Proměnlivost a evoluce rostlin

Petr Smýkal
Katedra botaniky, PřF UPOL
2012/13

Hybridizace
a
vznik nových druhů

ATE X. Assyrian bas-relief. Two figures of Ashur-nasir-pal, attended by priests in ceremonial attire, assisting the pollination rite before a conventionalized pistillate date tree (center). The right hand of each of the priests rries the staminate inflorescence of the date, the left hand holds the pollination tray or basket. Slab 2, Nimrud llery, British Museum.

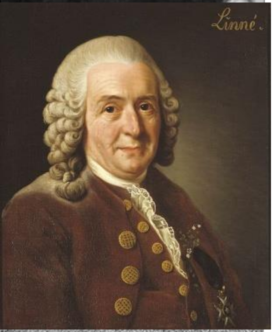
Babylonie a Asyrie, 900 př.n.l

Datlovník (*Phoenix dactylifera*)

Oddělené pohlaví, nutnost opylení

Mendelovi předchůdci

Rudolf J. Cammerer (1665-1721)
Uber das Geshlecht der Pflanzen (1694) – sex discovery in plants (pollens and ovaries) hybrids in plants

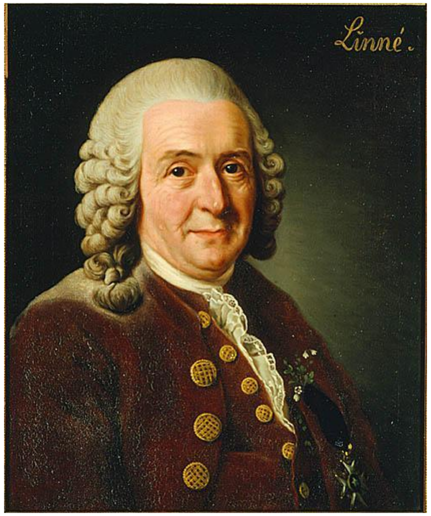


Carolus Linnaeus (1707-1778)
Initially concept of given / created number of species
Later observation of hybrids – „ it is without any doubt that new species might originate by hybridization“ (1759)

Joseph Koelreuter (1733-1806)
Making hybrids of tobacco, carnation (1760) – frequent sterility of hybrids, their origin is rare and has to be forced. Not discrete traits but „species essence“.

Carl F. Gaertner (1772-1850)
Hybrids in further generations (F2) have tendency to revert to original parental forms (hybrid instability), (1827) description of F2 maize hybrids (ratio 3,18 yellow : 1 coloured seeds)

Carl von Linne *(Carolus Linnaeus)*
(1707 – 1778)



Systema Naturae, *Genera Plantarum*,
Critica Botanica (1737) – znalost variability rostlin, fixní počet druhů
Platae Hydridae (1751) – 100 druhů/hybridů

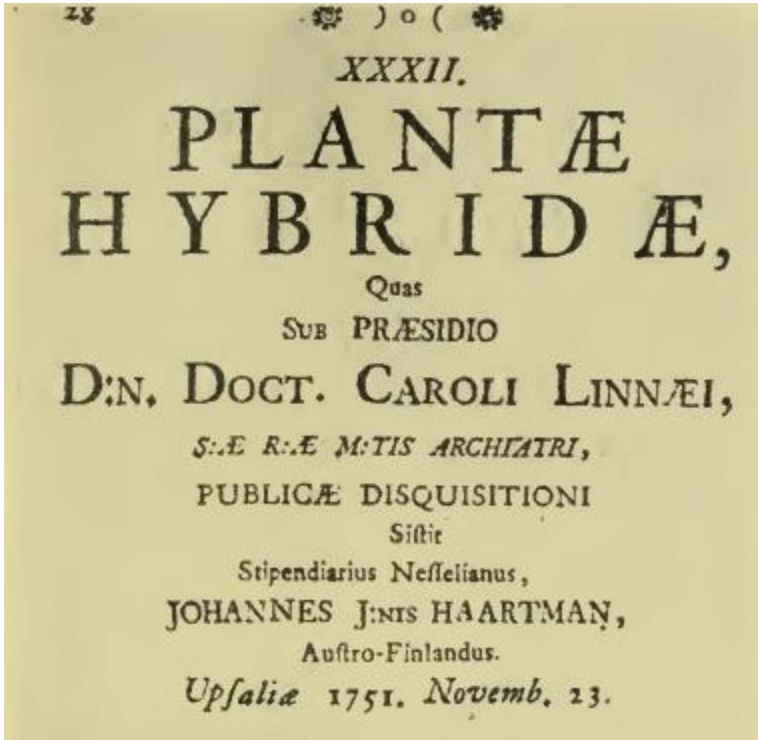
*Species Plantarum (*1753) začátek botanické nomenklatury a popis 5900 druhů.
Hierarchický umělý, binomický systém.
Pojmenoval 12,000 druhů (7700 rostlin, 4300 živočichů), 1105 rodů.

Carl von Linne *(Carolus Linnaeus)*

(1707 – 1778)

1757 – popis prvního vědecky doloženého hybrida
Tragopogon pratensis x T. porrifolius

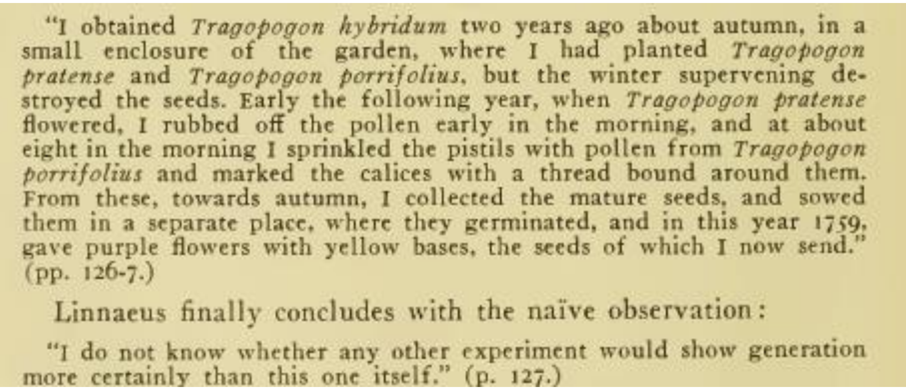
1760 – cena akademie v Petrohradě
význam i pro sexualitu u rostlin



28) o (

XXXII.

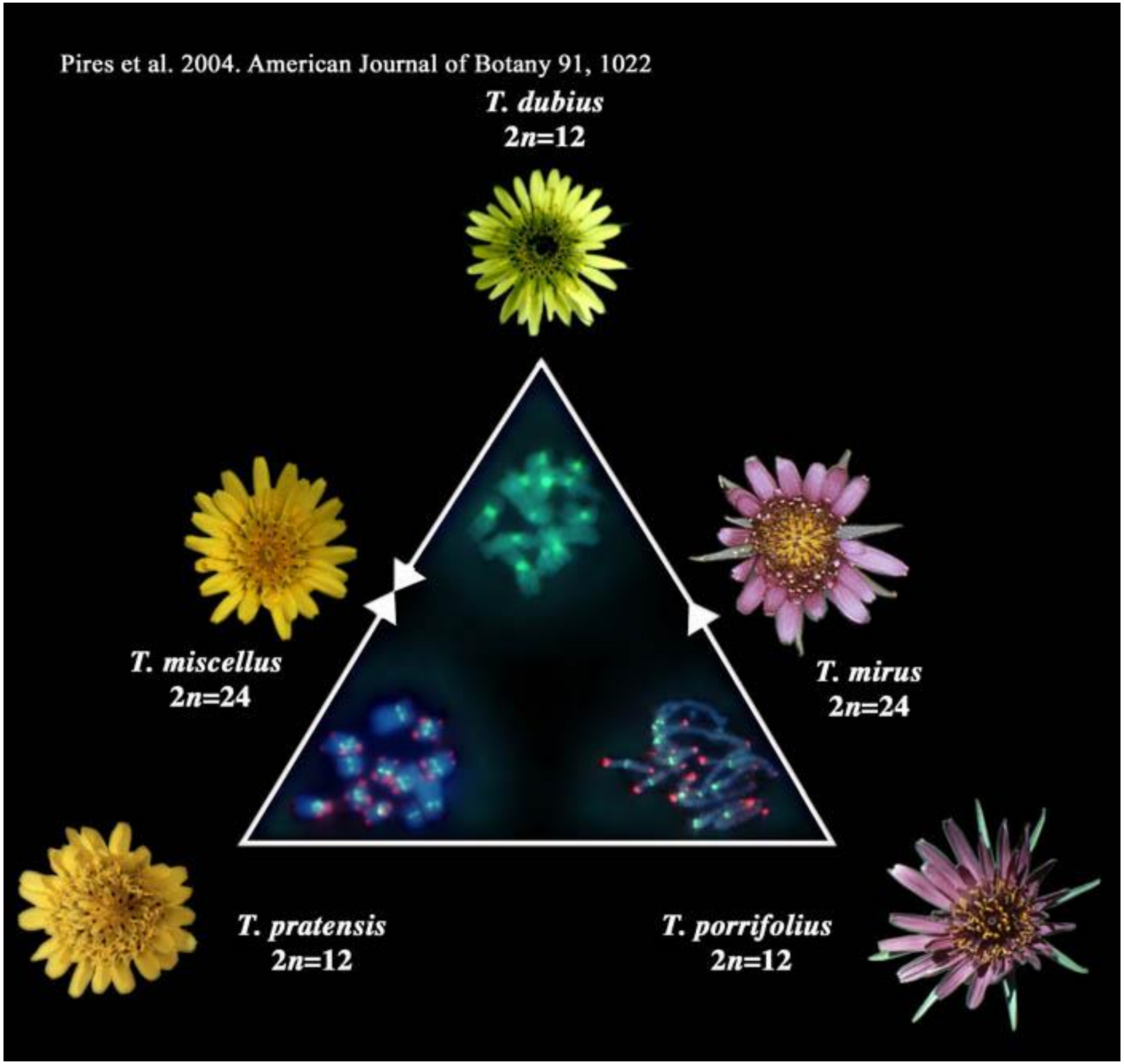
PLANTÆ
HYBRIDÆ,
Quas
Sub PRÆSIDIO
D:N. DOCT. CAROLI LINNÆI,
S:Æ R:Æ M:TIS ARCHIATRI,
PUBLICÆ DISQUISITIONI
Siſtit
Stipendiarius Neſſelianus,
JOHANNES J:NIS HAARTMAN,
Auſtro-Finlandus.
Upſaliæ 1751. Novemb. 23.



"I obtained *Tragopogon hybridum* two years ago about autumn, in a small enclosure of the garden, where I had planted *Tragopogon pratense* and *Tragopogon porrifolius*, but the winter supervening destroyed the seeds. Early the following year, when *Tragopogon pratense* flowered, I rubbed off the pollen early in the morning, and at about eight in the morning I sprinkled the pistils with pollen from *Tragopogon porrifolius* and marked the calices with a thread bound around them. From these, towards autumn, I collected the mature seeds, and sowed them in a separate place, where they germinated, and in this year 1759, gave purple flowers with yellow bases, the seeds of which I now send." (pp. 126-7.)

Linnaeus finally concludes with the naïve observation:

"I do not know whether any other experiment would show generation more certainly than this one itself." (p. 127.)



Diploidní druhy
2n = 2X = 12
evropské druhy zavlečené do Severní Ameriky
T. dubius, T. pratensis, a*T. porrifolius*

Ownby (1950) první pozorování hybridů v oblasti Palouse států Washington a Idaho

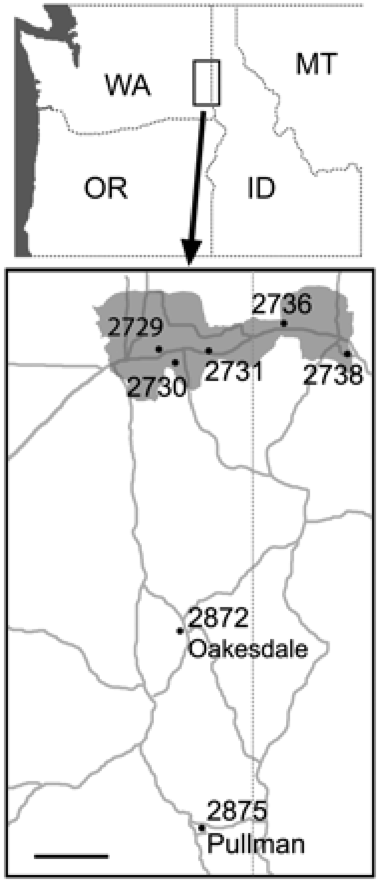
F1 hybridi jsou sterilní

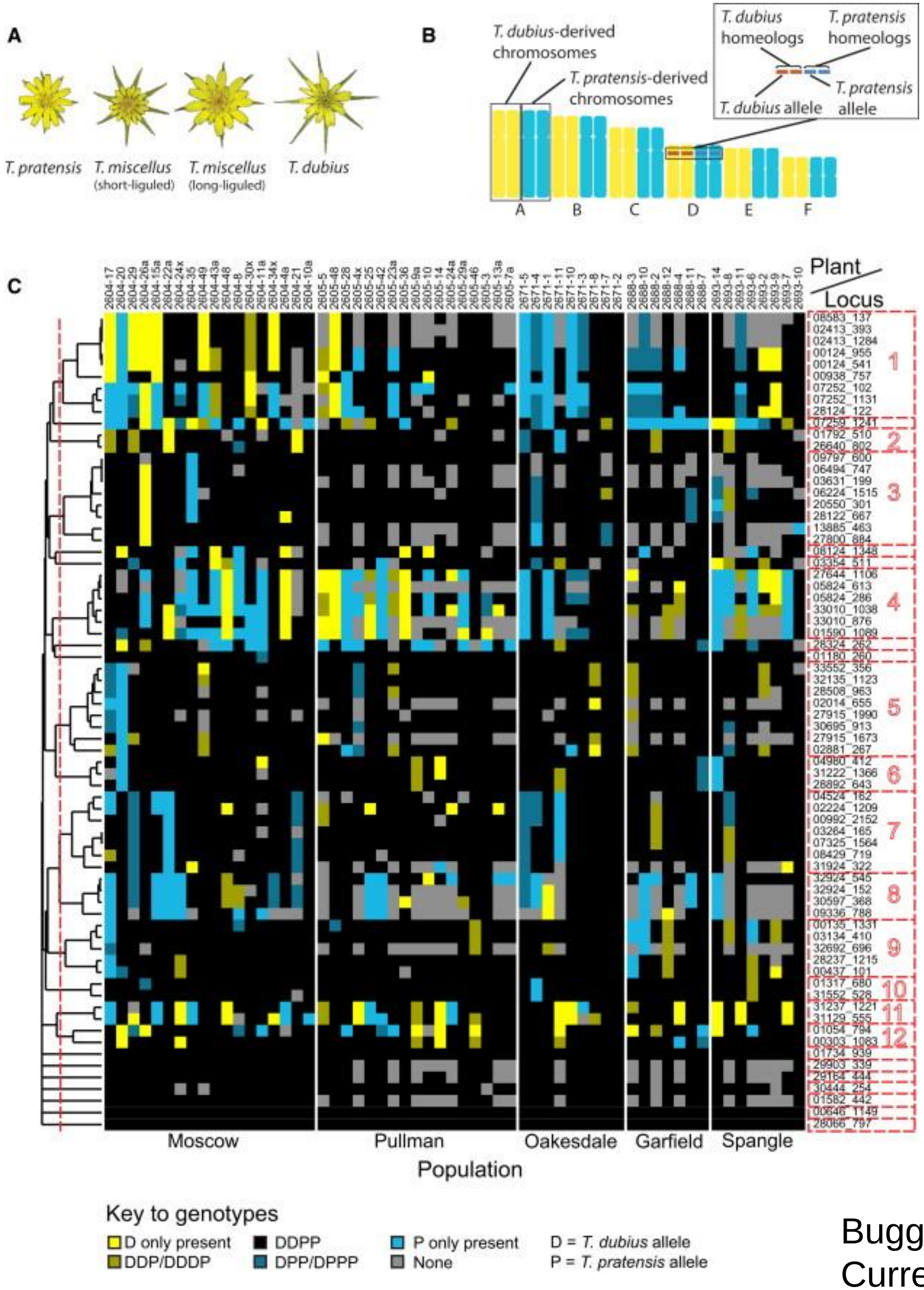
Ale tetraploidní hybridi
2n= 4x = 24
jsou fertilní a reprodukčně isolovaní od rodičovských druhů

Vznik vícenásobně

Hybridní druhy *Tragopogon*

Soltis et al. (1995) pomocí molekulárních markerů zjistil, že *T. miscellus* vznikl nejméně 9-13x a *T. mirus* 7-11x.
Častá polyploidizace během velmi krátké doby (50-60 let) od zavlečení.





Rapid, Repeated, and Clustered Loss of Duplicate Genes in Allopolyploid Plant Populations of Independent Origin

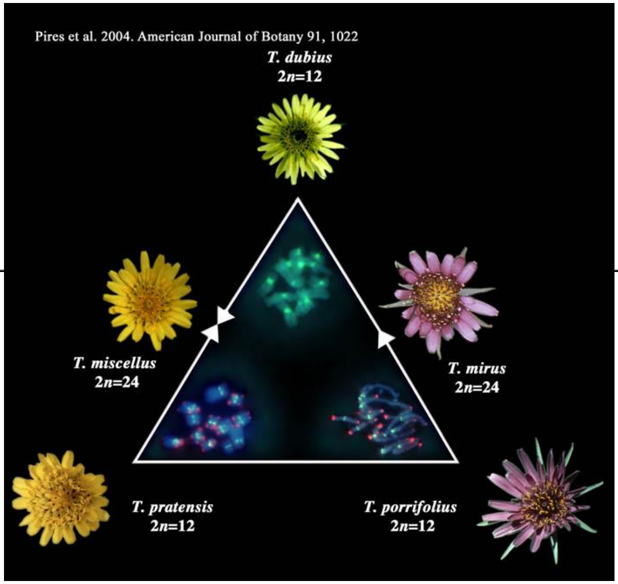
Whole-genome duplication (WGD; polyploidizationubiquitous in plant evolution. **We examined presence/absence of 70 homeologous loci in 59 *Tragopogon miscellus* plants from five natural populations of independent origin**; this allotetraploid arose 80 years ago via hybridization between diploid parents and WGD.

Buggs et al.
Current Biology, Volume 22, Issue 3, 248-252, 2012

Molecular cytogenetic analysis of recently evolved *Tragopogon* (Asteraceae) allopolyploids reveal a karyotype that is additive of the diploid progenitors

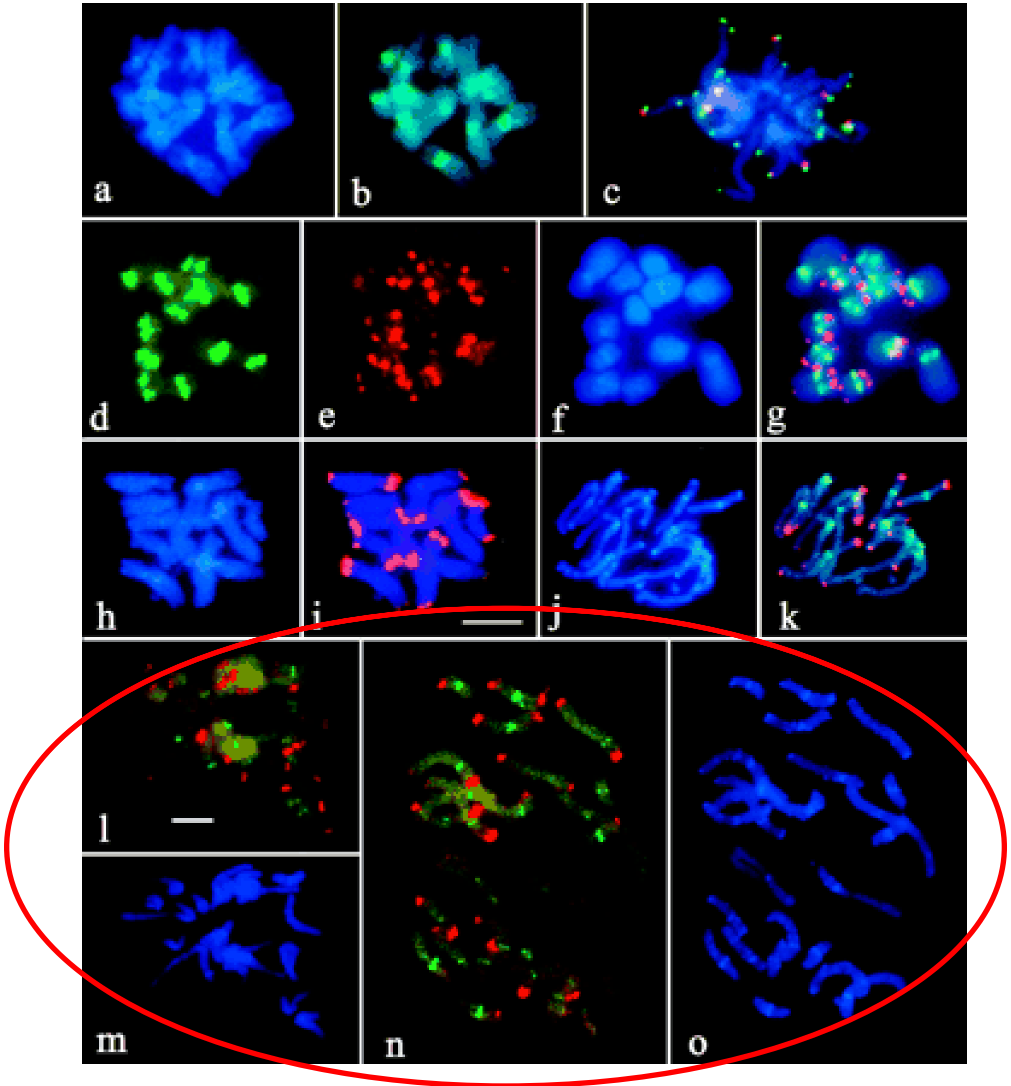
Pires et al. *Am. J. Bot. July 2004 vol. 91 no. 7 1022-1035*

