gene transmission, reproductive assurance

Outcrossing,
including self-incompatible



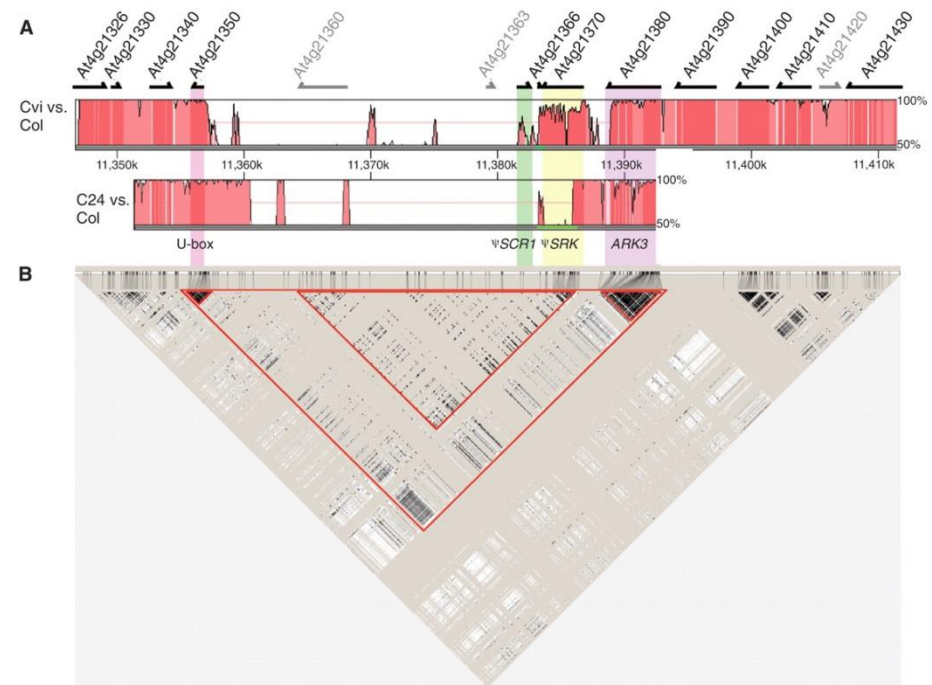
Inbreeding, for example
by loss of self-incompatibility

Current Biology

Current Biology 16, R726–R735, September 5, 2006 ©2006 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2006.07.068

Arabidopsis thaliana, a member of the Brassicaceae, is a highly selfing plant that is separated from its closest relative, the self-incompatible *A. lyrata*, by about 5 million years

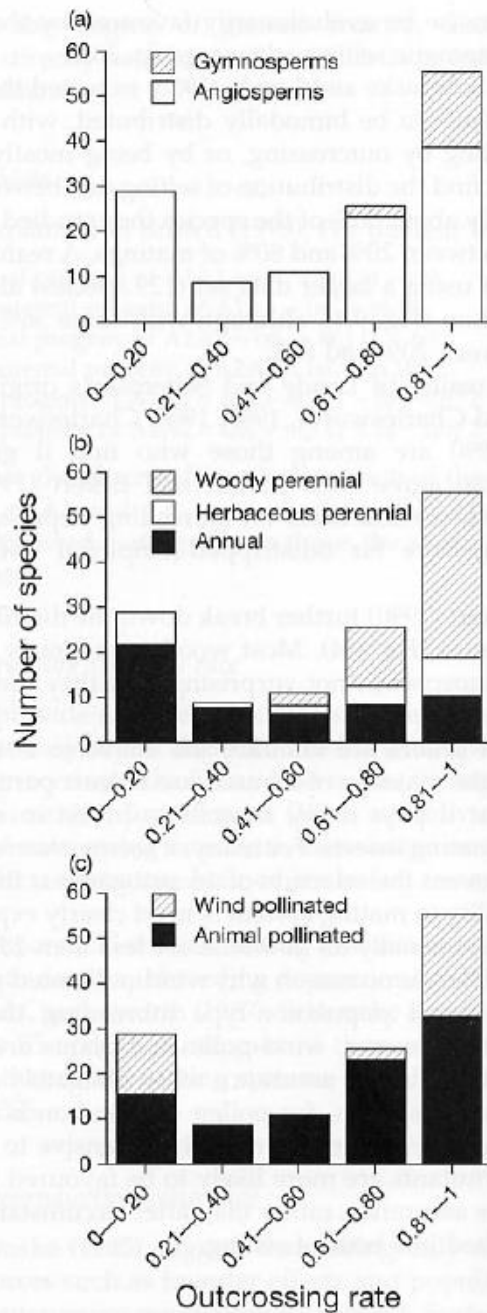
In the Brassicaceae, the main components of the *S* locus are the tightly linked *S*-locus cysteine-rich protein (*SCR*) and *S*-locus receptor kinase (*SRK*) genes, which encode male and female specificity determinants of self-incompatibility, respectively. Because *A. thaliana* is self-compatible, the self-incompatibility system must be inactive, and both *SCR* and *SRK* are pseudogenes (Ψ *SCR* and Ψ *SRK*).



It was found that the *S* locus of *A. thaliana* harbored considerable diversity, which is an apparent remnant of polymorphism in the outcrossing ancestor. Thus, the fixation of a single inactivated *S*-locus allele cannot have been a key step in the transition to selfing. An analysis of the genome-wide pattern of linkage disequilibrium suggests that selfing most likely evolved roughly **a million years ago or more**.