Species	Collection number	Locality	4C DNA amount ± SD (pg)	TGP7, TPRMBO and TRS	18–26S and 5S
T. dubius	2613	Pullman, WA	10.83 ± 0.65 11.76 ± 0.79	X	X
T. dubius	2614	Rosalia, WA	10.80 ± 0.96		
T. dubius	2615	Spokane, WA	na	X	X
T. porrifolius	2612	Potlatch, ID	13.17 ± 0.83	TRS only	X
T. porrifolius	2611	Pullman, WA	12.50 ± 1.21	X	5S only
T. porrifolius	2607	Troy, ID	na	X	18S only
T. pratensis	2598	Colton, WA	11.59 ± 1.13	X	X
T. pratensis	2608	Moscow, ID	12.44 ± 0.87	X	X
T. pratensis	2609	Spangle, WA	11.08 ± 0.60	X	
T. mirus	2601	Finch's Pullman, WA	24.33 ± 1.26 24.32 ± 1.41 25.11 ± 1.75		X
T. mirus	2603	Rosalia, WA	20.90 ± 1.23 24.93 ± 1.55 25.64 ± 1.44		
T. mirus	2602	Palouse, WA	na		
T. miscellus	2604	Moscow, ID	20.30 ± 1.50		
T. miscellus	2605	Pullman, WA	20.99 ± 1.14		
T. miscellus	2606	Spangle, WA	21.76 ± 0.87		


Pires et al. 2004. American Journal of Botany 91, 1022

Molecular cytogenetic analysis of recently evolved *Tragopogon* (Asteraceae) allopolyploids reveal a karyotype that is additive of the diploid progenitors

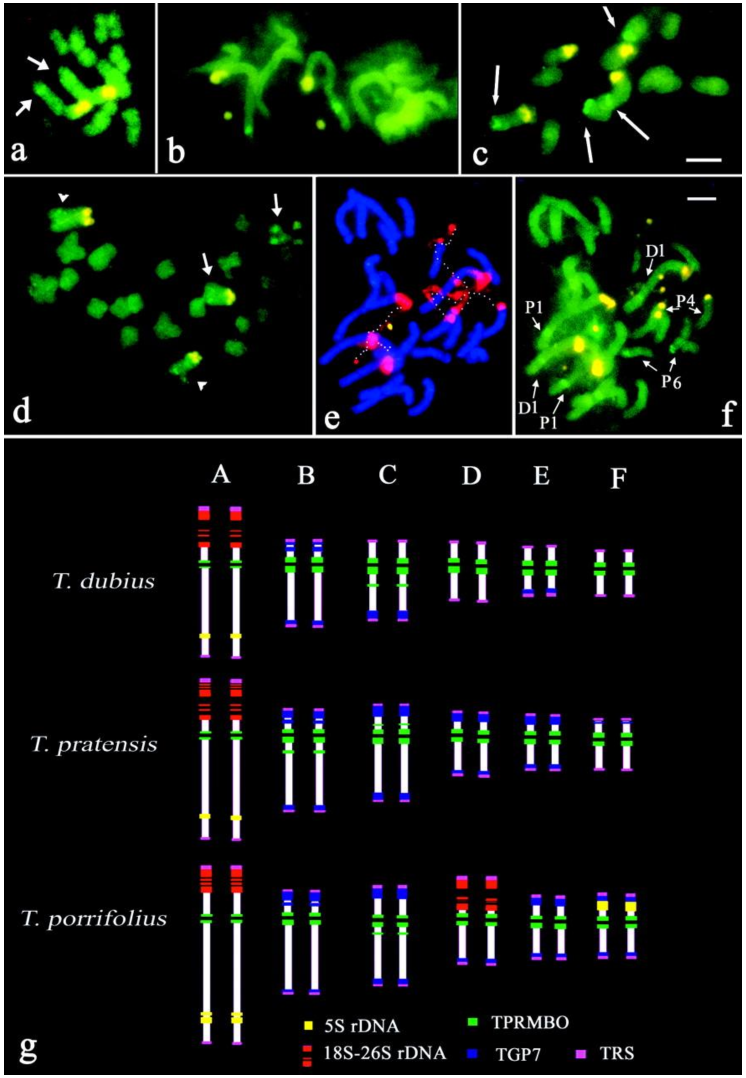
Pires et al. *Am. J. Bot. July 2004 vol. 91 no. 7 1022-1035*



Fluorescent in situ hybridization to *Tragopogon dubius* (a–c), *T. pratensis* (d–g), *T. porrifolius* (h–k), *T.* ***miscellus*** **(l, m) and** ***T. mirus*** **(n, o)**. Metaphases of diploid *T. dubius*: (a) 4,6-diamidine-2-phenylindole, dihydrochloride (DAPI)-stained (blue) and (b) TPRMBO-labeled metaphase showing the probe hybridizes to centromeric repeats (green); (c) metaphase labeled with TGP7 (red, eight sub-telomeric signals) and TRS (green, at the telomeres of all chromosomes). Metaphase of diploid *T. pratensis* labeled with (d) TPRMBO, (e) TGP7, note the few weaker signals dispersed at pericentromeric regions, (f) DAPI-stained and d–f merged (g). Metaphases of diploid *T. porrifolius*: (h) DAPI-stained metaphase and (i) probed with TGP7; (j) DAPI-stained metaphase and (k) labeled with TGP7 (red) and TPRMBO (green). Metaphase of allopolyploids *T. miscellus* (l, m) and *T. mirus* (n, o): (l, n) FISH with TPRMBO (green) and TPG7 (red) and (m, o) DAPI stained (blue).

Molecular cytogenetic analysis of recently evolved *Tragopogon* (Asteraceae) allopolyploids reveal a karyotype that is additive of the diploid progenitors

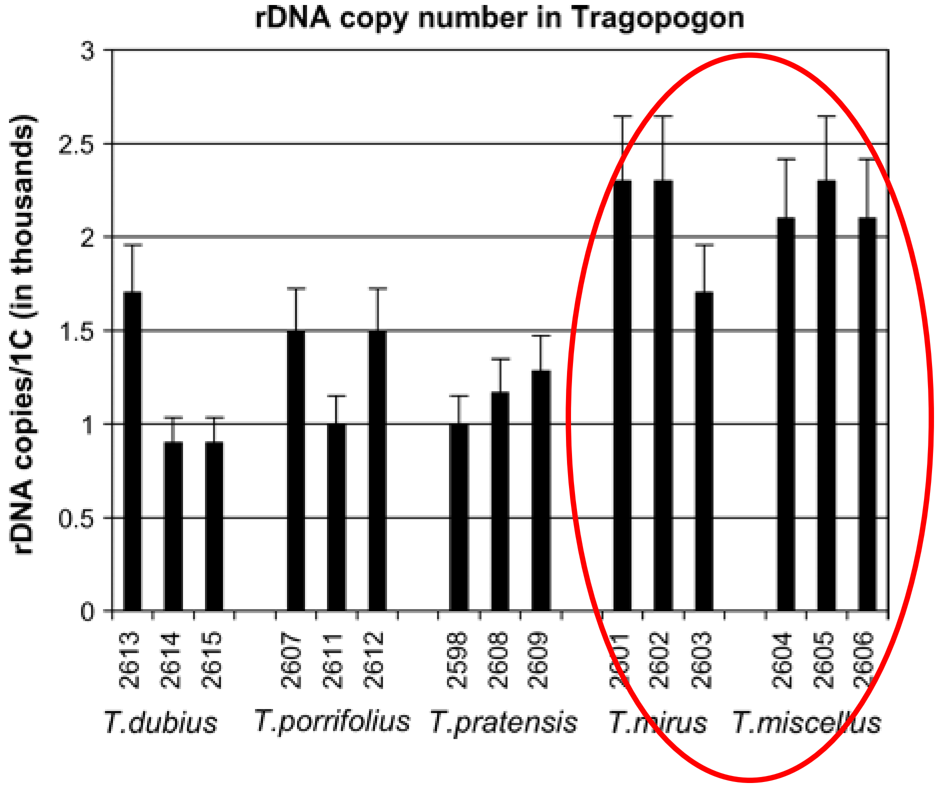
Pires et al. *Am. J. Bot. July 2004 vol. 91 no. 7 1022-1035*

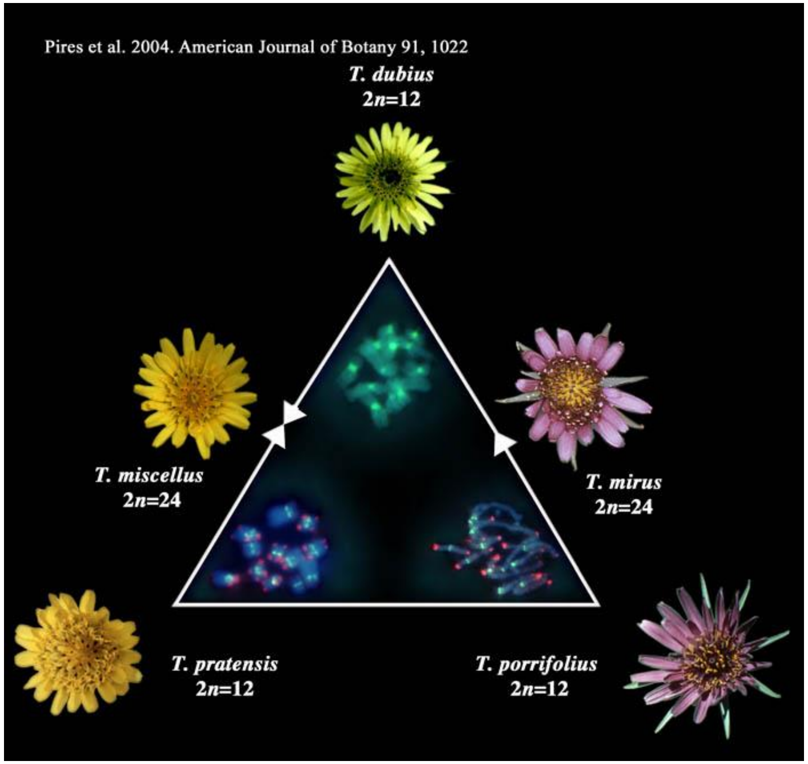


Fluorescent in situ hybridization to *T. dubius* (a), *T. pratensis* (b), *T. porrifolius* (c), *T. miscellus* (d) and *T. mirus* (e–f) with 18S–5.8S–26S rDNA (red or yellow) and 5S rDNA (green). (a) Metaphase of *T. dubius* with a pair of 5S rDNA locus (green, arrow) on the same pair of largest chromosome with terminal 18S–5.8S–26S rDNA (yellow) on the short arm. (b) Early metaphase of *T. pratensis* with a pair of 5S rDNA locus on the same pair of largest chromosome with terminal 18S–5.8S–26S rDNA. (c) Metaphase of *T. porrifolius* with a pair of terminal 5S rDNA (green, arrow), a pair of terminal 18S–5.8S– 26S rDNA (yellow), and an interstitial pair of 5S rDNA (green, arrow) on the largest chromosome pair with terminal 18S–5.8S–26S rDNA (yellow). **(d) Metaphase of *T. miscellus* with two pairs of terminal 18S–5.8S–26S rDNA loci (yellow) on the largest chromosomes with interstitial 5S rDNA (green, arrow on the long arms. (e) Early metaphase cell of *T. mirus* with six loci of 18S–5.8S–26S rDNA (red, decondensed rDNA indicated by dotted lines**) and (f) with six 5S rDNA loci (green, arrow) identified as D1 from *T. dubius* and P1 and P6 from *T. porrifolius*. P4 identifies the pair of 18S-5.8S-26S rDNA locus from *T. porrifolius* (yellow, arrow). (g) Karyotypes of diploid *T. dubius*, *T. pratensis*, and *T. porrifolius* showing all the mapped repetitive sequences for 5S rDNA, 18S-5.8S-26S rDNA, TPRMBO, TPG7, and TRS. The names of the chromosome pairs follow Ownbey and McCollum's karyotype nomenclature (1954)The gaps on the short arm of chromosome A of all species and on chromosome D of *T. porrifolius* represent secondary constrictions observed on some metaphases associated with the 18S–5.8S–26S rDNA.

Rapid Concerted Evolution of Nuclear Ribosomal DNA in Two Tragopogon Allopolyploids of Recent and Recurrent Origin

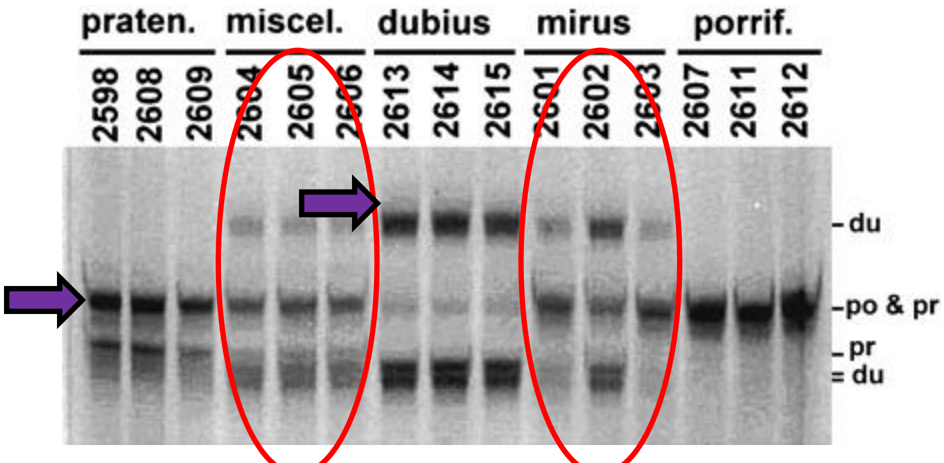
Kovařík et al. *Genetics February 1, 2005 vol. 169 no. 2 931-944*



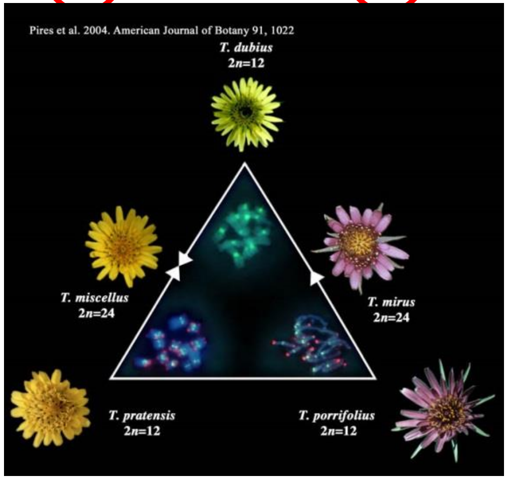

Pires et al. 2004. American Journal of Botany 91, 1022

Rapid Concerted Evolution of Nuclear Ribosomal DNA in Two Tragopogon Allopolyploids of Recent and Recurrent Origin

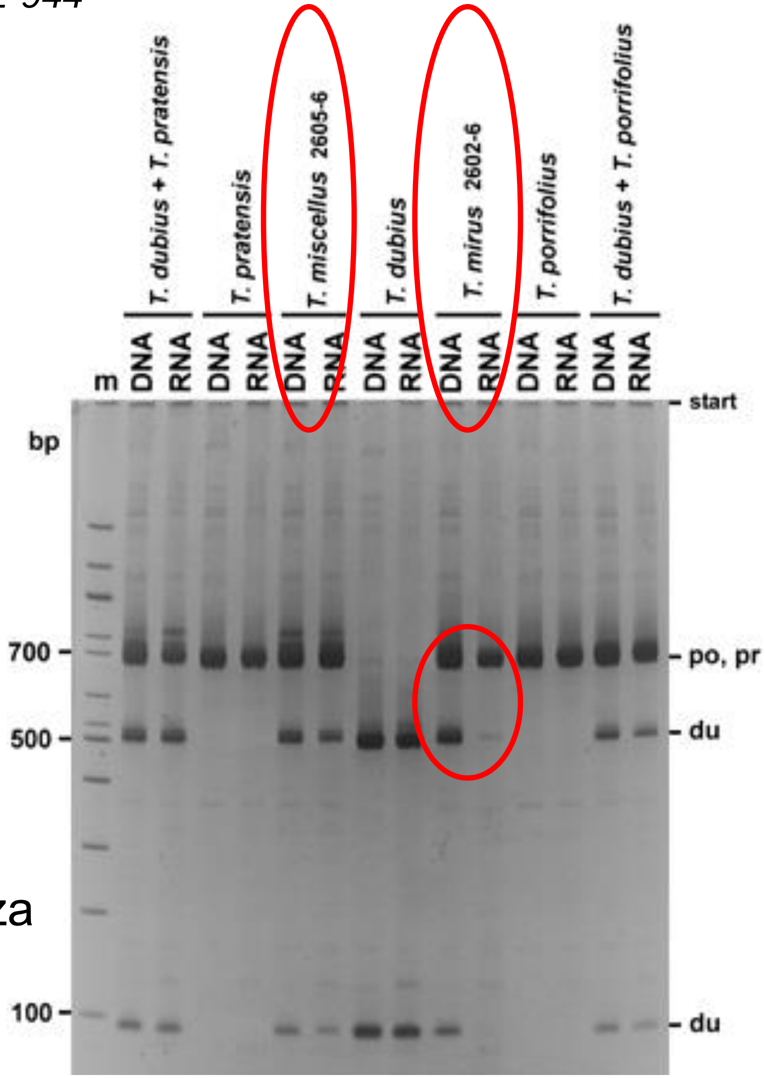
Kovařík et al. *Genetics February 1, 2005 vol. 169 no. 2 931-944*



ITS
analýza


Pires et al. 2004. American Journal of Botany 91, 1022

RT-PCR analýza
Exprese rRNA



Rapid Concerted Evolution of Nuclear Ribosomal DNA in Two Tragopogon Allopolyploids of Recent and Recurrent Origin

Kovařík et al. *Genetics February 1, 2005 vol. 169 no. 2 931-944*

ITS seq

	Accession/source	Total no. of sequenced clones	*T. dubius* clones (%)	*T. pratensis* clones (%)	Recombinant clones (%)
		***T. miscellus* populations**			
Present day	2606	15	7	80	13
	2605	28	14	68	18
	2604	24	25	58	17
	1	15	7	93	0
	4	20	30	70	0
Herbarium	Ownbey T-93-0; from 1953, Sheridan, WY	30	40	53	7
	Ownbey 3196; from 1949, Moscow, ID	20	43	52	5
	Accession/source	Total no. of sequenced clones	*T. dubius* clones (%)	*T. porrifolius* clones (%)	Recombinant clones (%)
		***T. mirus* populations**			
Present day	2603	29	10	69	21
	2602	21	46	29	25
	2601	31	29	61	10
	9	20	45	55	0
	21	15	20	80	0
Herbarium	Ownbey 3195; from 1949, Pullman, WA	17	47	40	13

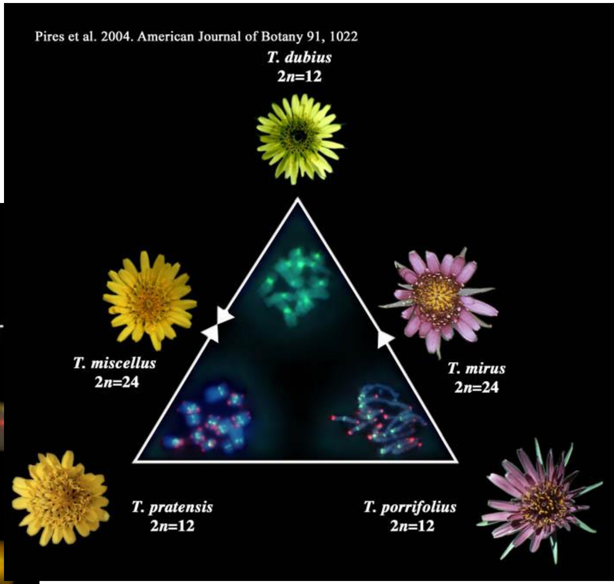
Rapid Concerted Evolution of Nuclear Ribosomal DNA in Two Tragopogon Allopolyploids of Recent and Recurrent Origin

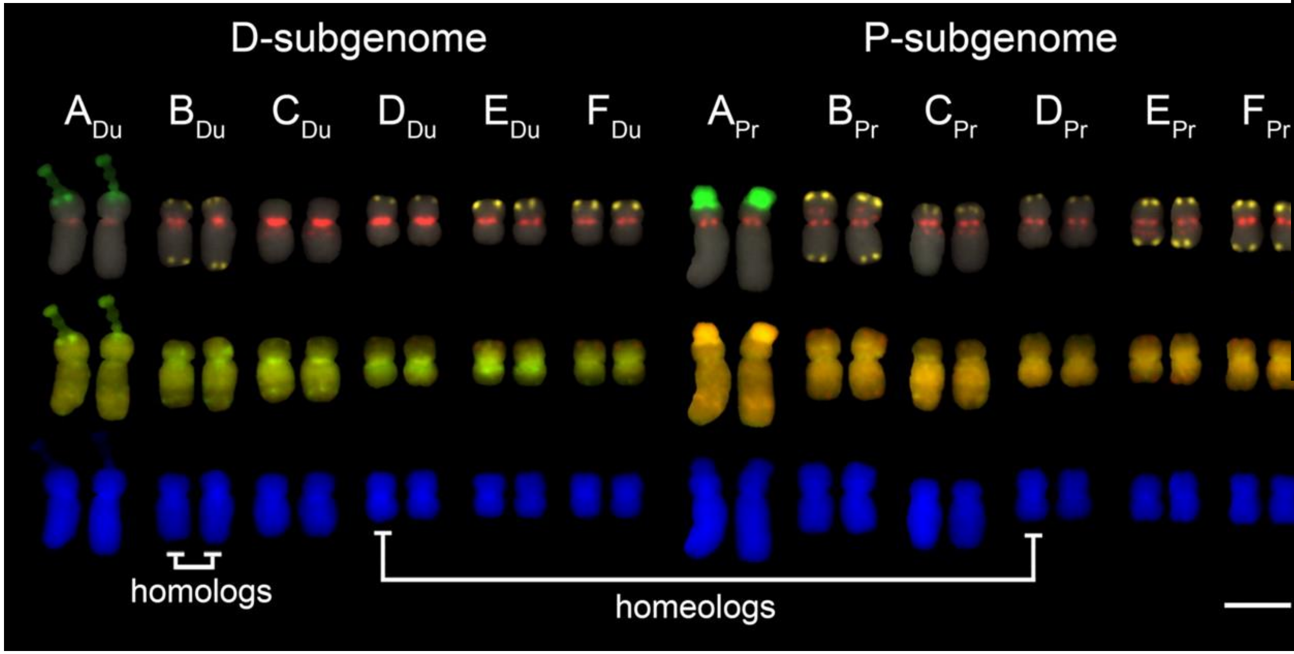
Kovařík et al. *Genetics February 1, 2005 vol. 169 no. 2 931-944*

Using the earliest herbarium specimens of the allotetraploids (1949 and 1953) to represent the genomic condition near the time of polyploidization, we found that the parental rDNA repeats were inherited in roughly equal numbers. **In contrast, in most present-day populations of both tetraploids, the rDNA of *T. dubius* origin is reduced and may occupy as little as 5% of total rDNA in some individuals**. However, in two populations of *T. mirus* the repeats of *T. dubius* origin outnumber the repeats of the second diploid parent (*T. porrifolius*), indicating bidirectional concerted evolution within a single species. In plants of *T. miscellus* having a low rDNA contribution from *T. dubius*, the rDNA of *T. dubius* was nonetheless expressed. We have apparently caught homogenization of rDNA repeats (concerted evolution) in the act, although it has not proceeded to completion in any allopolyploid population yet examined.