Selfing and Outcrossing

- Why not self?
 - High levels of homozygosity.
 - Expression of deleterious recessive alleles (DRA's).
 - Heterozygous genotypes have high fitness because normal alleles are dominant.
 - Overdominance for fitness (heterosis).
 - Heterozygous genotype is the most fit (e.g., sickle cell anemia, spots on *Clarkia* petals [Vince Eckhart]).
 - Loss of segregation and recombination for the generation of novel genetic variation.
 - Selfing populations less able to respond to environmental change?
 - The heterozygosity/fitness debate.
 - Are high levels of heterozygosity better because of dominance or overdominance?



Selekce mezi samo- a cizosprašností je závislá na druhu a prostředí

Samosprašné druhy jsou většinou jednoleté a invazivní druhy.

Selekce na menší květy

Redukce samičích částí

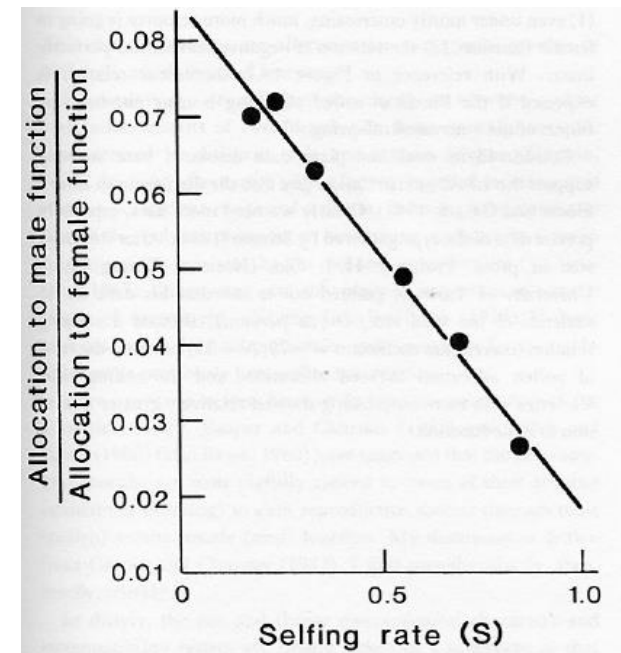


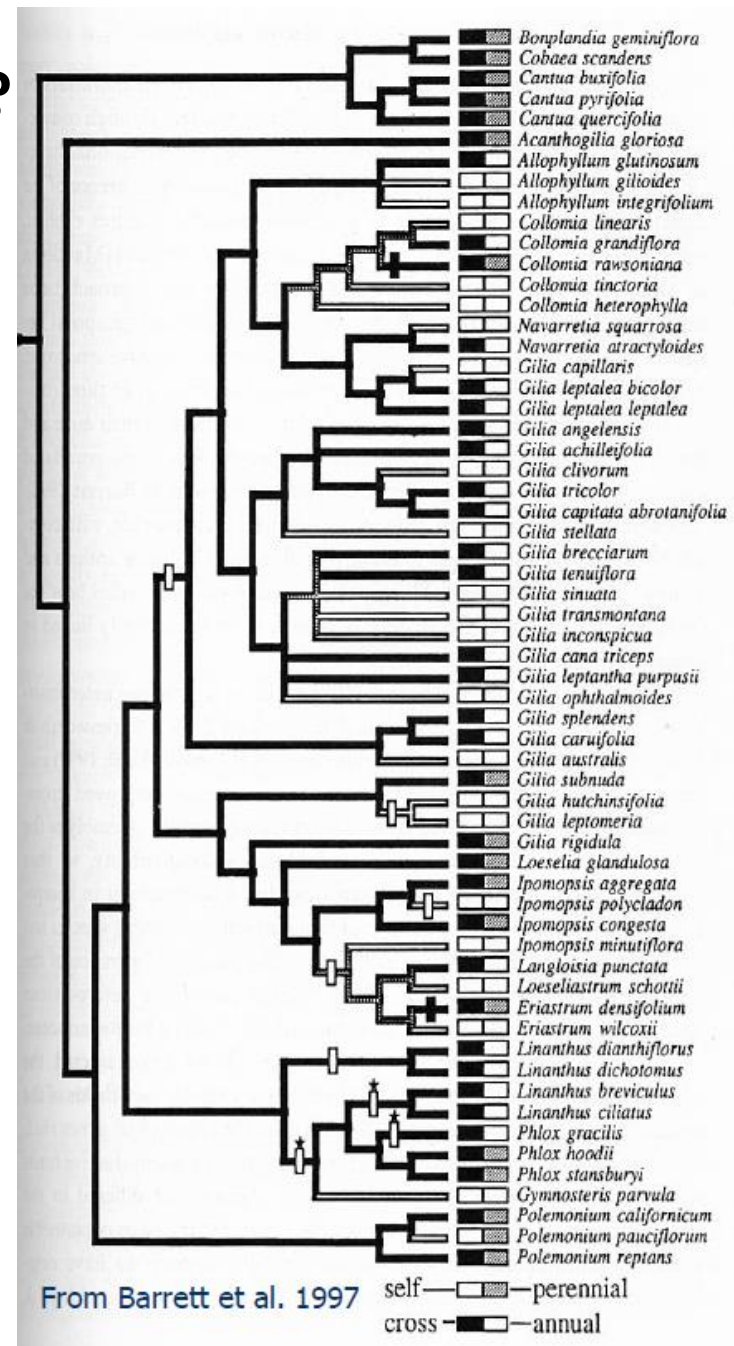
FIGURE 16.3. Resource allocation to male versus female function related to the selfing rate (S), for several populations of *Gilia achilleifolia*. For levels of inbreeding depression (δ) in the range 0.35–0.65, we expect a negative, linear relationship (as in Fig. 14.7). The observed data are very close to the theoretically expected results. Further discussion in text. (Data from Schoen, 1981; see for measurement details).

Je samosprašnost evoluční „dead-end“?

Samosprašnost je fylogeneticky odvozená a vznikla mnohonásobně.

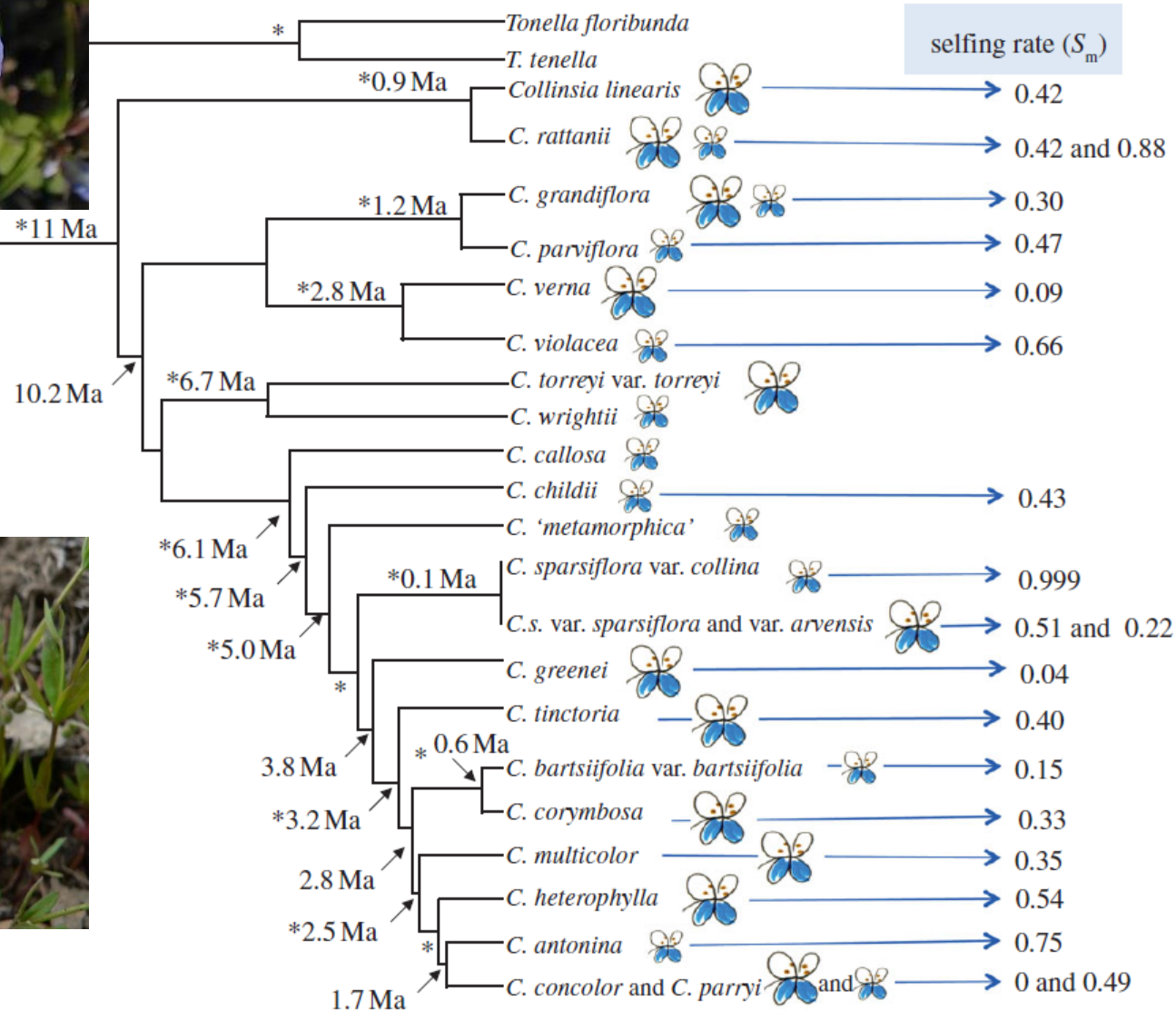
Samosprašné druhy jsou méně rozmanité.

Samosprašné linie (druhy) nejsou fylogeneticky dlouhověké.