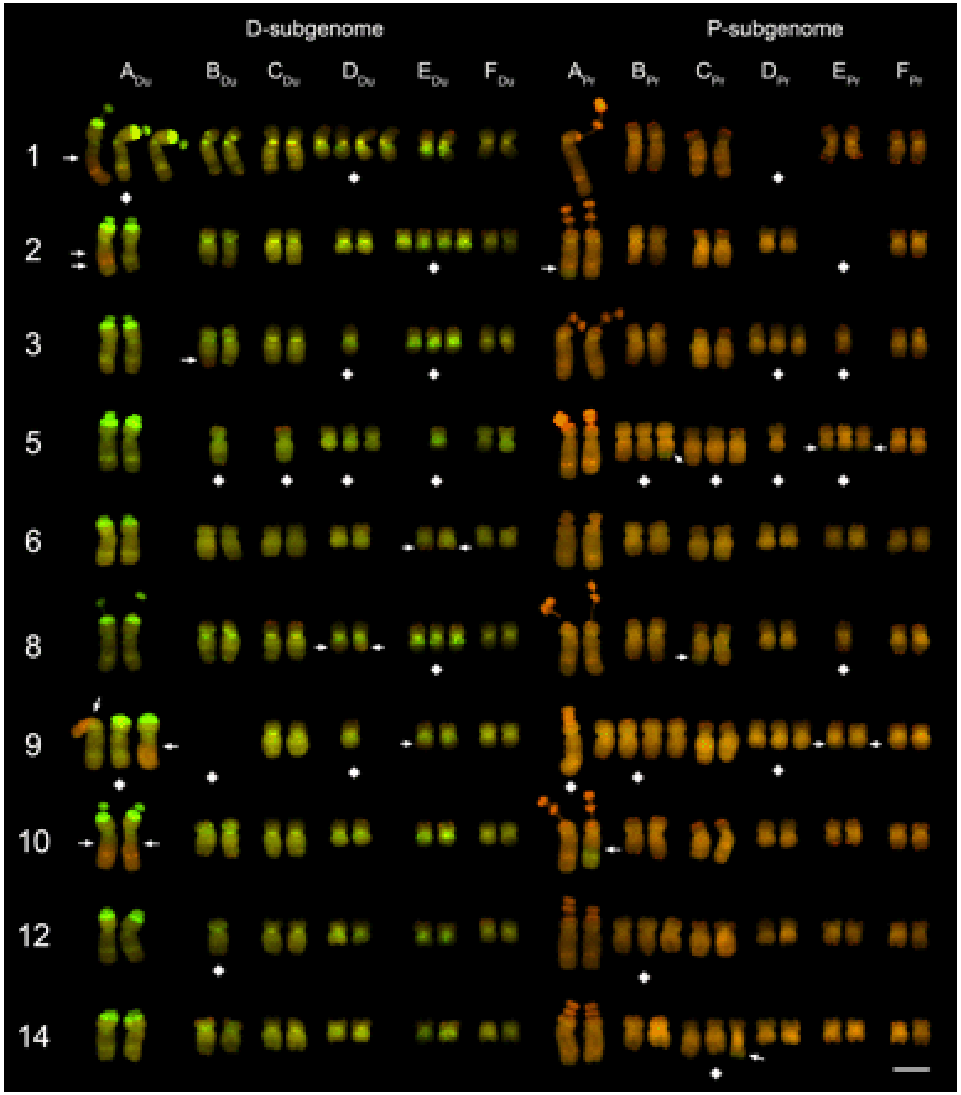
Extensive chromosomal variation in a recently formed natural allopolyploid species, *Tragopogon miscellus* (Asteraceae)

Chester et al. *PNAS January 24, 2012 vol. 109 no. 4 1176-1181*


Pires et al. 2004. American Journal of Botany 91, 1022



Mitotic karyotype of a *T. miscellus* plant showing an additive chromosome complement. Metaphase chromosomes (from plant 2875–1-1) were first subjected to FISH (top row) using probes for 35S rDNA (green), a centromeric repeat (TPRMBO; red), and a subtelomeric repeat (TGP7; yellow). The same spread was then reprobed with total genomic DNA (GISH; middle row) of *T. dubius* (green) and *T. pratensis* (red); chromosomes were counterstained with DAPI (gray). The lower row shows the same chromosomes with only DAPI staining (blue). Each chromosome is present in two copies (disomic).

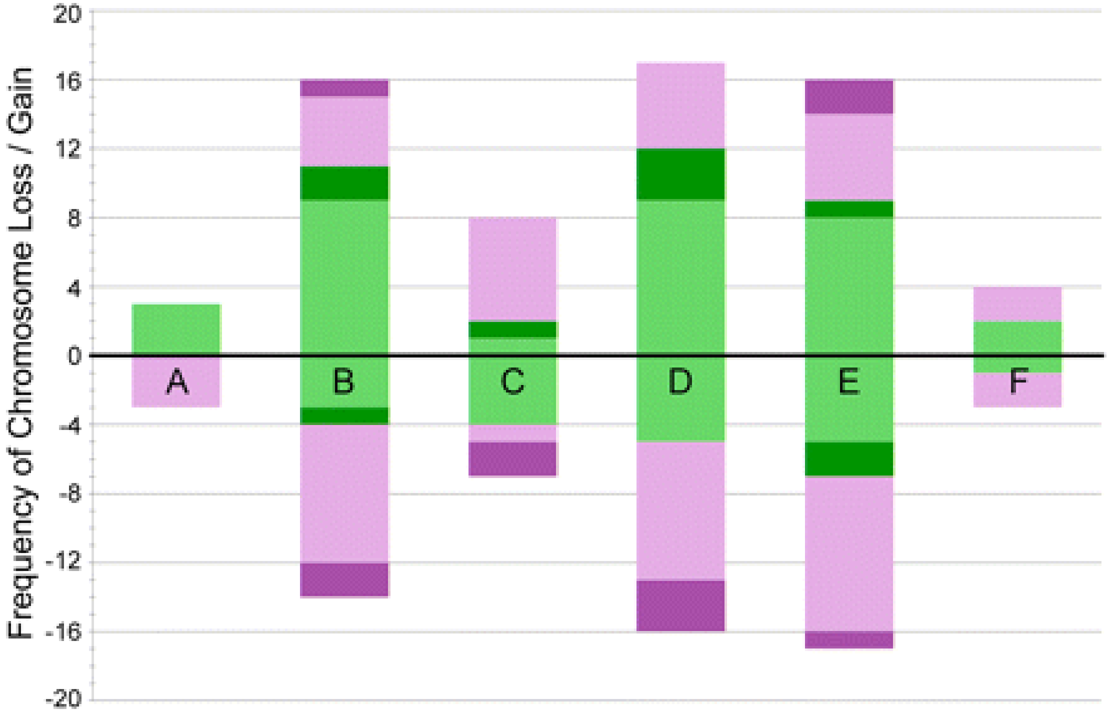


Mitotic karyotypes of 10 *T. miscellus* individuals from Oakesdale, WA.

GISH was carried out with total genomic DNA probes of *T. dubius* (green) and *T. pratensis* (red).

Arrows indicate the positions of translocation breakpoints.

Diamond symbols show aneuploid chromosomes (i.e., those that are not disomic).
(Scale bar: 5 µm.)



Stacked bar chart showing the **number of chromosome losses and gains from GISH karyotypes** of seed-grown plants.

On the *y*-axis are the numbers of aneuploid chromosomes observed in the 48 plants grown from seed, which were not chromosomally additive of the parents. Each bar on the *x*-axis represents one of the six homeologous chromosome groups, A–F, of *T. pratensis* (magenta) and *T. dubius* origin (green).

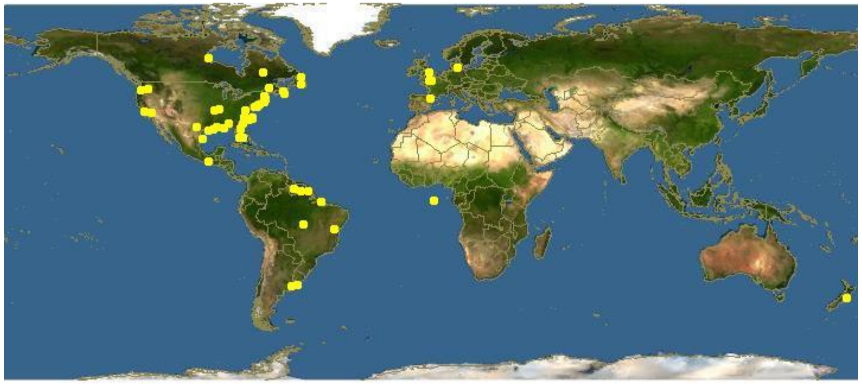
Cases of chromosome loss (either monosomy or nullisomy) and gain (either trisomy or tetrasomy) are shown below and above the origin, respectively.
The severity of the aneuploidy is indicated by color intensity, with monosomy or trisomy shown by lighter colors and nullisomy or tetrasomy indicated by darker colors.

Extensive chromosomal variation in a recently formed natural allopolyploid species, *Tragopogon miscellus* (Asteraceae)

Chester et al. *PNAS January 24, 2012 vol. 109 no. 4 1176-1181*

Using genomic and fluorescence in situ hybridization, we uncovered massive and repeated patterns of chromosomal variation in all populations. **No population was fixed for a particular karyotype; 76% of the individuals showed intergenomic translocations, and 69% were aneuploid for one or more chromosomes. Importantly, 85% of plants exhibiting aneuploidy still had the expected chromosome number, mostly through reciprocal monosomy-trisomy of homeologous chromosomes (1:3 copies) or nullisomy-tetrasomy (0:4 copies).** The extensive chromosomal variation still present after *ca*. 40 generations in this biennial species suggests that substantial and prolonged chromosomal instability might be common in natural populations after whole genome duplication.

hybridní *Spartina*



Spartina - *S.alterniflora × townsendii* (*S. alterniflora× S. maritima*)

Evropský druh *Spartina maritima* (2n = 2X = 60) v roce 1870 přišla do kontaktu se zavlečených americkým druhem *S. alterniflora* (2N = 2X = 62).
Vznikl amfidiploidní druh *S. x townsendii* (2n = 2X = 62), který byl sterilní (Marchant 1963, 1966).
V okolí anglického Southamptonu vznikl alloploid *S. anglica* (2n = 4X = 120, 122, or 124), který byl fertilní.
Další, pravděpodobně reciproční hybrid *S. x neyrautii* byl nalezel v roce1892 ve Francii.
Oba hybridi vykazovaly velmi nízkou genetickou diverzitu – pravděpodobně vznikly jen jednou, nebo z geneticky uniformních rodičů

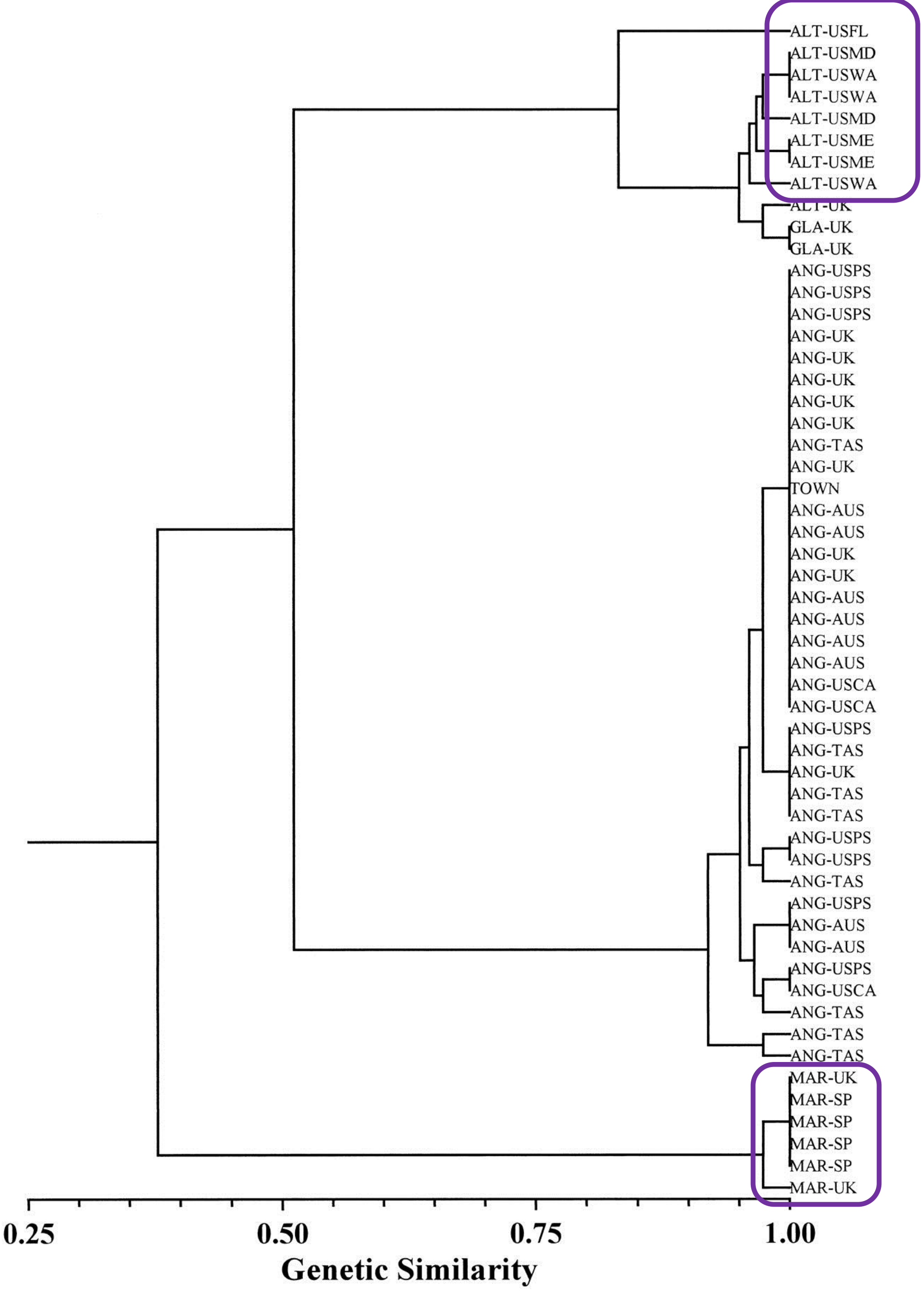
Spartina anglica *(2n=122-124)*

(S. alterniflora × S. maritima)

Delivering
Alien
Invasive
Species
Inventories
for **E**urope

Origin and genetic diversity of *Spartina anglica* (Poaceae) using nuclear DNA markers

Ayres and Strong, *Am. J. Bot. October 2001 vol. 88 no. 10 1863-1867*

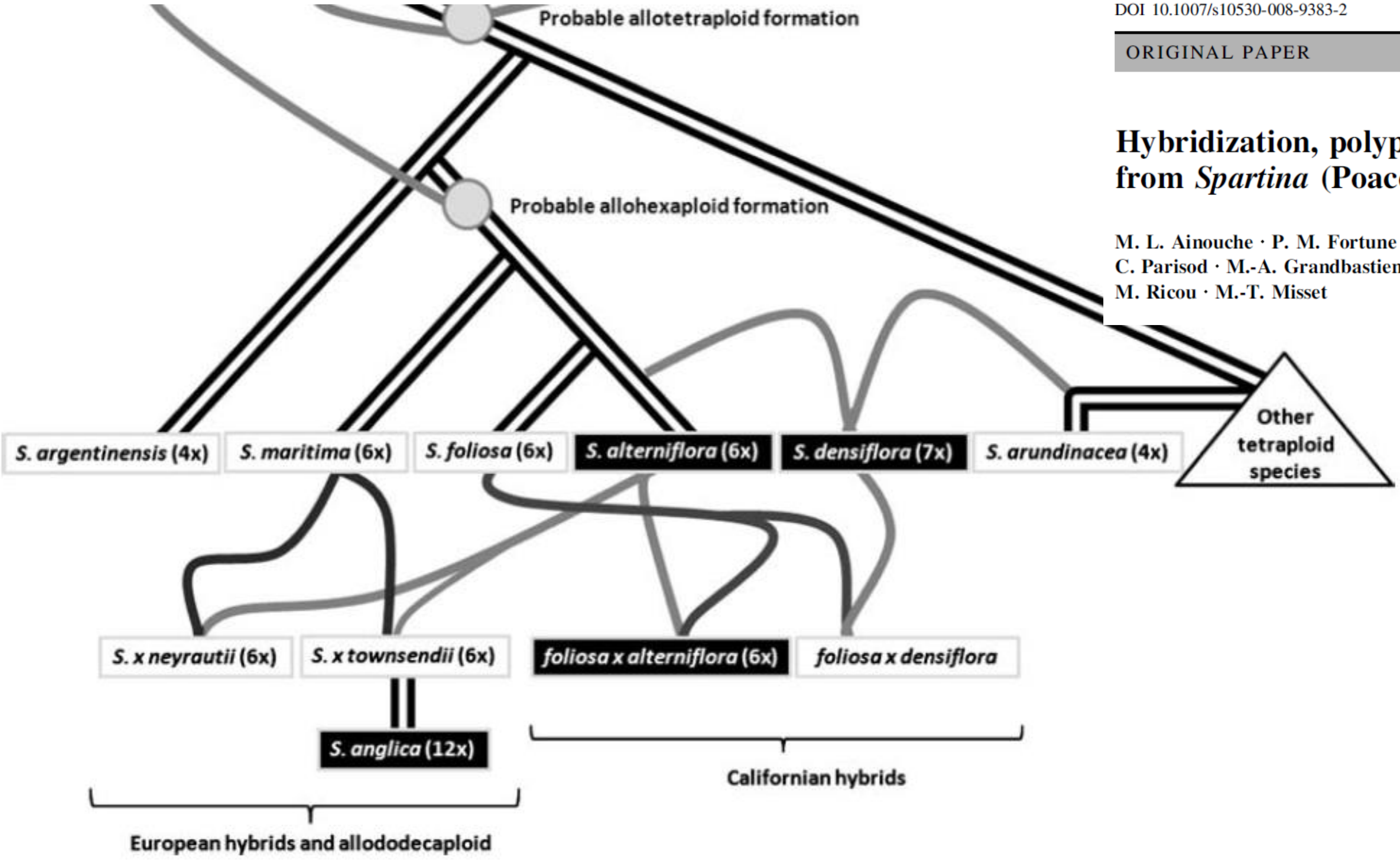


Nízká genetická diverzita hybridu ale možnost vícenásobného vzniku

Dendrogram portraying genetic similarity among species, populations, and individuals of *Spartina* (ALT = *S. alterniflora*; GLA = *S. alterniflora glabra*; MAR = *S. maritima*; ANG = *S. anglica*; TOWN = *S. ×townsendii*). Populations: US = United States; FL = Florida; MD = Maryland; ME = Maine; WA = Washington; PS = Puget Sound, Washington; CA = California; UK = United Kingdom; AUS = Australia; TAS = Tasmania; SP = Spain

Spartina alterniflora x foliosa

This invasive Spartina is primarily a result of hybridization between the native Pacific cordgrass (*Spartina foliosa*) and smooth cordgrass (*Spartina alterniflora*) from the East Coast which was introduced by the Army Corps of Engineers in the 1970s. The resulting hybrid plants, discovered and documented by scientists at UC Davis in the late 1990's, were found to be extremely invasive "ecosystem engineers" that threatened the integrity of marshes, mudflats, flood control channels,



Biol Invasions
DOI 10.1007/s10530-008-9383-2

ORIGINAL PAPER

Hybridization, polyploidy and invasion: lessons from *Spartina* (Poaceae)

M. L. Ainouche · P. M. Fortune · A. Salmon ·
C. Parisod · M.-A. Grandbastien · K. Fukunaga ·
M. Ricou · M.-T. Misset

Hybrids involving *S. alterniflora* (introduced) and *S. foliosa* (native) have arisen in California (Ayres *et al.*, 1999) where they compete with the native plants.