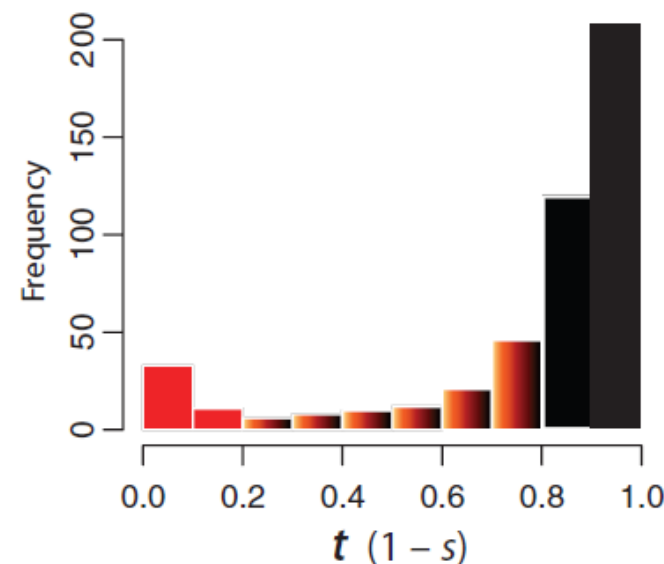
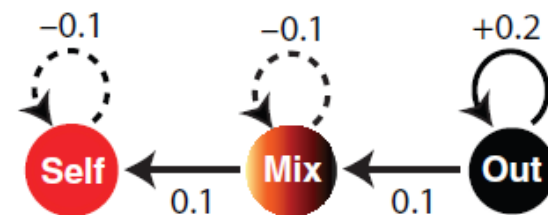
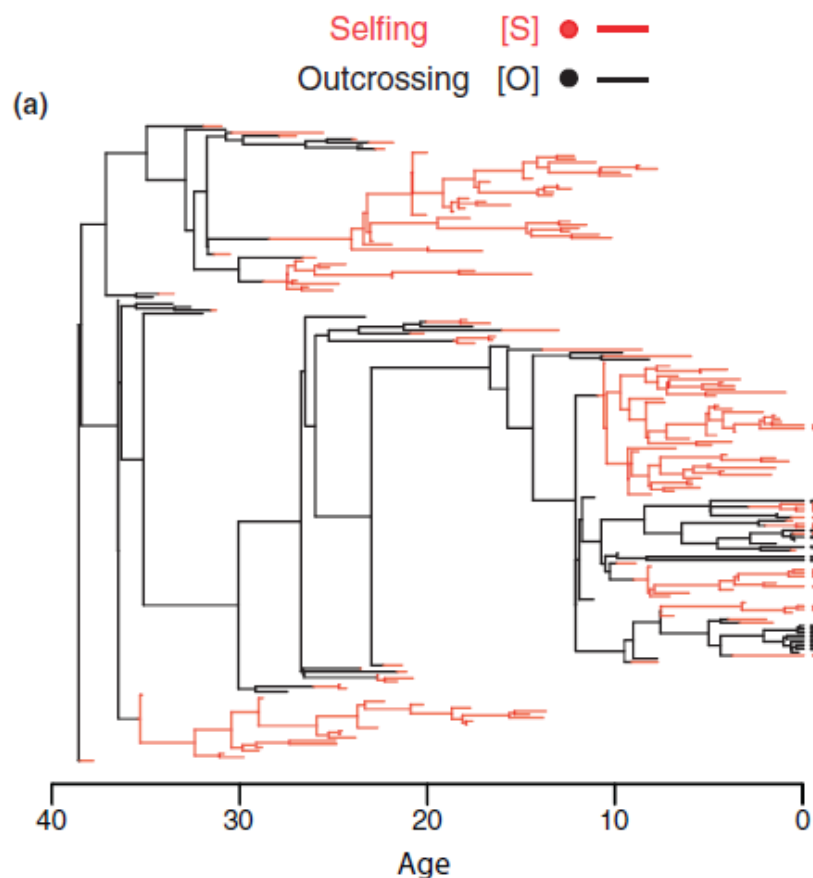
Collinsia verna



Collinsia parviflora

Is self-fertilization an evolutionary dead end?

Boris Igic^{1*} and Jeremiah W. Busch^{2*}



Speciace/ extinkce
(na linii za milion let)

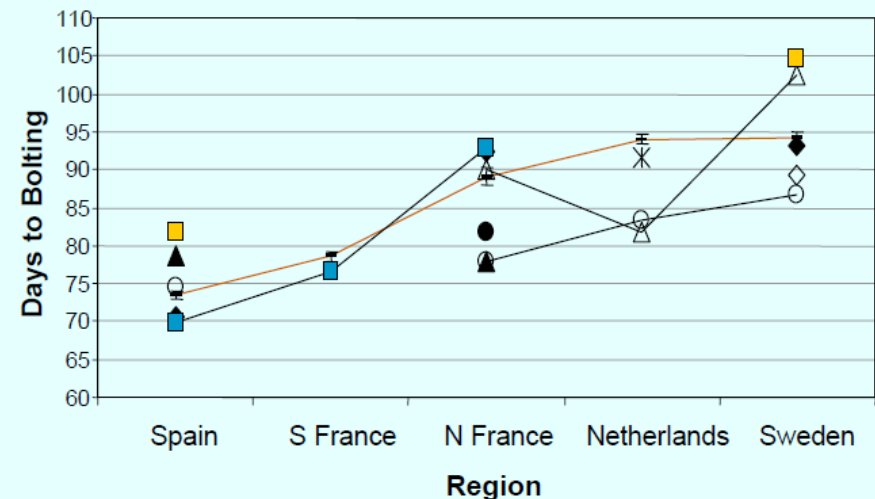
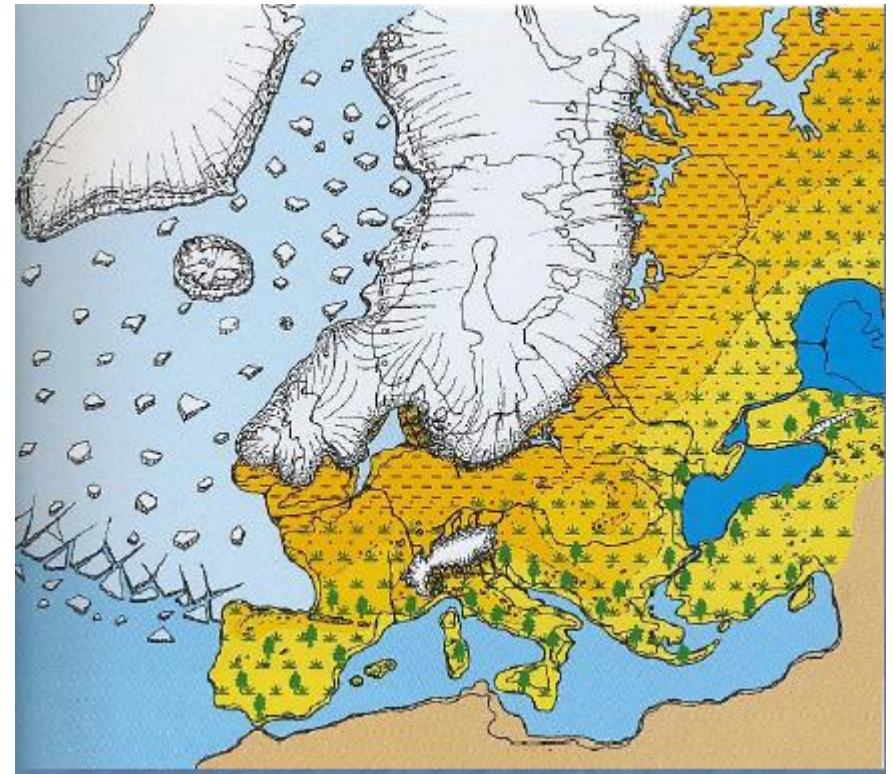
Vyvíjejí se samosprašné druhy ?

Příklad *Arabidopsis thaliana* v Evropě

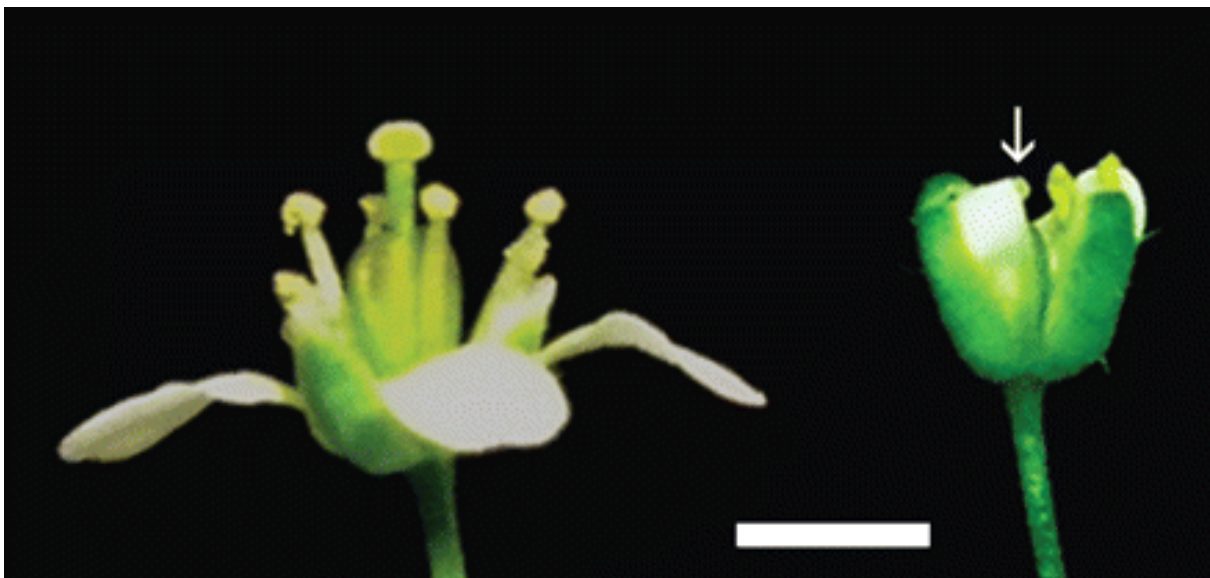
Po poslední době ledové se téměř kompletně samosprašné linie rozšířili z jižních refugií.

Existence rekombinací a menší míry cizosprašnosti je dostatečná pro variabilitu.

Jednotlivé linie postupně během 10,000 let akumulovaly mutace vedoucí až ke 30% fenotypové variabilitě.



Která z nich je cizosprašná ?