In addition, interspecific hybridization is reported in this area between the hexaploid *S. foliosa* and the introduced alloheptaploid *S. densiflora* (Ayres *et al.*, 2008).

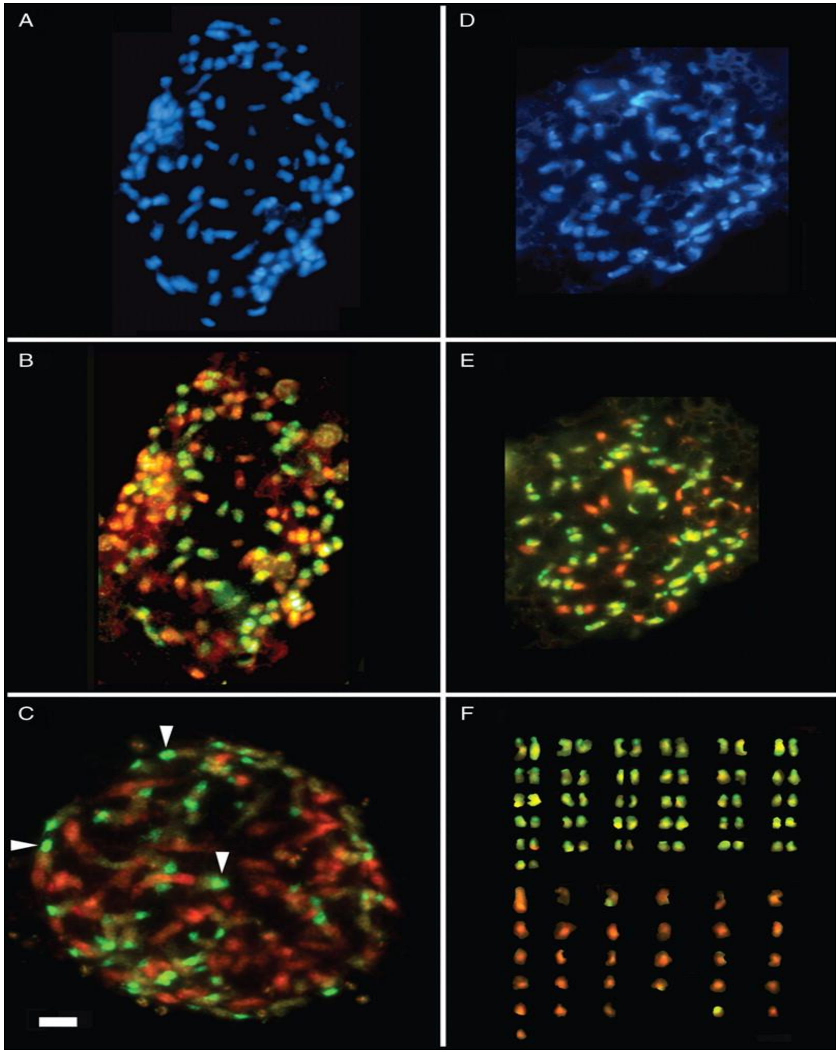
Furthermore *S. densiflora* originated in South America following hybridization between a hexaploid species (likely to be *S. alterniflora*) and a tetraploid species related to *S. arundinacea*, also from the southern hemisphere (Fortune *et al.*, 2008).

Backcrossing of the F_1 *S. densiflora* × *S. foliosa* hybrids ($2n = 66$) has resulted in individuals with $2n = 94$–96, exhibiting either '*foliosa*' or '*alterniflora*' plastid sequence types (Ayres *et al.*, 2008).

indicate the extensive reticulate evolution in the genus.

Flow cytometry and GISH reveal mixed ploidy populations and *Spartina* nonaploids with genomes of *S. alterniflora* and *S. maritima* origin

Renny-Byfield et al. *Ann Bot (2010) 105 (4): 527-533.*



Root tip metaphases (A, B, D–F) and prophase nucleus (C) after DAPI staining (blue fluorescence) (A, D) and GISH (B, C, E, F) using digoxigenin-labelled probes of *S. alterniflora* genomic DNA (green, detected using FITC-conjugated anti-digoxigenin IgG) and biotin-labelled probes of *S. maritima* genomic DNA (orange, detected using Cy3-conjugated streptavidin). Shown in (A–C) are cells from an **AAMM dodecaploid individual with approx. 120 chromosomes, approx. 60 of which are of *S. maritima* origin and approx. 60 of *S. alterniflora* origin.**

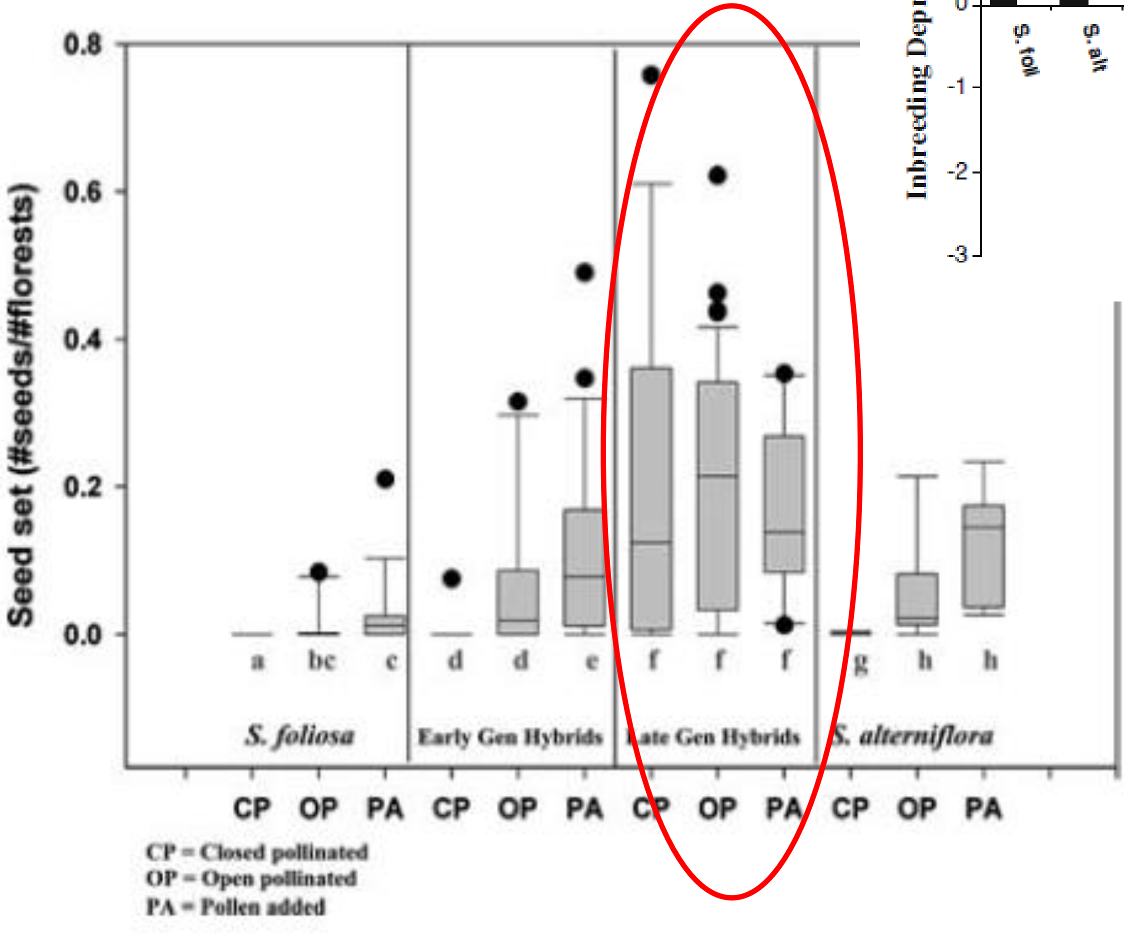
nonaploids were the rarest, occurring at a frequency of approx. 10·7 % (= 6 individuals), whereas dodecaploids and hexaploids occurred at higher frequencies of 17·8 % (= 10 individuals) and 71 % (= 40 individuals),

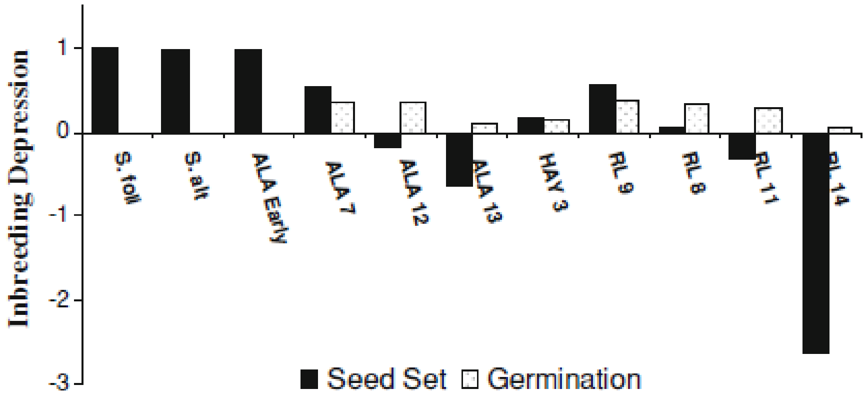
Biol Invasions (2009) 11:1131–1144
DOI 10.1007/s10530-008-9385-0

ORIGINAL PAPER

The rapid evolution of self-fertility in *Spartina* hybrids (*Spartina alterniflora* × *foliosa*) invading San Francisco Bay, CA

Christina M. Sloop · Debra R. Ayres ·
Donald R. Strong





Inbrední deprese rodičů
a časných hybridů

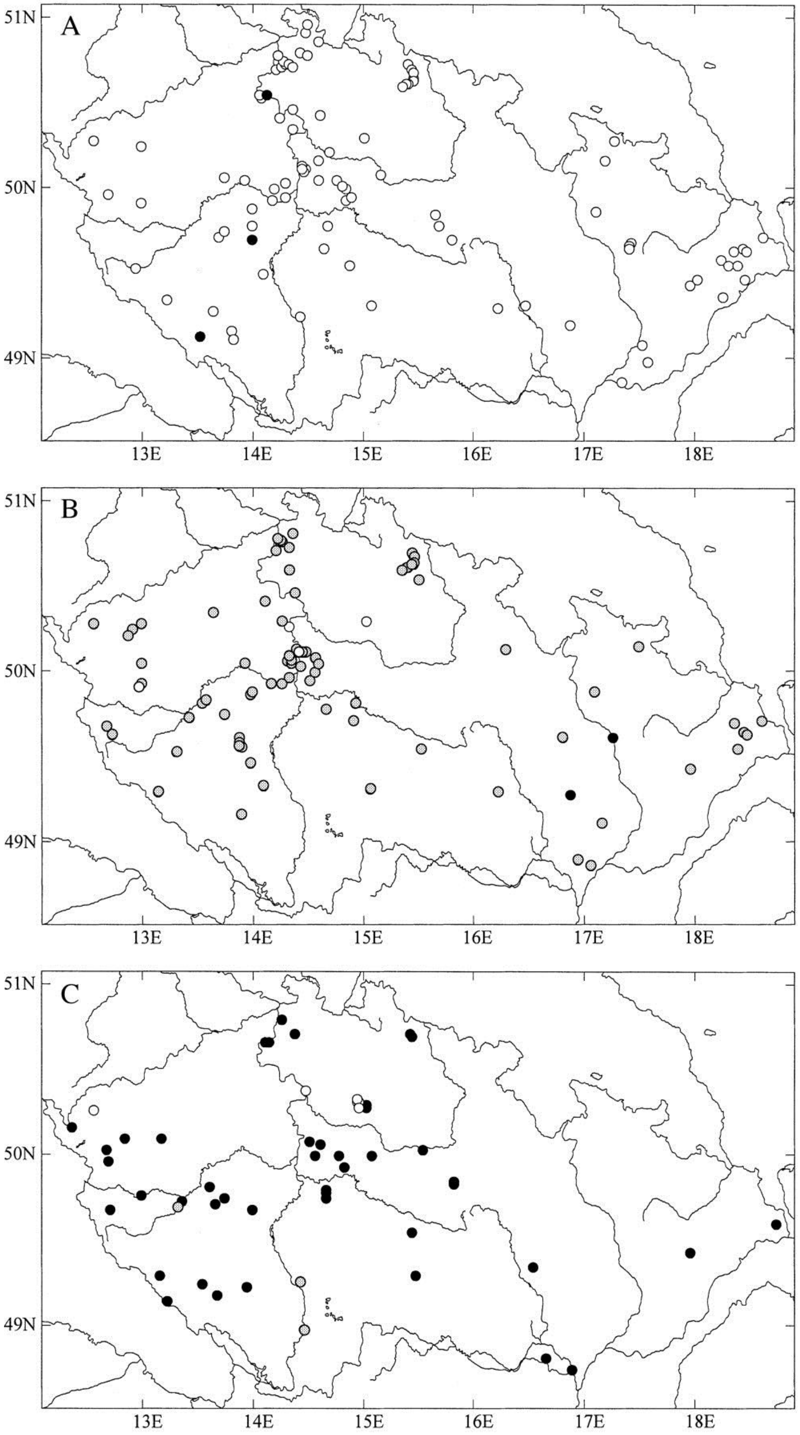
„pozdní hybridi“ mají lepší
klíčení a více semen při
samosprášení
než cizosprášení

Větší fitness

Reynoutria x bohemica

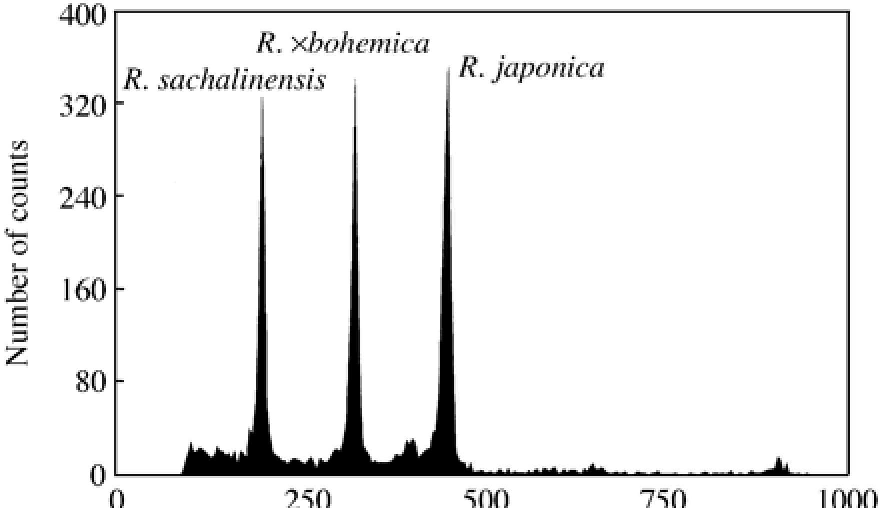
Variation in DNA-ploidy Levels of *Reynoutria* Taxa in the Czech Republic

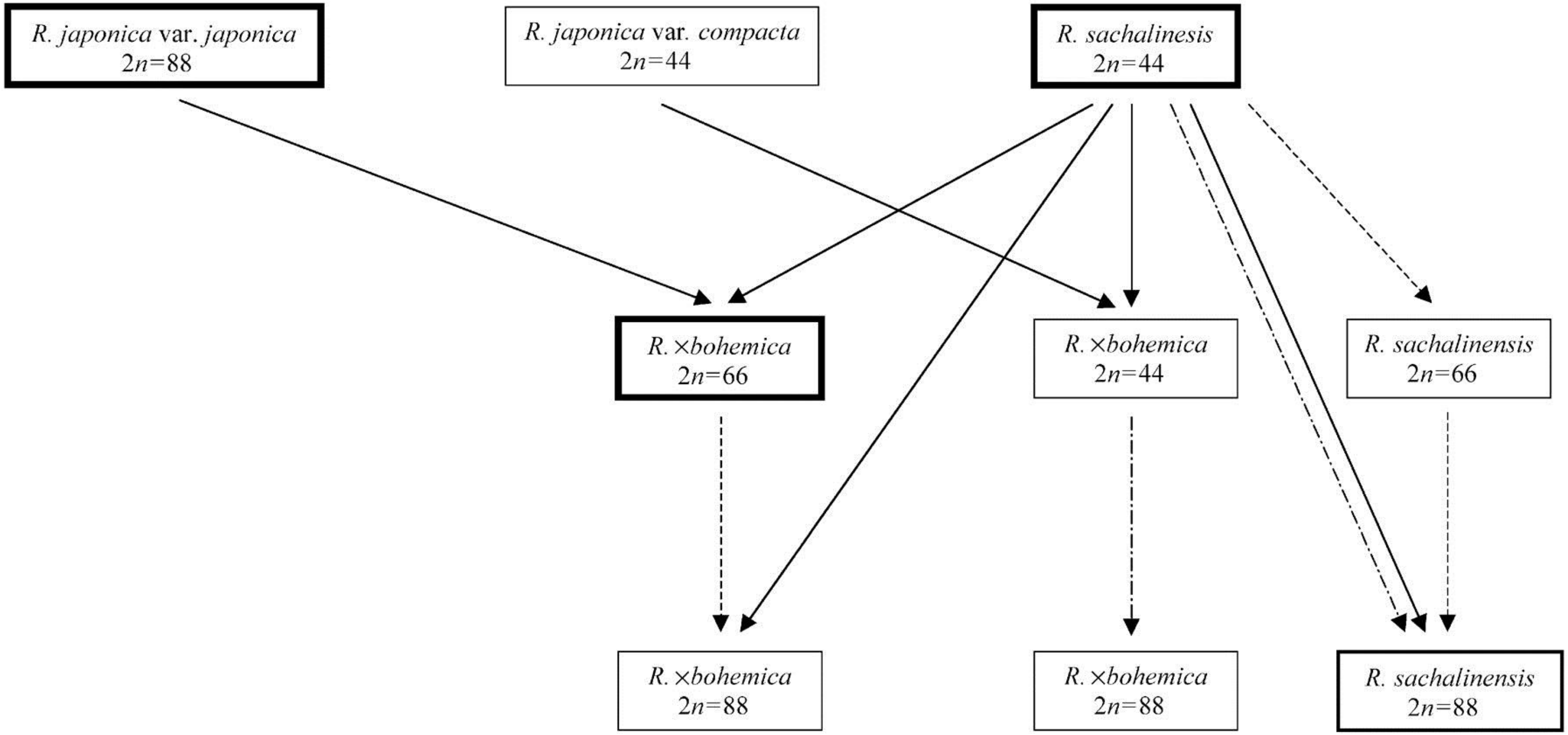
Mandák et al. *Ann Bot (2003) 92 (2): 265-272*



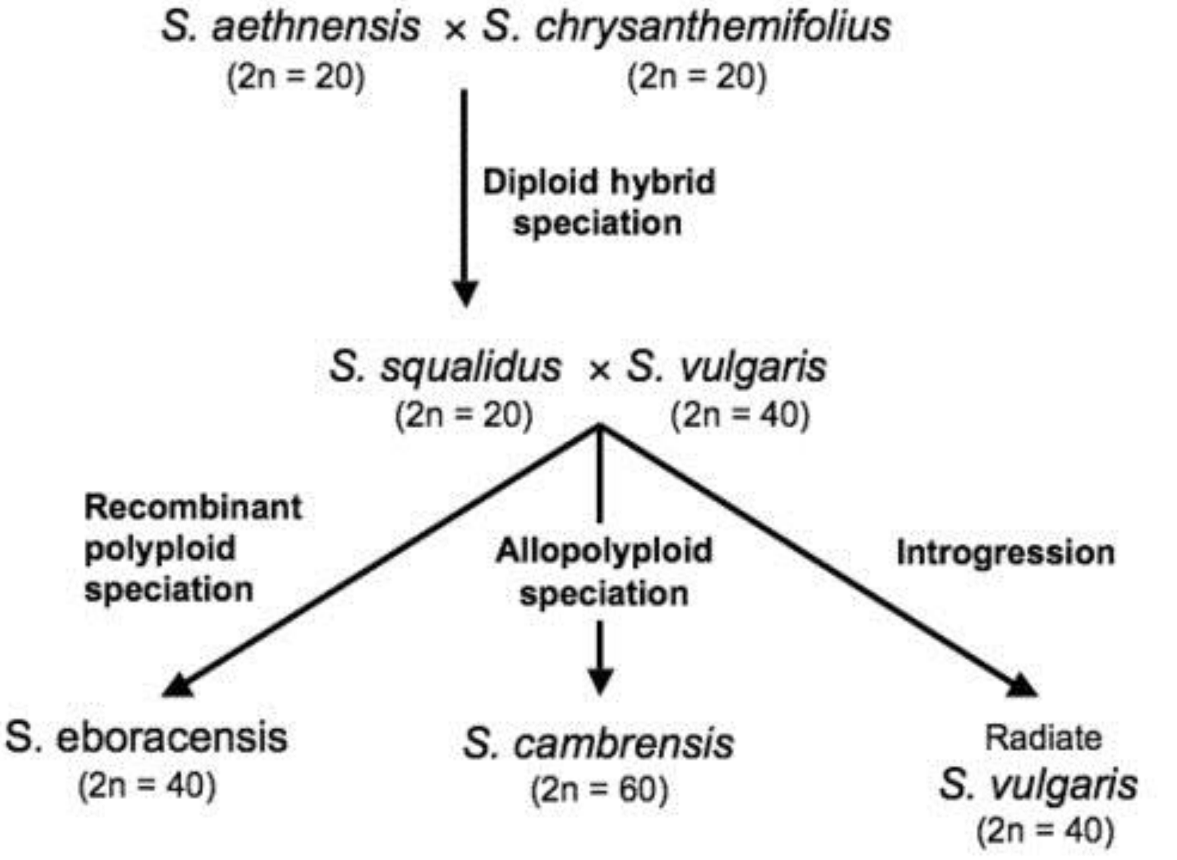
Distribution of the 257 *Reynoutria* clones used in this study. A, *Reynoutria japonica* var. *japonica* (white circles) and *R. japonica* var. *compacta* (black circles). B, *R. ×bohemica*; C, *R. sachalinensis*.