Capsella grandiflora

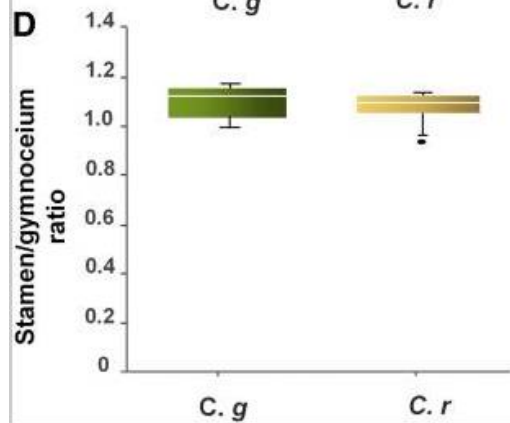
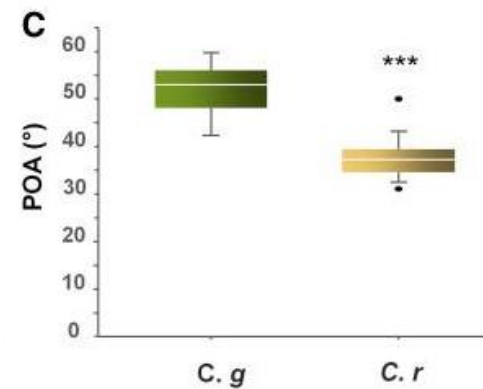
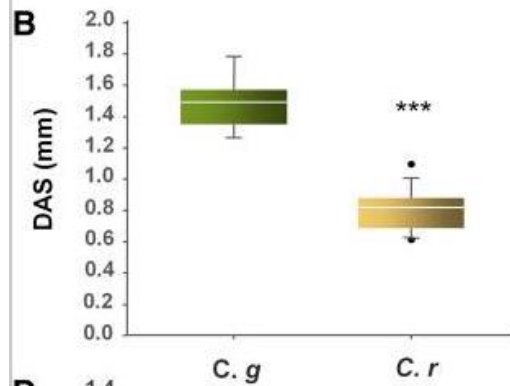
Capsella rubella

Cizosprašná

Capsella grandiflora

Samosprašná

Capsella rubella



The selfing syndrome: a model for studying the genetic and evolutionary basis of morphological adaptation in plants

Table 1.
Summary of quantitative-genetic studies of the selfing syndrome

Genus	Crossed species/strains	Mating system (outcrossing rate)	Traits investigated	No. of QTLs found	% of the total phenotypic variance/phenotypic difference between parents explained by all the QTLs	% of the total phenotypic variance/phenotypic difference between parents explained by the strongest QTLs	References
<i>Mimulus</i>	<i>M. platycalyx</i>	Predominantly selfing (0.1–0.2)	Flower width	0			Lin and Ritland (1997)
			Flower length	1	7.8	7.8	
	<i>M. guttatus</i>	Predominantly outcrossing (0.6–0.9)	Pistil length	1	28.6	28.6	
			Long stamen length	3	38.3	17.7	
			Short stamen length	3	33.6	12.4	
<i>Solanum (Lycopersicon)</i>	<i>S. esculentum</i>	Selfing	Anther–stigma separation	2	21.2	10.7	Bernacchi and Tanksley (1997)
			Self-incompatibility	4	46.8	30	
	<i>S. hirsutum</i>	Self-incompatible obligate outcrosser	Unilateral incongruity	6	72.5	34.3	
			Bud type	7	95.7	17.5	
			Corolla indentation	2	23.2	12.3	
			Rachis length	3	62.2	37	
			Flower size	3	29.8	11.4	
			Inflorescence vegetative meristem	2	17.9	9.7	
			Flower number	1	28.4	28.4	
			Stigma exsertion	1	19.7	19.7	
<i>Solanum (Lycopersicon)</i>	<i>S. pimpinellifolium</i> LA1237	Selfer (0)	Flowers per inflorescence	3	55.3	29.8	Georgiady et al. (2002)
			Petal length	2	34.6	22	
	<i>S. pimpinellifolium</i> LA1581	Outcrossing (0.37)	Total anther length	3	82.2	36.7	
			Fertile anther length	2	27.2	19.6	
			Sterile anther length	5	42.8	31	
			Style length	3	66.1	42.2	

Figure 1. Processes affecting macroevolutionary diversification of outcrossers (top panel) and selfers (bottom panel), and factors that may enhance rates of transition. (a) Transitions from outcrossing to selfing are thought to be common, while the reverse is rare. (b) Selfing may often evolve as a speciation process, where the ancestral outcrossing lineage persists. (c) Speciation rates within outcrossers can be enhanced by higher rates of sexual and genomic conflicts, whereas selfers may experience accelerated rates of speciation owing to greater mating isolation and more rapid post-zygotic isolation owing to underdominant alleles. (d) Extinction rates in outcrossers can be enhanced by the lack of available mates, whereas extinction rates in selfers may be increased by reduced adaptive potential and by the accumulation of deleterious mutations.