Black circles indicate tetraploids (2*n* = 44),
grey circles hexaploids (2*n* = 66),
and open circles octoploids (2*n* = 88).




R. japonica var. *japonica*
2*n*=88
R. japonica var. *compacta*
2*n*=44
R. sachalinesis
2*n*=44
R. ×*bohemica*
2*n*=66
R. ×*bohemica*
2*n*=44
R. sachalinensis
2*n*=66
R. ×*bohemica*
2*n*=88
R. ×*bohemica*
2*n*=88
R. sachalinensis
2*n*=88

příklad *Senecio*



Current Biology

Adaptation and selection in the *Senecio* (Asteraceae) hybrid zone on Mount Etna, Sicily

---

Adrian C. Brennan[1]*, Jon R. Bridle[2]*, Ai-Lan Wang[1,3], Simon J. Hiscock[2] and Richard J. Abbott[1]

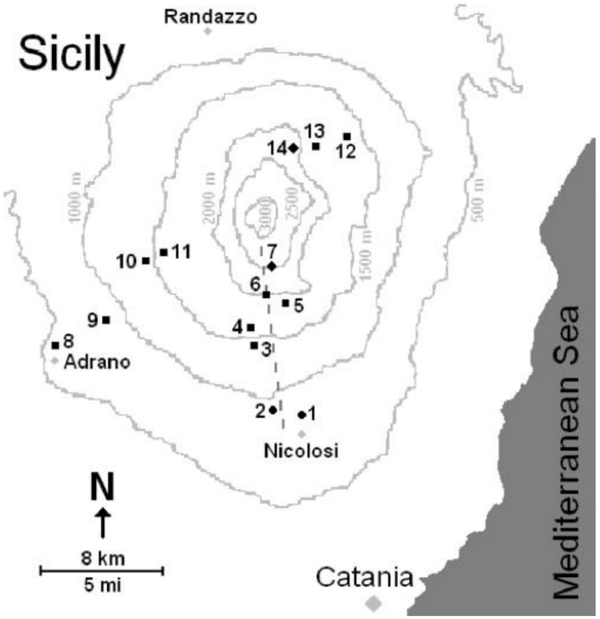


Fig. 1 Map of sample populations of *Senecio aethnensis*, *Senecio chrysanthemifolius* and their hybrids from Mount Etna, Sicily. Black markers and numbers indicate the locations and identities of different sample sites. The dark grey dashed line represents the southern transect line onto which nearby sample sites (1–7) were mapped for the hybrid cline analysis. The pale grey lines mark approximate 500 m altitude above sea level contours on Mt Etna and also indicate approximate ranges of the *Senecio* taxa: *S. chrysanthemifolius* occurs at 500–1000 m; the hybrid occurs at 1000–2000 m; and *S. aethnensis* occurs at 2000–3000 m. Black diamonds and circles indicate reference *S. aethnensis* and *S. chrysanthemifolius* sites, respectively, while black squares indicate all other sample sites. Grey diamonds represent towns and cities in the area.

Homoploidní hybridi *Helianthus*

Helianthus petiolaris

X

Helianthus annus

Helianthus deserticola

Ekologická selekce homoploidních hybridních druhů

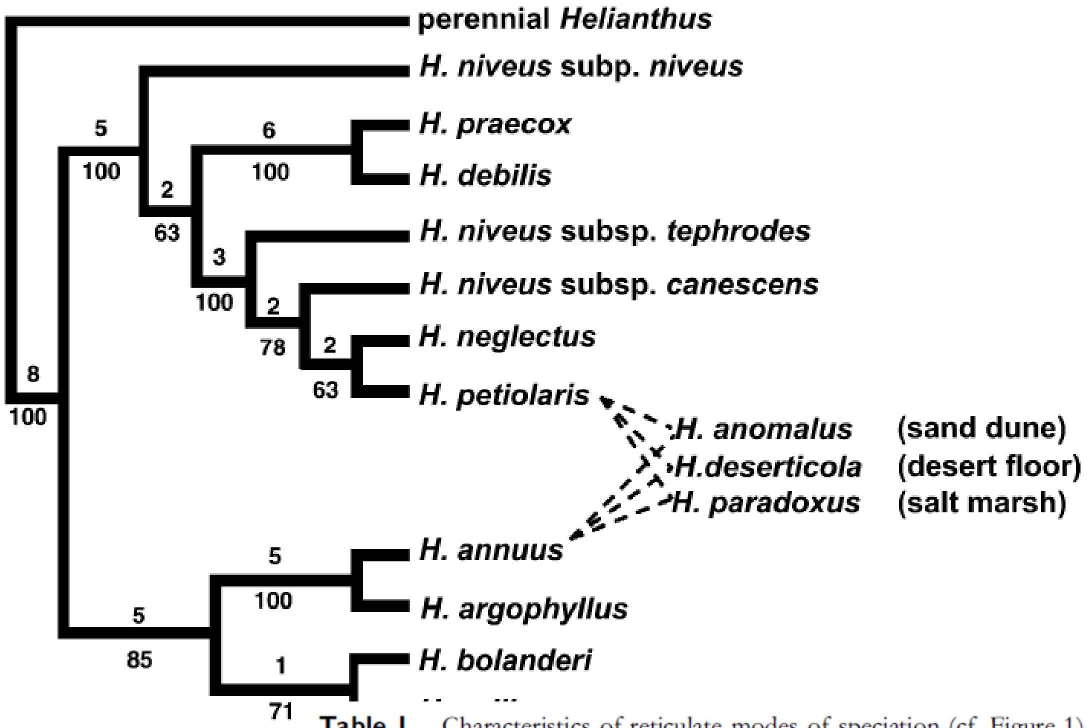
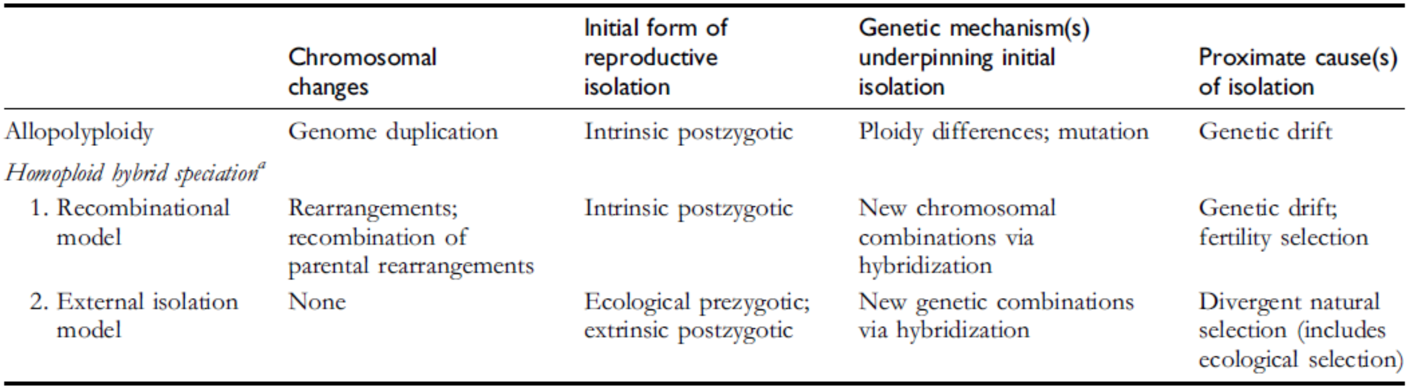


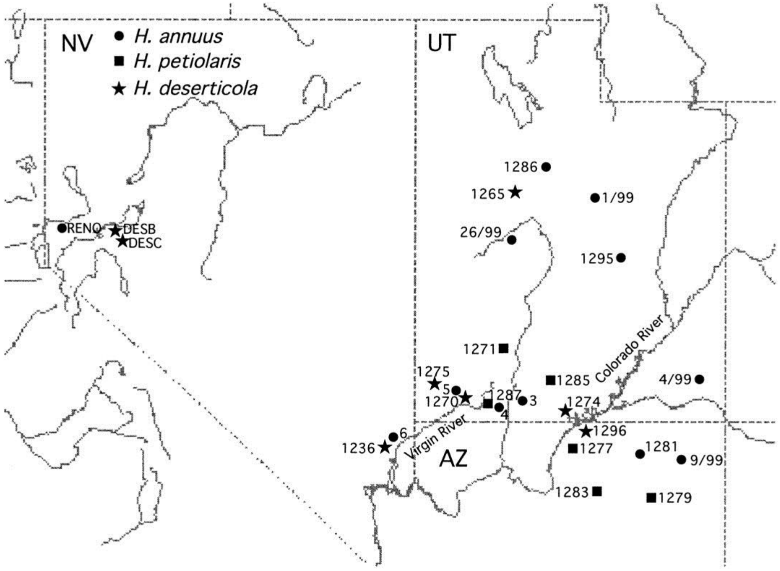
Table 1. Characteristics of reticulate modes of speciation (cf. Figure 1).

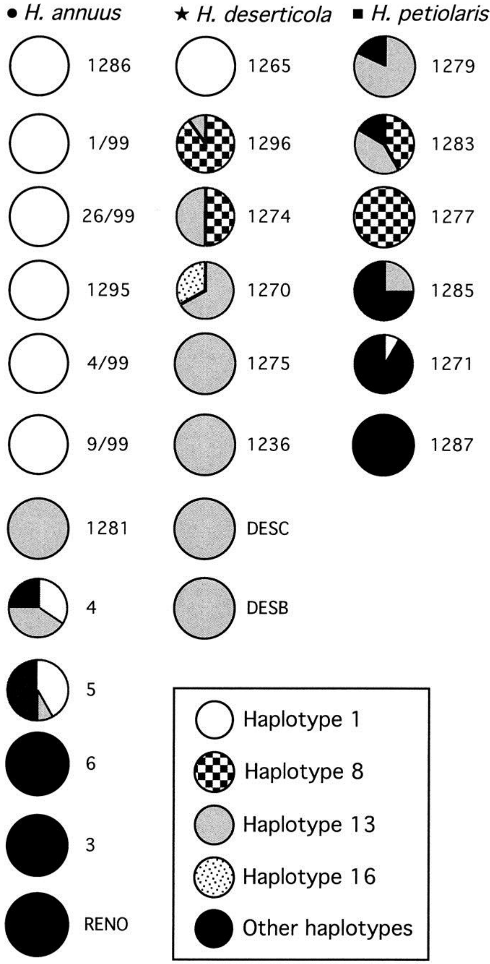


	Chromosomal changes	Initial form of reproductive isolation	Genetic mechanism(s) underpinning initial isolation	Proximate cause(s) of isolation
Allopolyploidy	Genome duplication	Intrinsic postzygotic	Ploidy differences; mutation	Genetic drift
Homoploid hybrid speciation[a]				
1. Recombinational model	Rearrangements; recombination of parental rearrangements	Intrinsic postzygotic	New chromosomal combinations via hybridization	Genetic drift; fertility selection
2. External isolation model	None	Ecological prezygotic; extrinsic postzygotic	New genetic combinations via hybridization	Divergent natural selection (includes ecological selection)

Origin(s) of the diploid hybrid species *Helianthus deserticola* (Asteraceae)

Gross et al. Am. J. Bot. December 2003 vol. 90 no. 12 1708-1719

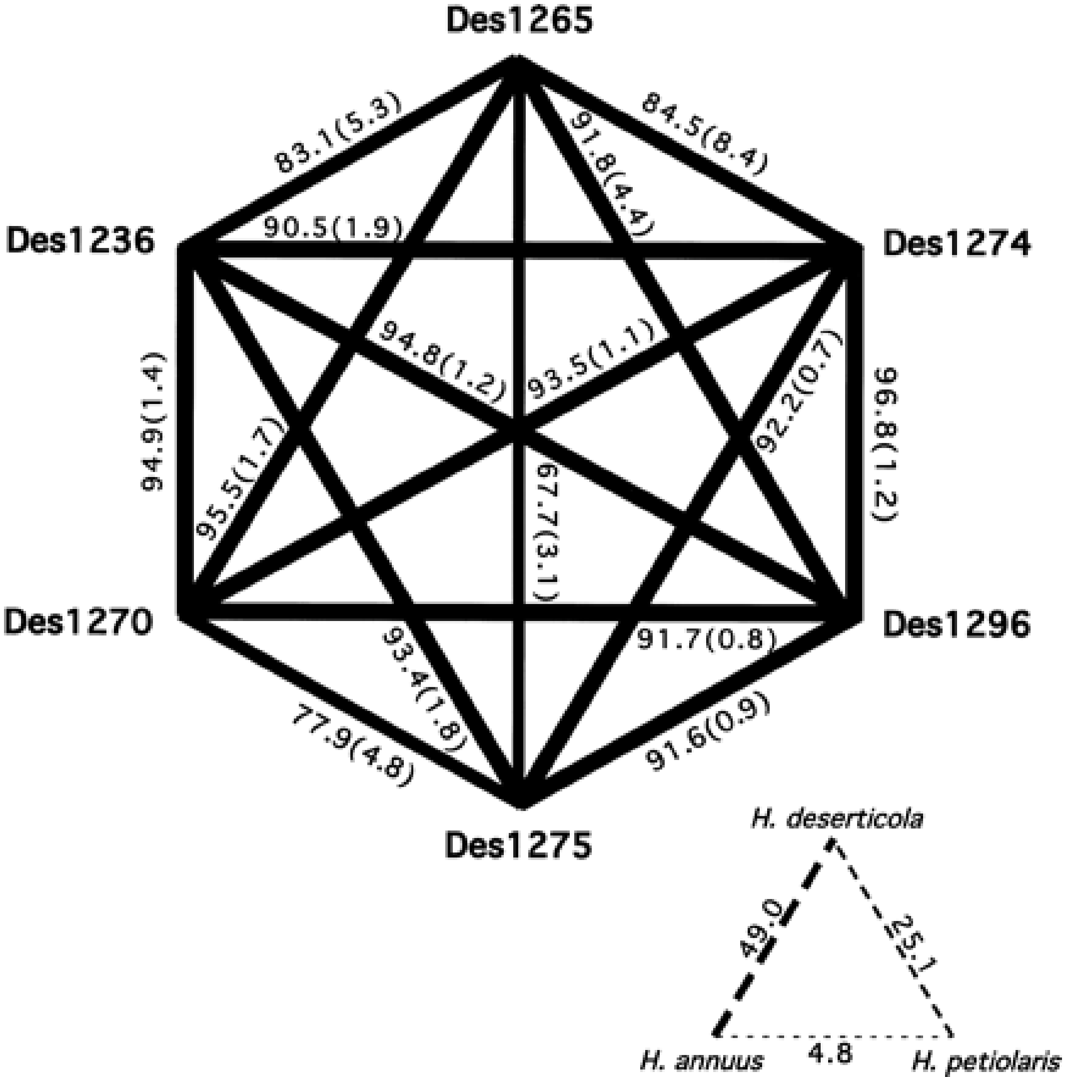




Range map showing locations of *Helianthus* populations from Utah, Arizona, and Nevada, USA, used in this study. Haplotype composition of each population is shown to the right of the map. For simplicity, only the four haplotypes found in *H. deserticola* are depicted, and the other 11 haplotypes are represented in black

Origin(s) of the diploid hybrid species *Helianthus deserticola* (Asteraceae)

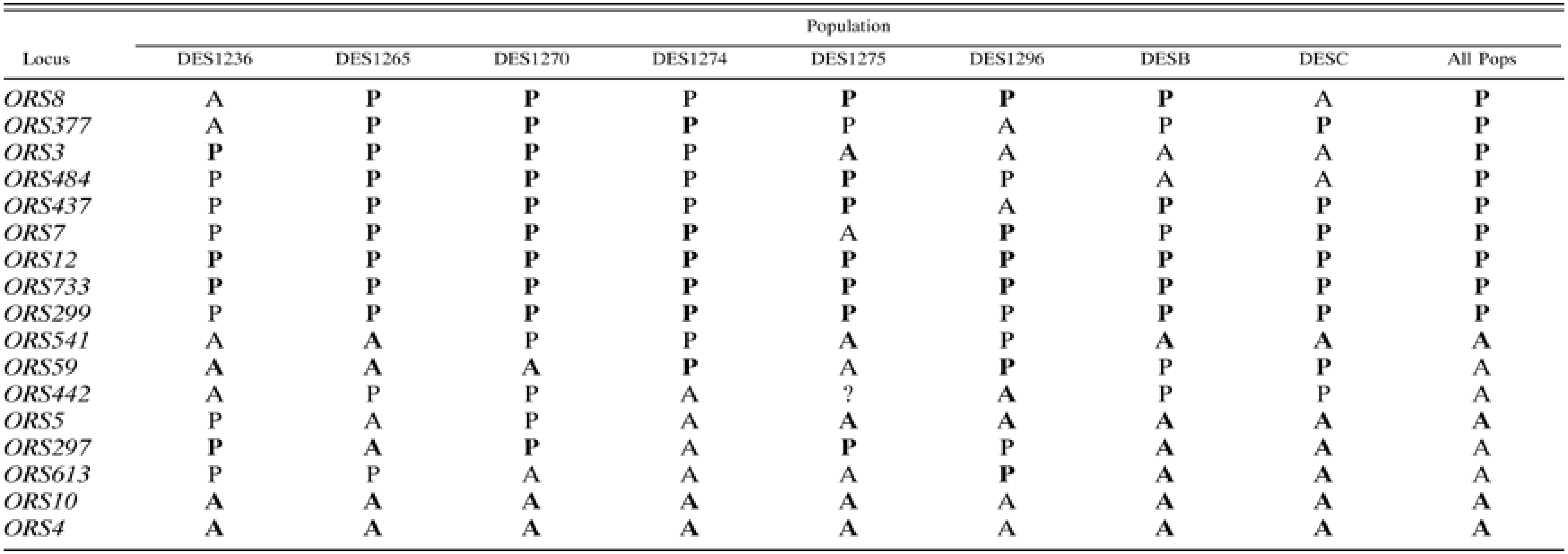
Gross et al. Am. J. Bot. December 2003 vol. 90 no. 12 1708-1719



Crossability relationships among populations of *Helianthus deserticola*

Origin(s) of the diploid hybrid species *Helianthus deserticola* (Asteraceae)

Gross et al. Am. J. Bot. December 2003 vol. 90 no. 12 1708-1719



	Population								
Locus	DES1236	DES1265	DES1270	DES1274	DES1275	DES1296	DESB	DESC	All Pops
ORS8	A	**P**	**P**	P	**P**	**P**	**P**	A	**P**
ORS377	A	**P**	**P**	**P**	P	A	P	**P**	**P**
ORS3	**P**	**P**	**P**	P	**A**	A	A	A	**P**
ORS484	P	**P**	**P**	P	**P**	P	A	A	**P**
ORS437	P	**P**	**P**	P	**P**	A	**P**	**P**	**P**
ORS7	P	**P**	**P**	**P**	A	**P**	P	**P**	**P**
ORS12	**P**	**P**	**P**	**P**	**P**	**P**	**P**	**P**	**P**
ORS733	**P**	**P**	**P**	**P**	**P**	**P**	**P**	**P**	**P**
ORS299	P	**P**	**P**	**P**	**P**	P	**P**	**P**	**P**
ORS541	A	**A**	P	P	**A**	P	**A**	**A**	**A**
ORS59	**A**	**A**	**A**	**P**	A	**P**	P	**P**	A
ORS442	A	P	P	A	?	**A**	P	P	A
ORS5	P	A	P	A	**A**	**A**	**A**	**A**	**A**
ORS297	**P**	**A**	**P**	A	**P**	P	**A**	**A**	A
ORS613	P	P	A	A	A	**P**	**A**	**A**	A
ORS10	**A**	**A**	**A**	**A**	**A**	A	**A**	**A**	**A**
ORS4	**A**	**A**	**A**	**A**	**A**	A	**A**	**A**	**A**

Parental origin of 17 loci, based on hybrid index scores;
A = *Helianthus annuus*, P = *H. petiolaris*.
The hybrid index scores ranged from 0 (*H. petiolaris*) to 1 (*H. annuus*), and each score was assigned an upper and lower support limit, representing two log-likelihood units

Origin(s) of the diploid hybrid species *Helianthus deserticola* (Asteraceae)

Gross et al. Am. J. Bot. December 2003 vol. 90 no. 12 1708-1719

Helianthus deserticola contains cpDNA haplotypes characteristic of both parental species, is polyphyletic with one parental species based on nine microsatellite loci, and has a high degree of interfertility among populations.