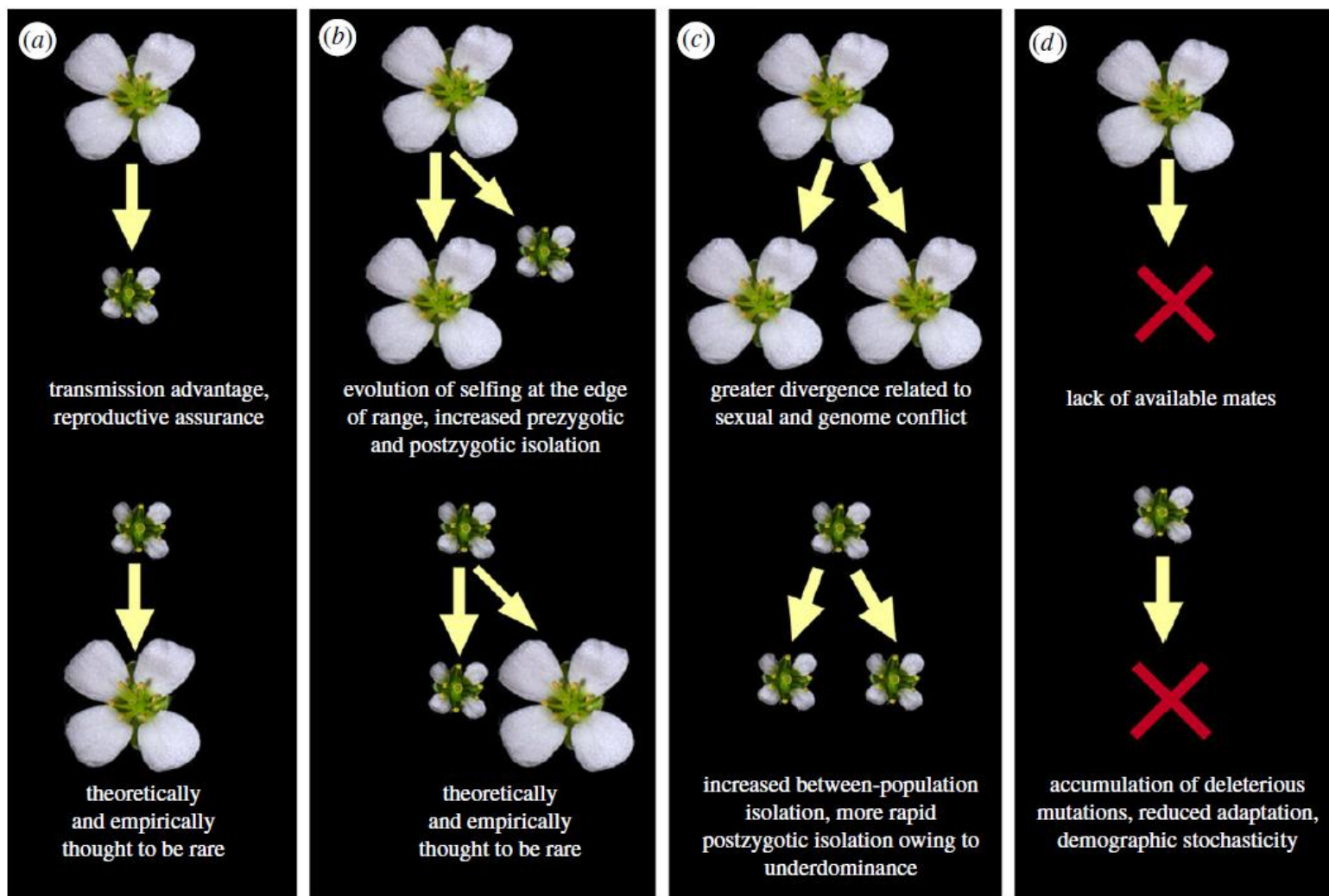
Cite this article: Wright SI, Kalisz S, Slotte T.

2013 Evolutionary consequences of self-fertilization in plants. *Proc R Soc B* 280: 20130133.

<http://dx.doi.org/10.1098/rspb.2013.0133>

CIZO-

**SAMO-
sprašnost**



III. Asexualní (nepohlavní) rozmnožování (= Apomixie)

často spojena s polyplodií

A. Vegetativní (= klonální)

Nezahrnuje tvorbu semen.

B. Agamospermie.

Znamená „semena bez gamet“ (nebo bez oplození).

[Taraxacum](#) (Asteraceae).

1. Adventivní embryonie

a. bez gametofytického stádia

b. embryo vzniká přímo ze somatické buňky (megasporocytu) vajíčka

2. Gametofytická apomixie.

Gametofyt vzniká, ale je diploidní (2N), ne haploidní

a. Diplosporie

b. Aposporie

c. Parthenogeneze



Výhody a nevýhody reprodukčních systémů.

1. Typ rozmnožování ovlivňuje/určuje genetické složení populace – homo-/heterozygotnost

inbrední deprese – recesivní alely v homozygotním stavu mohou redukovat zdatnost („cena za samosprašnost“)

outbrední deprese - zdatnost (fitnes) může být snížena, jestliže některé geny jsou adaptační pro dané prostředí

Výhody autogamie (samosprašení)

Jistější rozmnožení , nezávislost na opylovačích

Nevýhody

Vysoká homozygotnost – menší variabilita, adaptabilita

Nevýhody allogamie (cizosprašení)

„Energetická náročnost“ – produkce nápadných květů a nektaru.
V případě osídlení nových území, může být snížena produkce semen.

Potřeba opylovačů.