The data are consistent with either a single origin followed by introgression with the parental species or multiple origins.

Analysis of microsatellite variation places the origin of *H. deserticola* between 170 000 and 63 000 years before present, making it unlikely that anthropogenic disturbances influenced its origin.

doi:10.1111/j.1420-9101.2010.01950.x

Are hybrid species more fit than ancestral parent species in the current hybrid species habitats?

L. A. DONOVAN*, D. R. ROSENTHAL*[1], M. SANCHEZ-VELENOSI*[2], L. H. RIESEBERG† &
F. LUDWIG*[3]

J. EVOL. BIOL. **23** (2010) 805–816

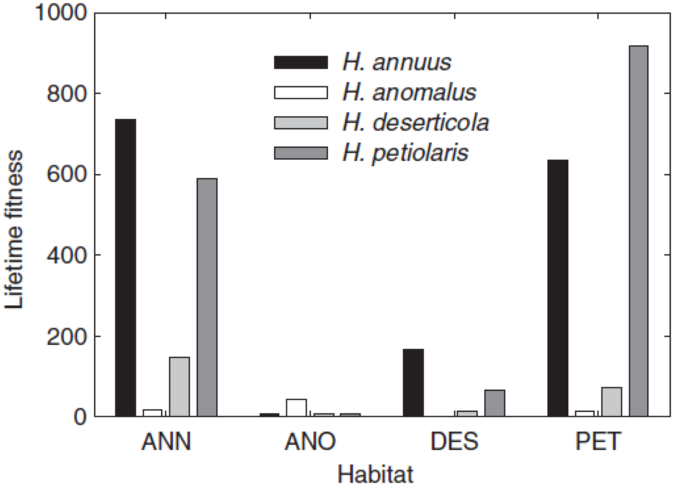


Fig. 3 Lifetime fitness of two hybrid species (*Helianthus anomalus*, *H. deserticola*) and their ancestral parent species (*H. annuus*, *H. petiolaris*) in each of the four species habitats (ANO, DES, ANN, PET, respectively).

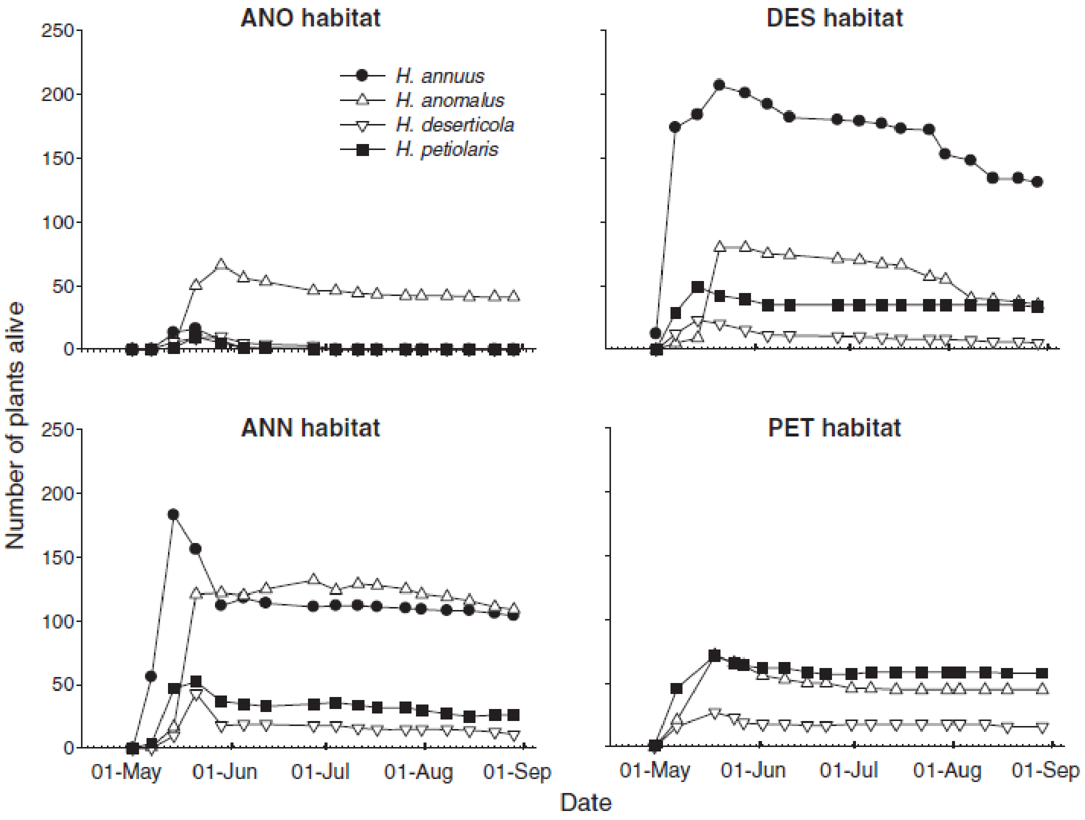


Fig. 1 Number of live plants in seed plots. Seeds of two hybrid species (*Helianthus anomalus*, *H. deserticola*) and their ancestral parent species (*H. annuus*, *H. petiolaris*) were planted into each of the four species habitats (ANO, DES, ANN, PET, respectively).

Heredity

Heredity (2012) 108, 159–166

www.nature.com/hdy

REVIEW

Hybrid fitness, adaptation and evolutionary diversification: lessons learned from Louisiana Irises

ML Arnold, ES Ballerini and AN Brothers

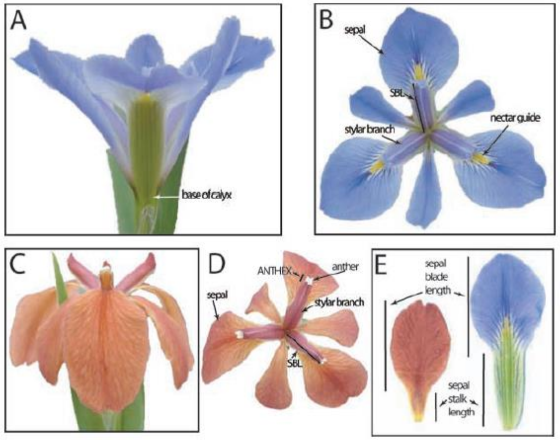
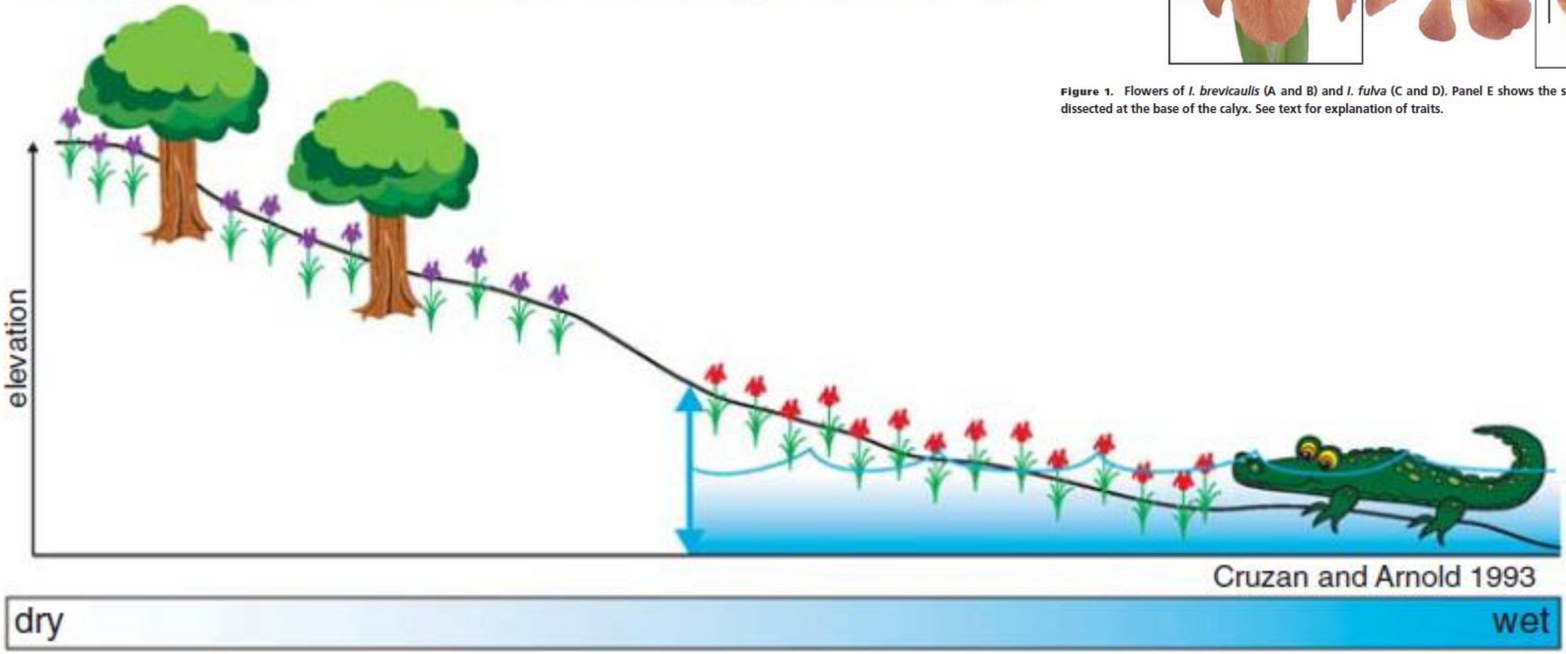


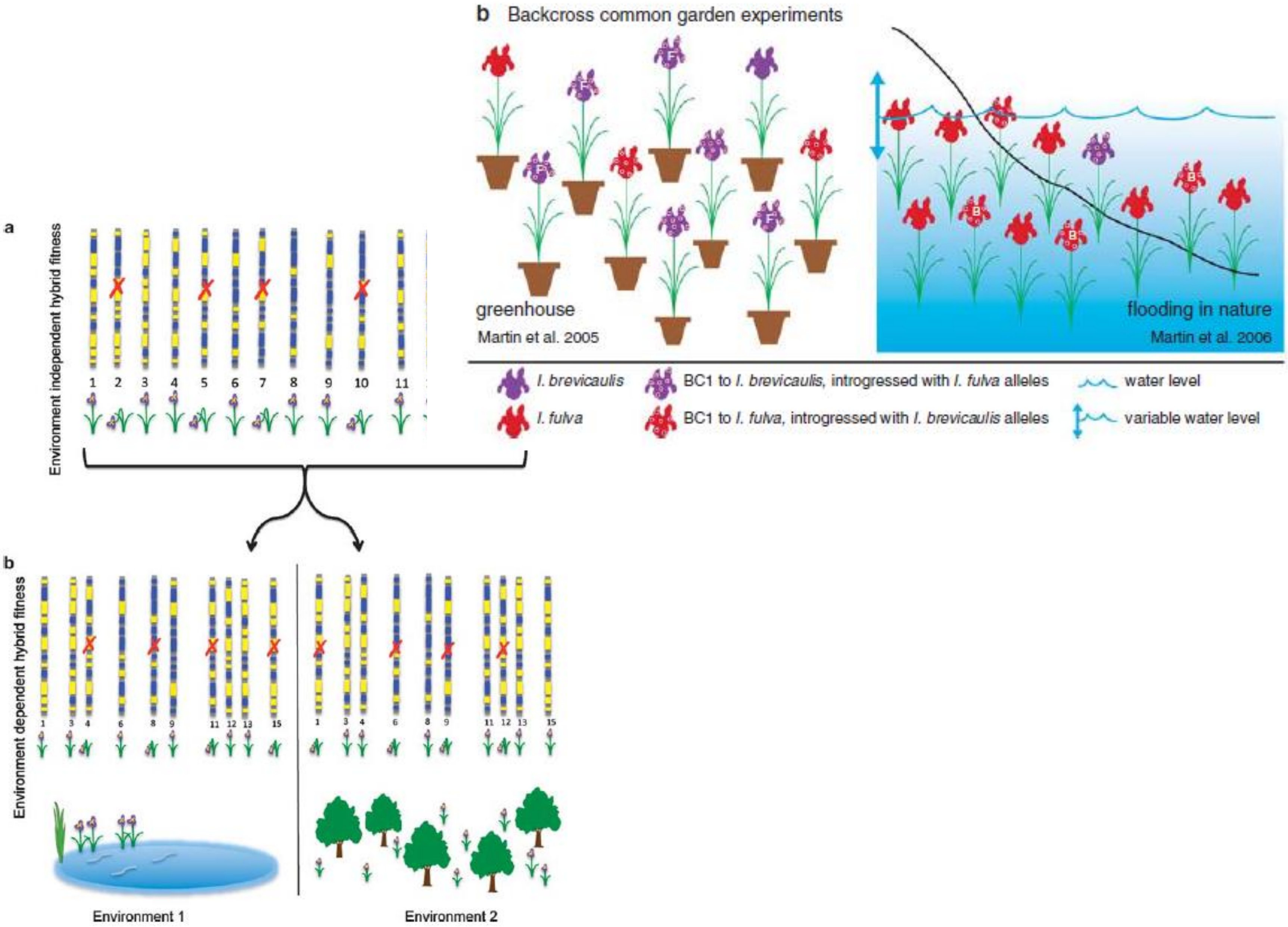
Figure 1. Flowers of *I. brevicaulis* (A and B) and *I. fulva* (C and D). Panel E shows the sepals of *I. fulva* (left) and *I. brevicaulis* (right) dissected at the base of the calyx. See text for explanation of traits.

a Distribution of *I. brevicaulis* and *I. fulva* in typical natural condi



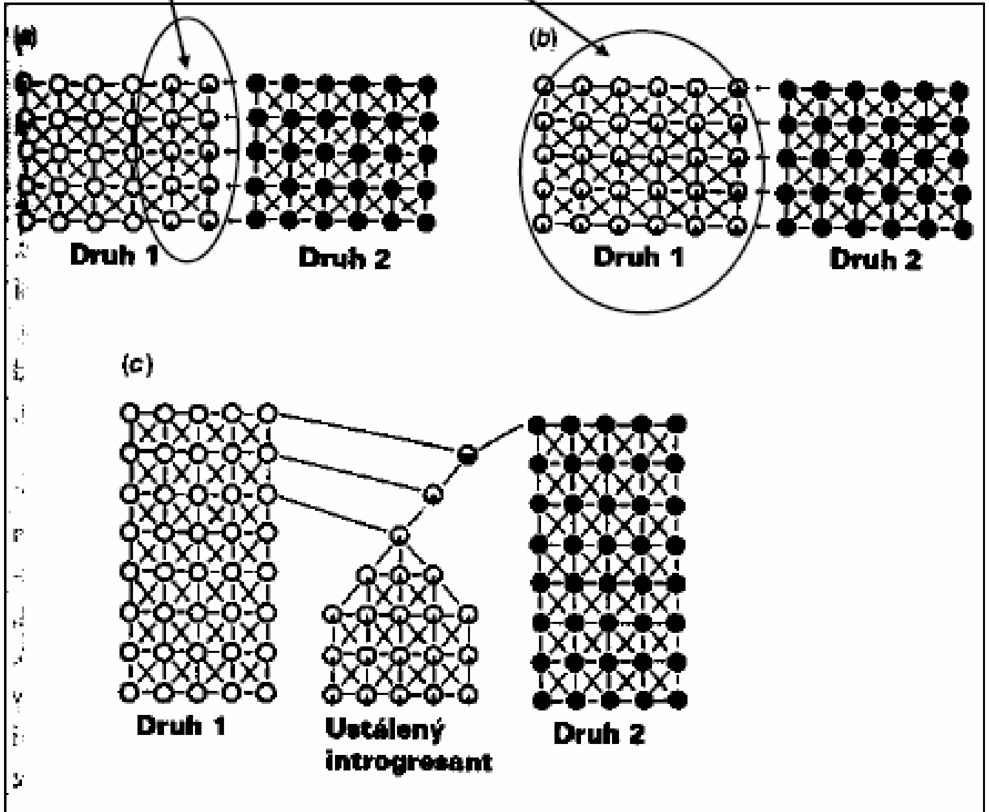
Cruzan and Arnold 1993

Variabilní zdatnost (fitness) hybridů - závislost na genotypu a prostředí



Introgrese

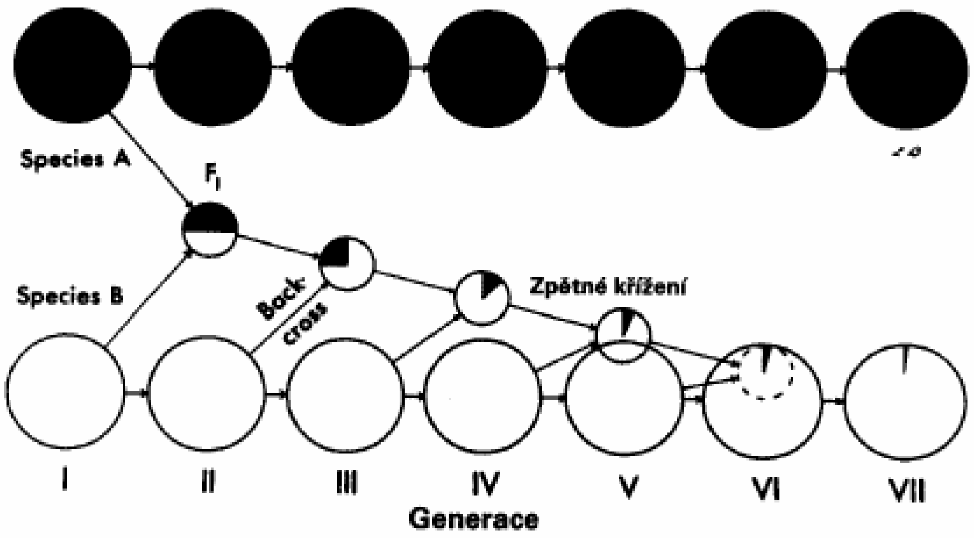
- Lokalizovaná
- Rozptýlená
- Ustálená



Obr. 11. 18. Lokalizovaná introgrese, rozptýlená introgrese a původ ustálené populace vzniklé introgresí. Otevřené kroužky = populace druhu 1; uzavřené kroužky = populace druhu 2; černé čáry = křížení mezi populacemi; šipky = směr introgrese. (*a*) Jednosměrná lokalizovaná introgrese z druhu 2 do druhu 1. (*b*) Jednosměrná rozptýlená introgrese z druhu 2 do druhu 1. (*c*) Původ ustálené introgresivní populace. (Rieseberg & Wendel, 1993)

Introgrese

- Geny jednoho druhu postupně vneseny do druhého sérií spontánních a následných zpětných křížení
- Opak Wallaceova efektu, zvýhodnění hybridů při existenci přechodných biotopů



Obr. 11.11. Graf znázorňující introgresi mezi dvěma druhy. Zpětné křížení F$_1$ hybridů s druhem B vede v konečném důsledku k přijetí některých genů druhu A druhem B. Přetištěno se svolením nakladatelství John Wiley & Sons, Inc., Benson (1962), *Plant taxonomy.* ©1962.

Asymmetric Introgressive Hybridization Among Louisiana Iris Species

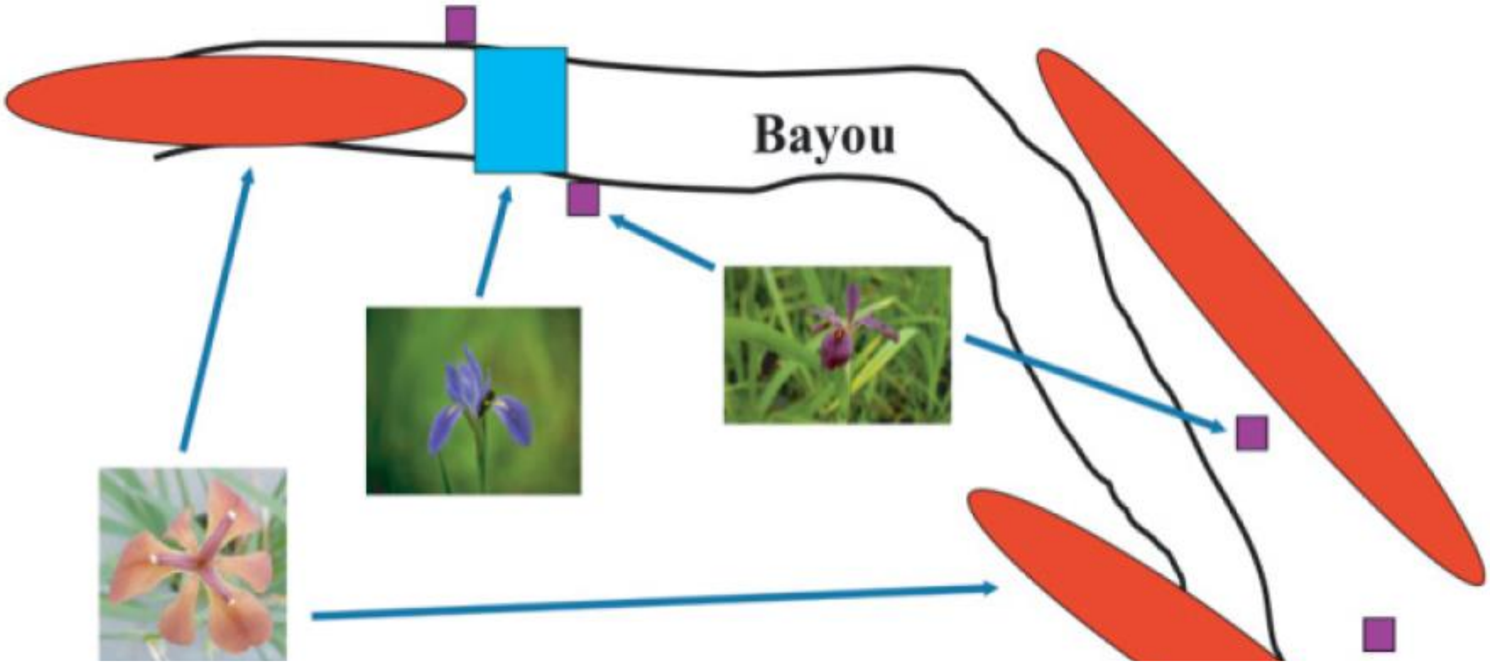
Michael L. Arnold [1,*], Shunxue Tang [2], Steven J. Knapp [3] and Noland H. Martin [4]

Genes **2010**, *1*, 9-22; doi:10.3390/genes1010009

Table 1. The frequency of homozygous *I. brevicaulis* (“bb”), heterozygous (“bf”) and homozygous *I. fulva* (“ff”) genotypes among adult plants and seeds from an *I. fulva* x *I. brevicaulis* natural hybrid zone [20].

	Adult Plant Genotypes			Seed Genotypes		
	bb	*bf*	*ff*	*bb*	*bf*	*ff*
Iris brevicaulis-like	17	20	0	29	89	9
Iris fulva-like	0	0	37	0	2	42

Figure 4. Schematic illustration of the distribution of 1) naturally occuring *I. fulva* plants (red ovals), 2) introduced *I. hexagona* (blue rectangle) and 3) *I. fulva* x *I. hexagona* F_1 plants (purple squares) [27,28].



The experimental population lies within a region typified by numerous natural hybrid zones between *I. fulva, I. brevicaulis* and *I. hexagona*, e.g., [16,25,26]. Originally, this population consisted only of naturally occuring *I. fulva* individuals. In 1989, we introduced 200 *I. hexagona* plants in a centralized block (Figure 4). Over three consecutive years, we collected and genotyped >5000 seeds from *I. fulva* and *I. hexagona* fruits formed by pollen transfer by natural pollinators. F_1 hybrid seed formation was very infrequent in the fruits of both species. However, there was a significant bias in the direction of hybrid formation (Figure 5) with F_1 seeds being formed at 50x the frequency in *I. hexagona* fruits (*i.e.,* 0.74%) relative to *I. fulva* fruits (*i.e.,* 0.03%; [27,28]).

Figure 5 Percentage of F_1 (0.03% and 0.74% in *I. fulva* and *I. hexagona* fruits, respectively) and first generation backcross seeds (B_f and B_h) formed on plants in an experimental population by natural pollinations [27,28]. The B_f and B_h hybrid seeds reflect the first generation of introgression into *I. fulva* and *I. hexagona*, respectively.

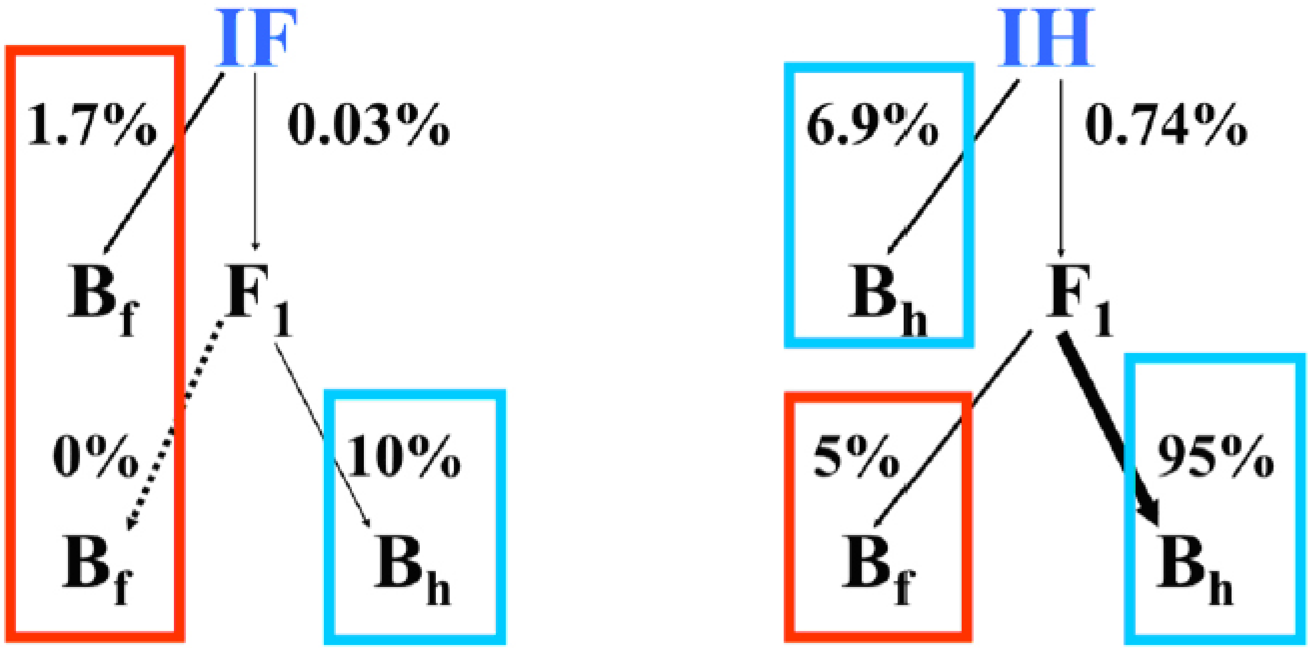
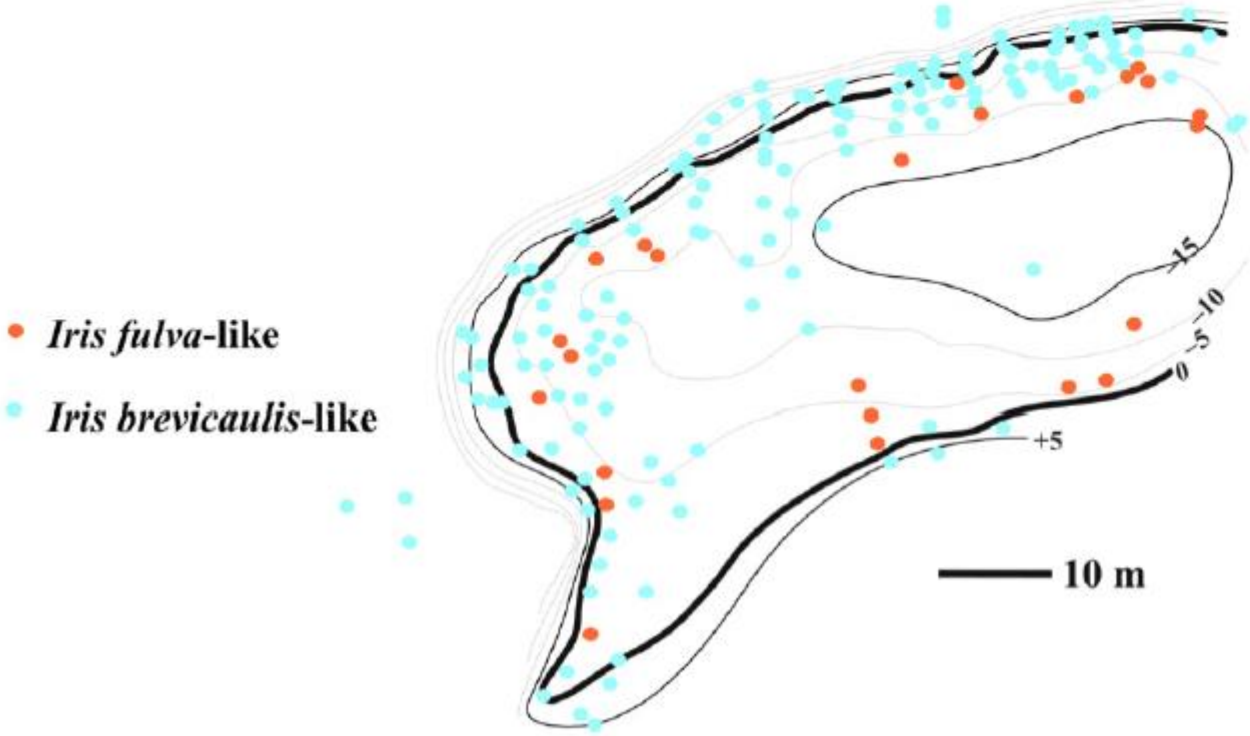


Figure 7 Spatial distribution of Louisiana Iris genotypes in a natural population containing "*I. brevicaulis*-like" and "*I. fulva*-like" genotypes. Each circle reflects a single plant. The numbers indicate elevations, with the "0" line indicating the water level of the pond. Negative values reflect flooded areas, and positive values reflect areas above the waterline [19].



Annals of Botany **111**: 563–575, 2013
doi:10.1093/aob/mct013, available online at www.aob.oxfordjournals.org

Breeding systems, hybridization and continuing evolution in Avon Gorge *Sorbus*

Shanna Ludwig[1], Ashley Robertson[1], Timothy C. G. Rich[2], Milena Djordjević[3], Radosav Cerović[3], Libby Houston[1], Stephen A. Harris[4] and Simon J. Hiscock[1,*]

[1]*School of Biological Sciences, University of Bristol, Bristol, UK,* [2]*Department of Biodiversity & Systematic Biology, National Museum of Wales, Cardiff, UK,* [3]*Fruit Research Institute, Čačak, Serbia and* [4]*Department of Plant Sciences, University of Oxford, Oxford, UK*

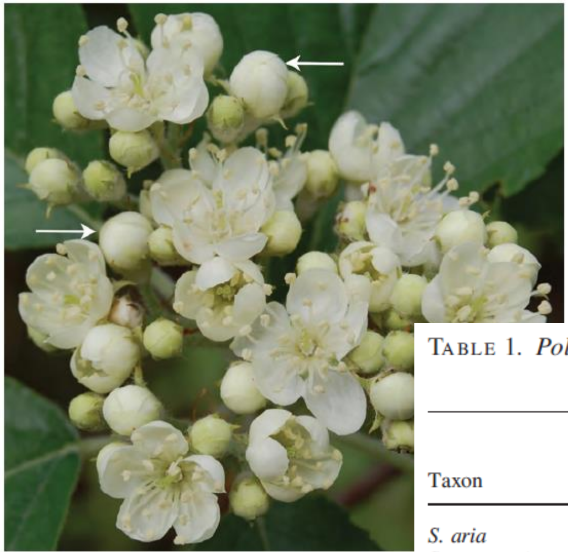


FIG. 1. Flowers of *S. aria* at various stages of ope

TABLE 1. *Pollination crosses, ploidy levels and pollen viability for each taxon; the total number of trees receiving treatment is shown in parentheses*

			Pollen treatment received				
Taxon	Ploidy*	Average pollen viability (%)[‡]	A	B	C	D	E
S. aria	$2x$[†]	84·75	(10)	(7)	*S. aucuparia* (1); *S. eminens* (5); *S. porrigentiformis* (6)		
S. aucuparia	$2x$[†]	93·28	(1)				
S. torminalis	$2x$[†]	81·50	(4)	(3)	*S. aria* (1); *S. eminens* (5); *S. porrigentiformis* (2)		
S. × avonensis	$3x$	N/A					
S. bristoliensis	$3x$[†]	38·20	(6)	(4)	*S. aria* (6); *S. porrigentiformis* (1)	(3)	(3)
S. leighensis	$3x$	23·00[§]	(7)	(5)	*S. aria* (7); *S. porrigentiformis* (6)	(7)	(1)
S. whiteana	$3x$[†]	63·00	(5)	(4)	*S. aria* (5); *S. porrigentiformis* (5)	(5)	(1)
S. wilmottiana	$3x$[†]	46·50	(7)	(6)	*S. aria* (5)	(4)	(3)
S. × robertsonii	$3x$	N/A					
S. eminens	$4x$[†]	80·71	(8)	(7)	*S. aria* (6); *S. torminalis* (1)	(3)	(2)
S. × houstoniae	$4x$	N/A					
S. porrigentiformis	$4x$[†]	57·25	(7)	(8)	*S. aria* (6)	(1)	

Key to pollen treatments: (A) pollen from the same tree; (B) pollen from a conspecific individual; (C) pollen from a different taxon (pollen parents shown); (D) emasculation with no pollen; (E) no pollen/bagged and left.

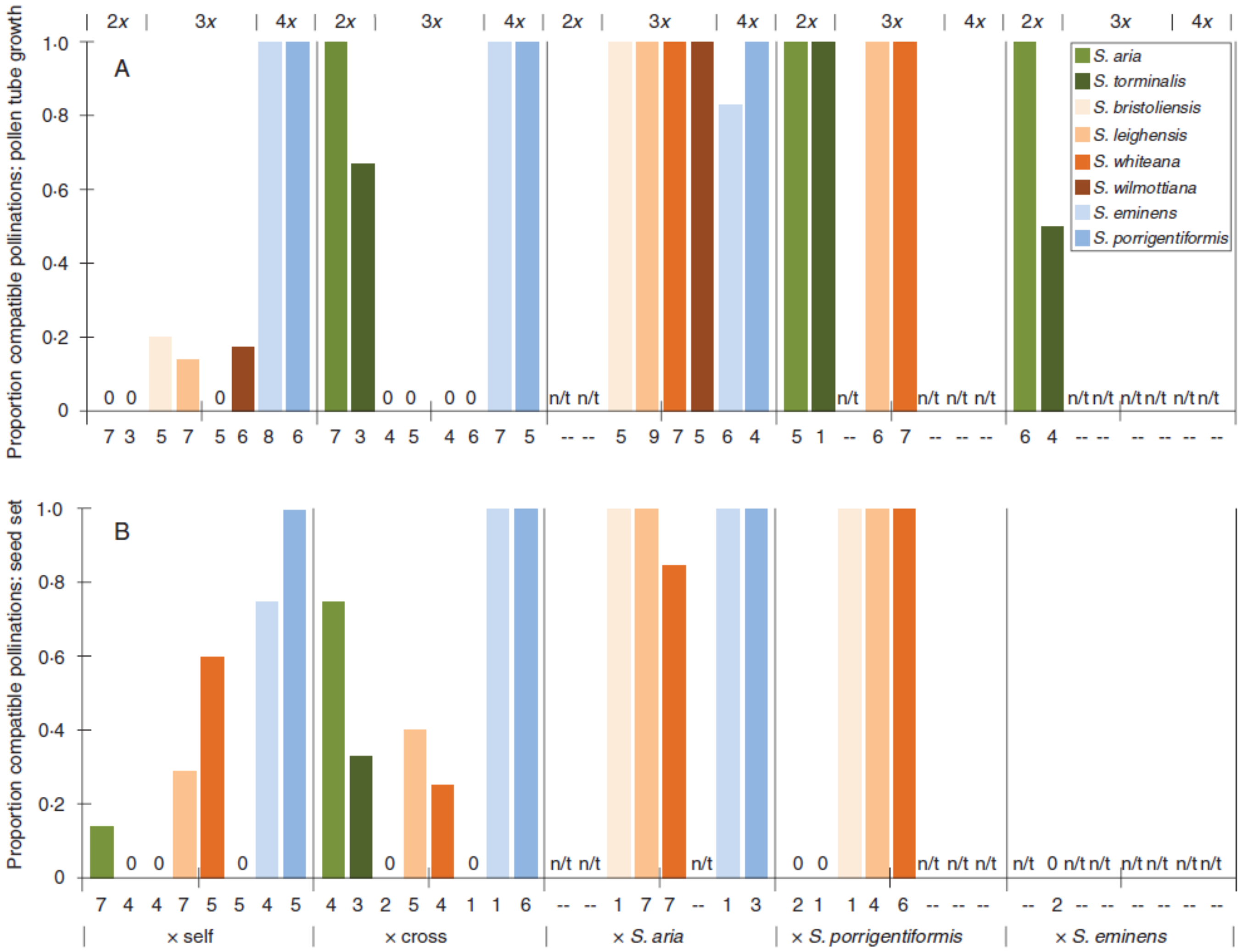


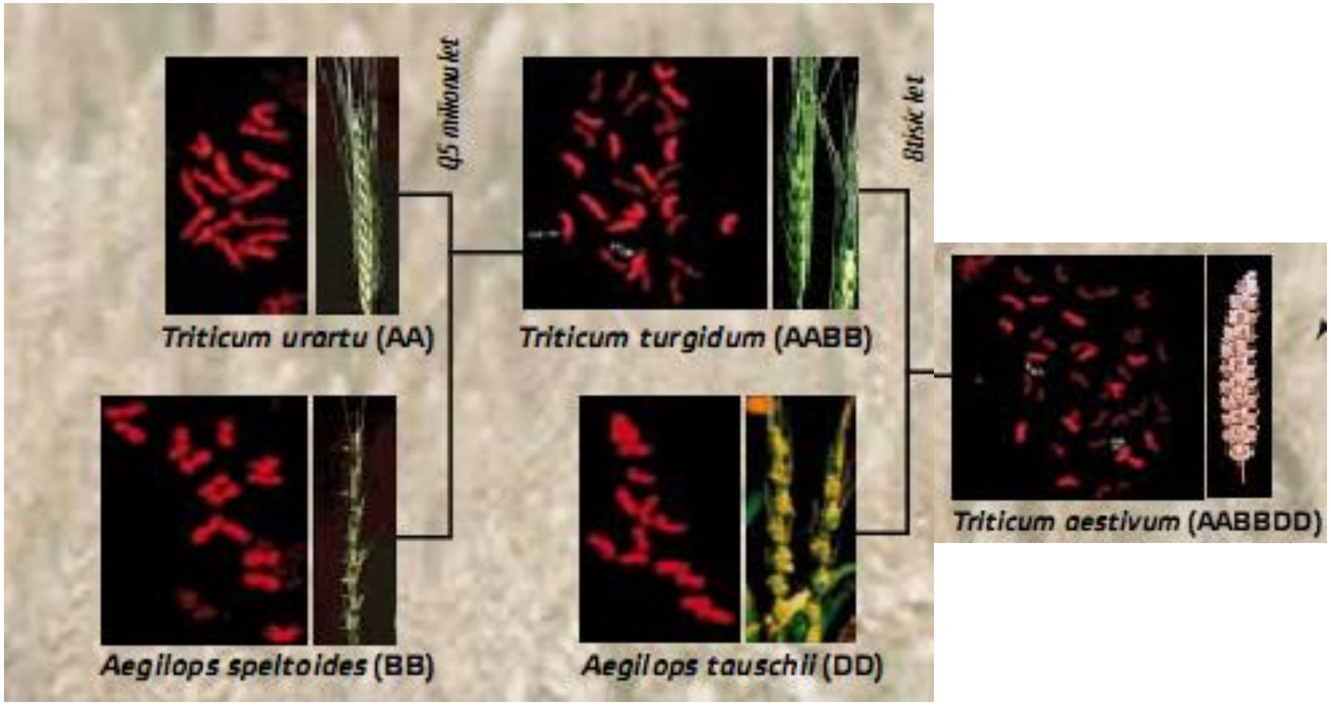
FIG. 3. Proportion of compatible pollinations based on pollen tube growth (A) and seed set (B). The horizontal axis gives the type of pollination combination

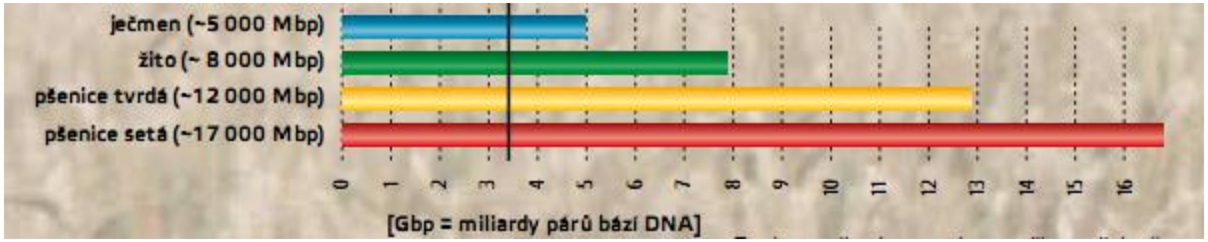
• *Key Results* Diploid *Sorbus* are outcrossing and self-incompatible (SI). Triploid taxa are pseudogamous apomicts and genetically invariable, but because they also display self-incompatibility, apomictic seed set requires pollen from other *Sorbus* taxa – a phenomenon which offers direct opportunities for hybridization. In contrast tetraploid taxa are pseudogamous but self-compatible, so do not have the same obligate requirement for inter-taxon pollination.