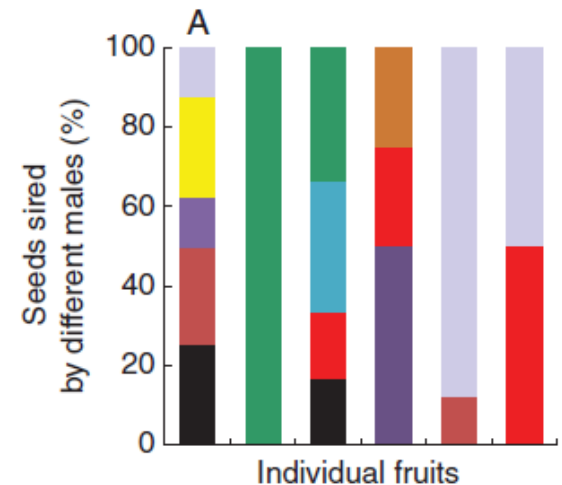
Díky cizosprašení se neustále mění genetické složení, a to i v případě výhodných adaptací. Výhodná je však heteroze.

Mnoho druhů proto kombinuje cizo- a samosprašnost v závislosti na podmínkách.

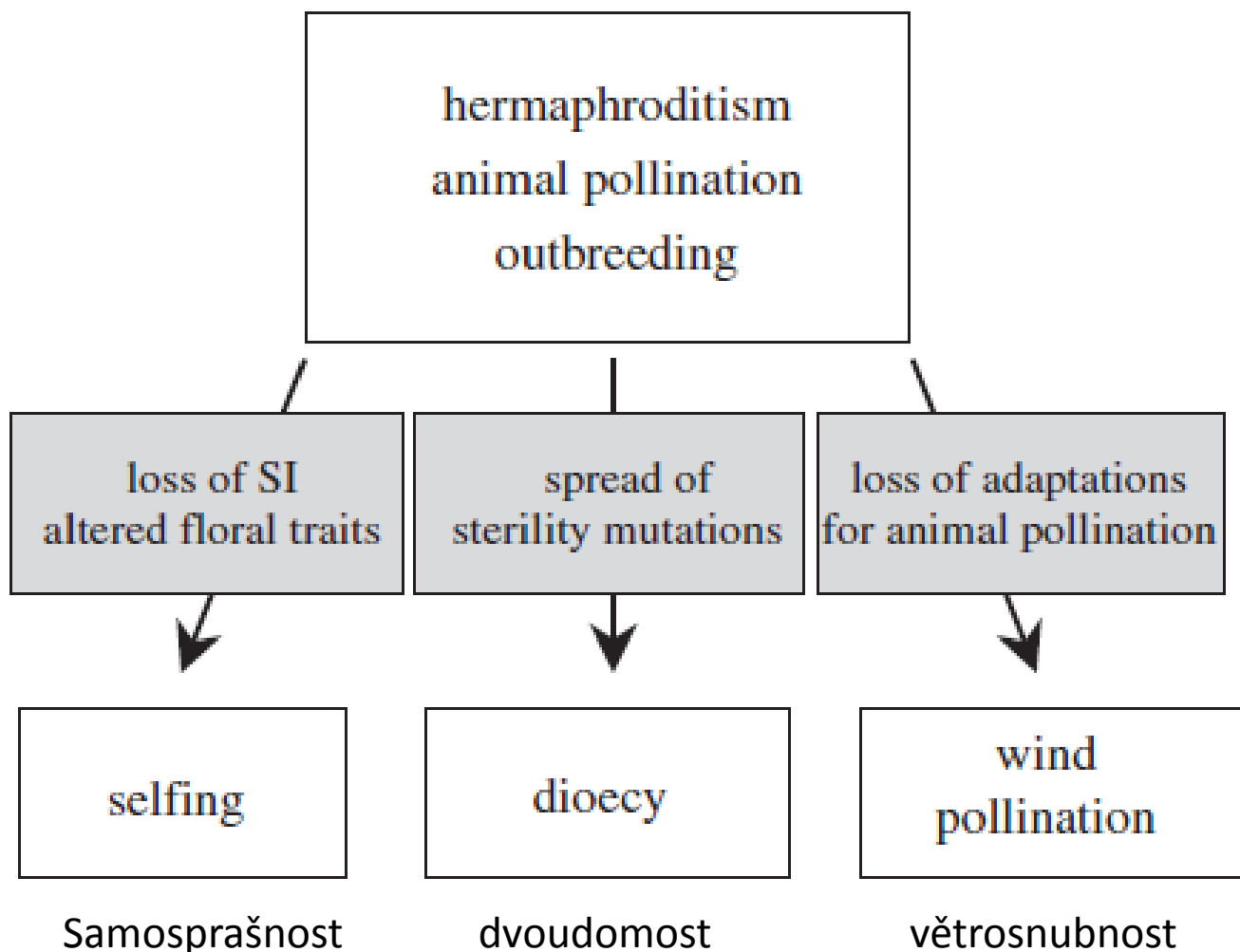
Výhody allogamie (cizosprašení)

Generuje genetickou variabilitu

Umožňuje tak adaptaci na měnící se prostředí



Evoluční změny v reprodukčních systémech rostlin



Evoluce reprodukčních systémů

Autoinkompatibilita (cizosparšnost) u krytosemenných
– pravděpodobně ancestrální stav.

Význam uzavřených plodolistů jako ochrana před
opylením vlastním pylem.

Autokompatibilita (samosprašnost) vznikla až následně.

Diverzita reprodukčních systémů je rozhodujícím
faktorem výměny genů v populaci.