Hybridní původ
některých domestikovaných rostlin

JAROSLAV DOLEŽEL

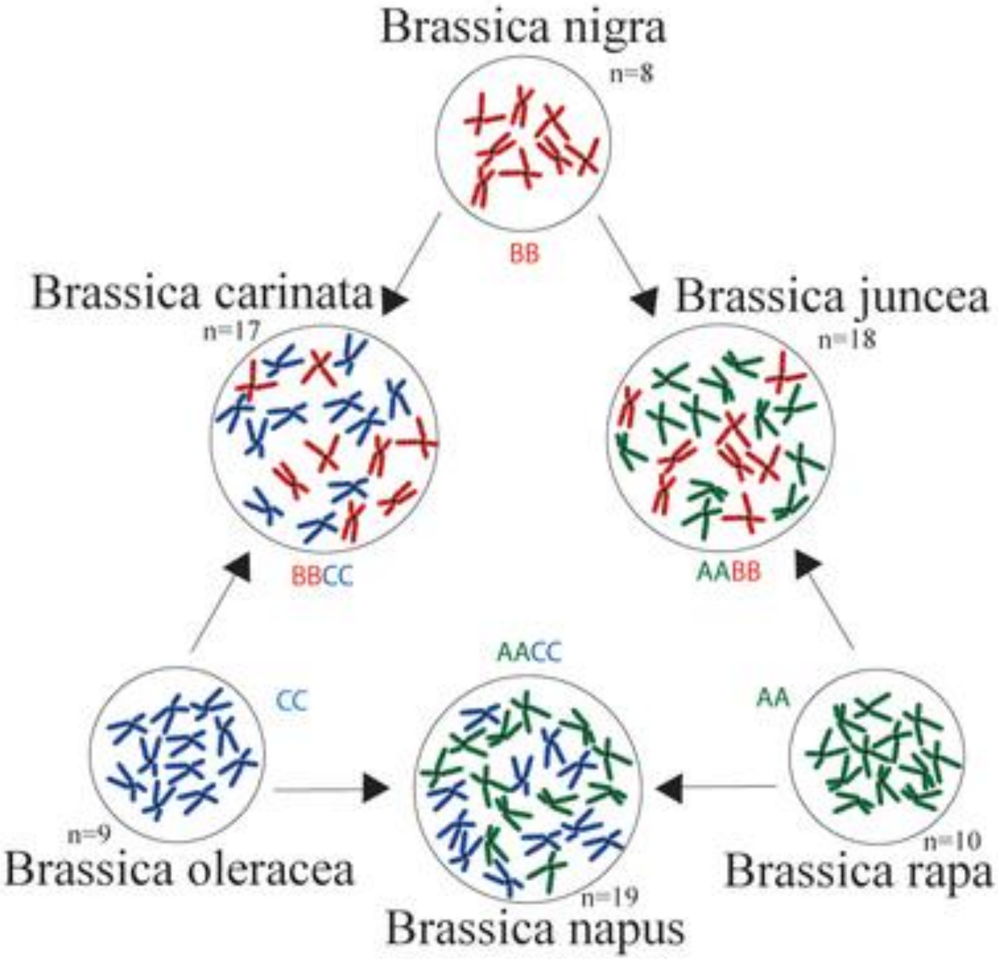
Tráva s trojím věnem





Vesmír 9/2009

Mezidruhová / mezirodová hybridizace
příklad -rod *Brassica*



Role hybridizace v evoluci

Hybridní rostliny mají mozaiku znaků typických pro jednoho nebo druhého rodiče a navíc vykazují nové (transgrese) spíše než přechodné znaky

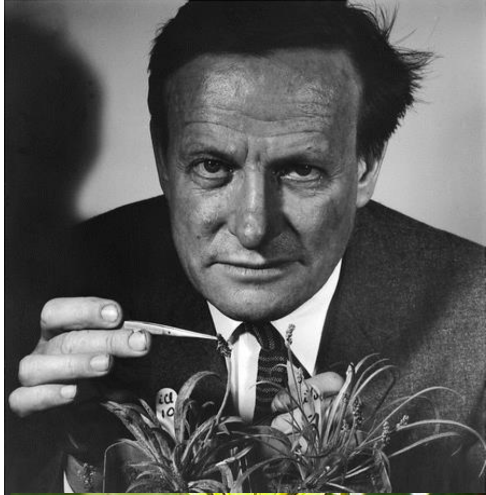
Hybridní jedinci jsou často fertilní a naopak vykazují větší zdatnost než rodiče

Průměrně se odhaduje, že asi 11% rostlinných druhů (tj. cca 30 tisíc) je hybridního původu, z toho 16-34% čeledí a 6-16% rodů

Kříženci zkreslují fylogenetické analýzy (morfologické i molekulární)

G.L. Stebbins

(1906-2000)



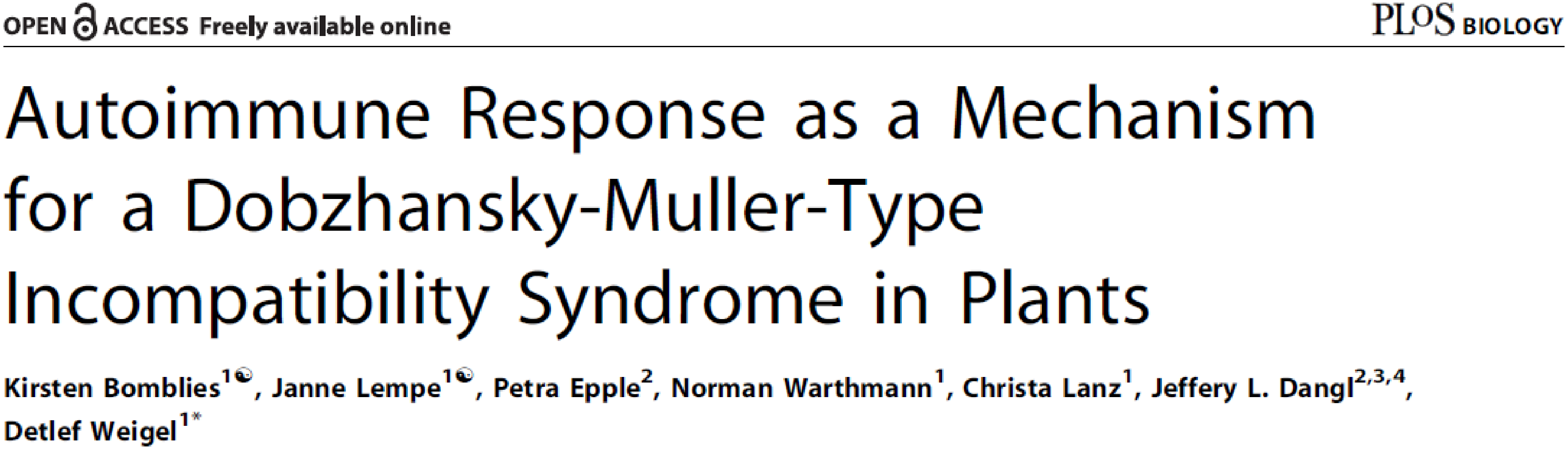
V roce 1940, získal fertilní hybridy pomoci uměle navozené polyploidie (aplikace kolchicinu) – vznik nových druhů (např. tráva *Ehrharta erecta*).

The American Species of Crepis: their interrelationships and distribution as affected by polyploidy and apomixis (1938)

Variation and Evolution in Plants (1950) - byl první kdo zavedl evoluční pohled do botaniky

Processes of Organic Evolution (1966), The Basis of Progressive Evolution (1969), and Chromosomal Evolution in Higher Plants (1971), *Flowering Plants: Evolution Above the Species Level* (1974) and *Darwin to DNA, Molecules to Humanity* (1982), co-author of the textbook *Evolution* (1977) with Theodosius Dobzhansky, Francisco Ayala, and James Valentine.

Hybridizace v rámci druhu
být vždy úspěšná



OPEN ACCESS Freely available online

PLoS BIOLOGY

Autoimmune Response as a Mechanism for a Dobzhansky-Muller-Type Incompatibility Syndrome in Plants

Kirsten Bomblies[1☯], Janne Lempe[1☯], Petra Epple[2], Norman Warthmann[1], Christa Lanz[1], Jeffery L. Dangl[2,3,4], Detlef Weigel[1*]

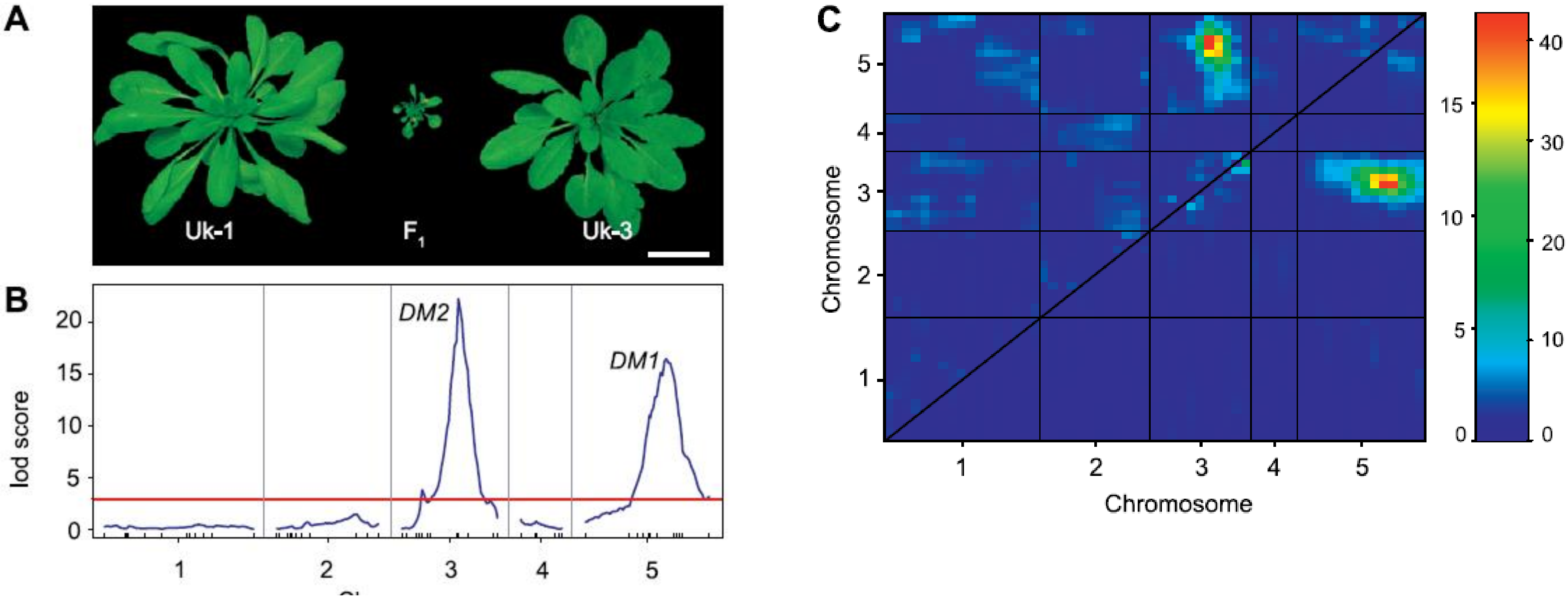
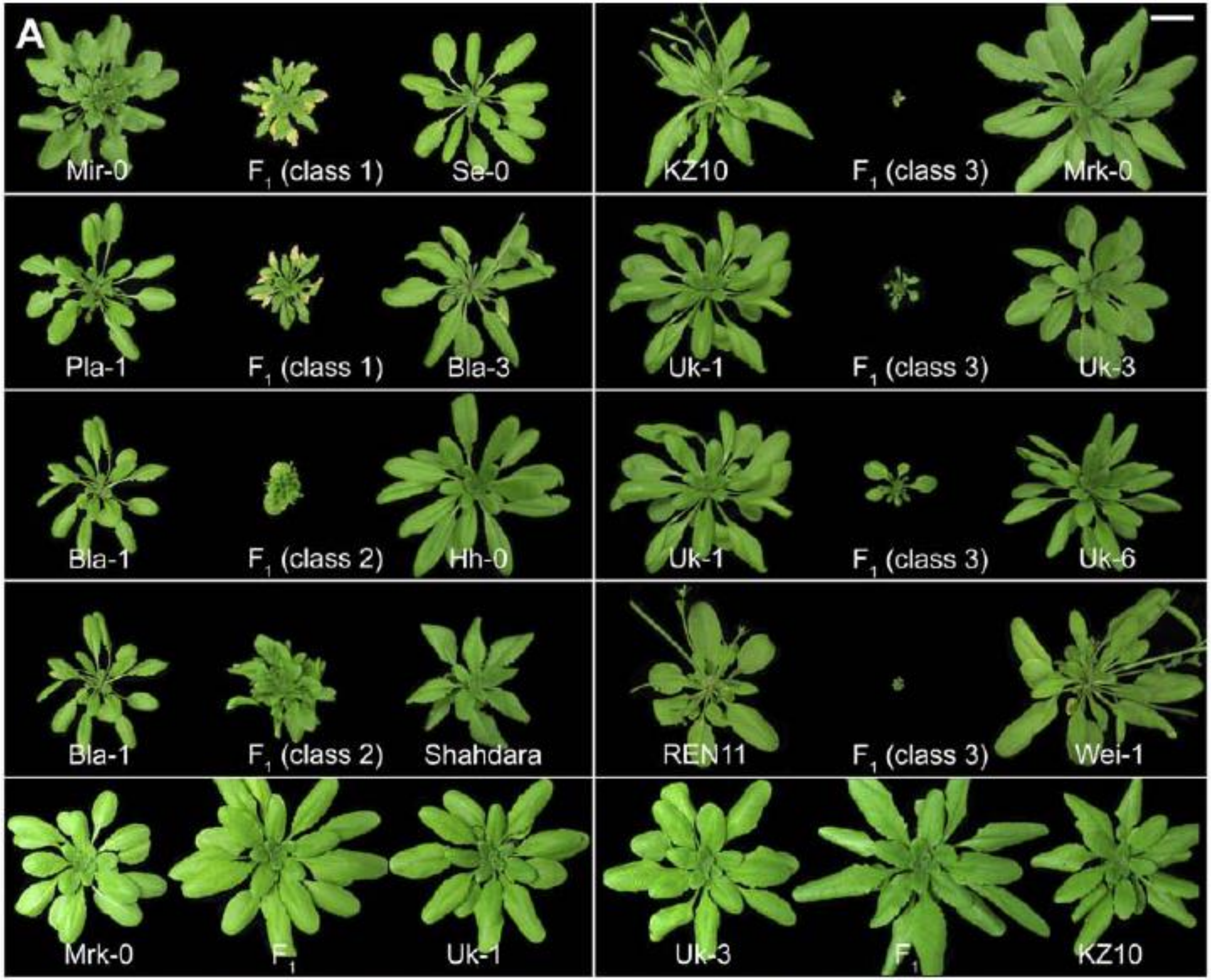


Table 1. F_2 Segregation Ratios

Cross	Phenotypic Class	Temperature	n	Phenotype				Model[c]	χ^2
				Normal	F_1-Like	Enhanced[a]	Other[b]		
Uk-1/Uk-3	3	16°C	149	64	36	49	—	I	0.91
		23°C	69	46	17	6	—	II	0.70
KZ10/Mrk-0	3	16°C	598	278	214	106	—	III	0.60
		23°C	589	463	126	0	—	IV	0.10
Bla-1/Hh-0	2	16°C	161	37	47	27	50	V	0.55
		23°C	106	87	14	5	—	IV	0.80
Mir-0/Se-0	1	16°C	327	153	174	0	—	VI	0.27


A
Mir-0
F1 (class 1)
Se-0
KZ10
F1 (class 3)
Mrk-0
Pla-1
F1 (class 1)
Bla-3
Uk-1
F1 (class 3)
Uk-3
Bla-1
F1 (class 2)
Hh-0
Uk-1
F1 (class 3)
Uk-6
Bla-1
F1 (class 2)
Shahdara
REN11
F1 (class 3)
Wei-1
Mrk-0
F1
Uk-1
Uk-3
F1
KZ10

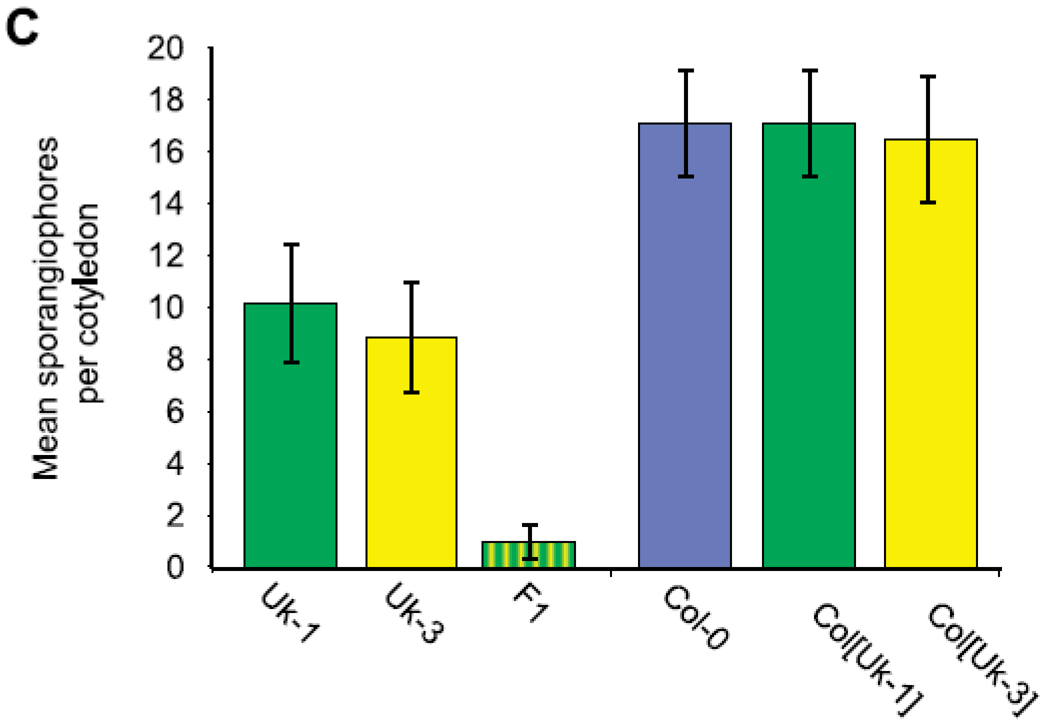


Figure 5. Susceptibility of Hybrids and Parental Accessions to *H. parasitica* Infection

Oenothera (pupalka)

Homozygotní druhy

Hybridi

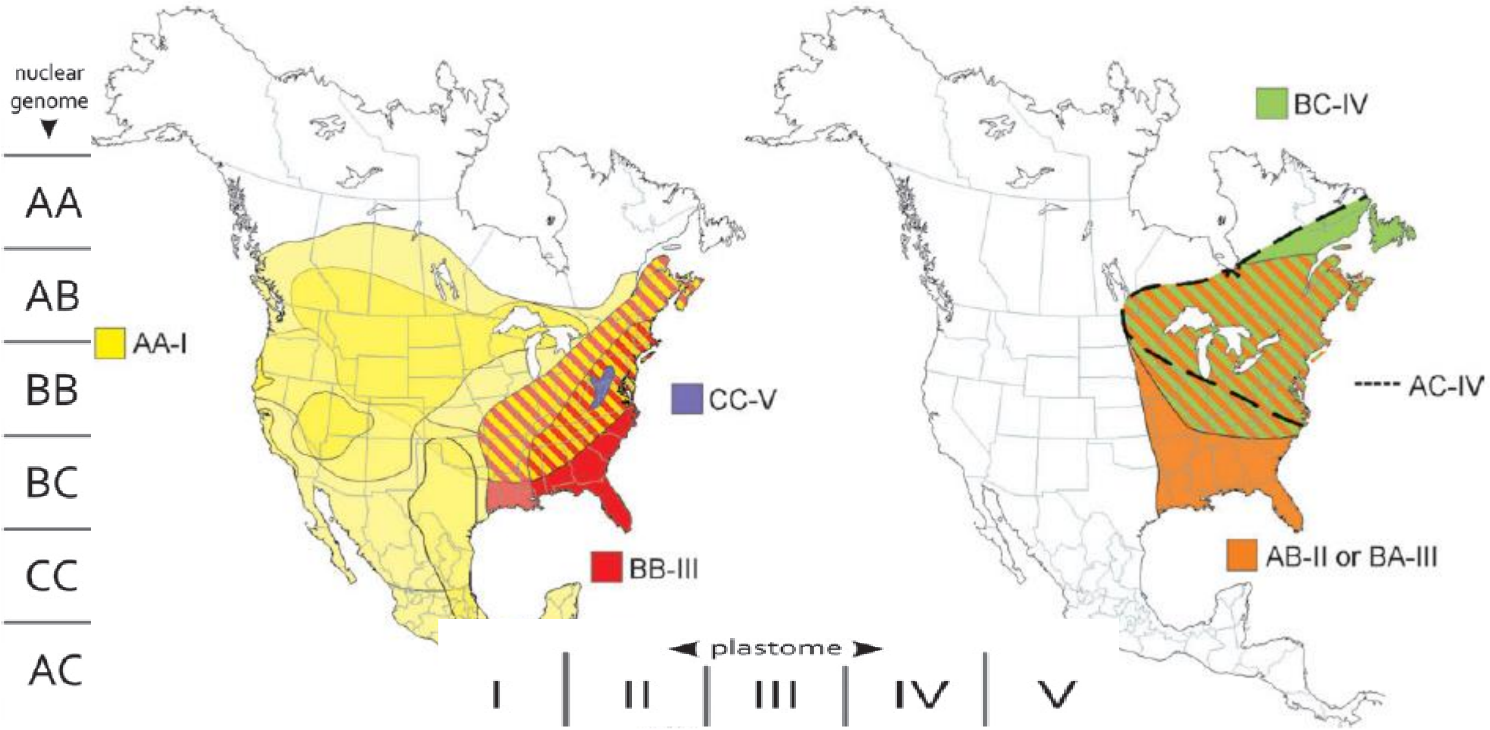
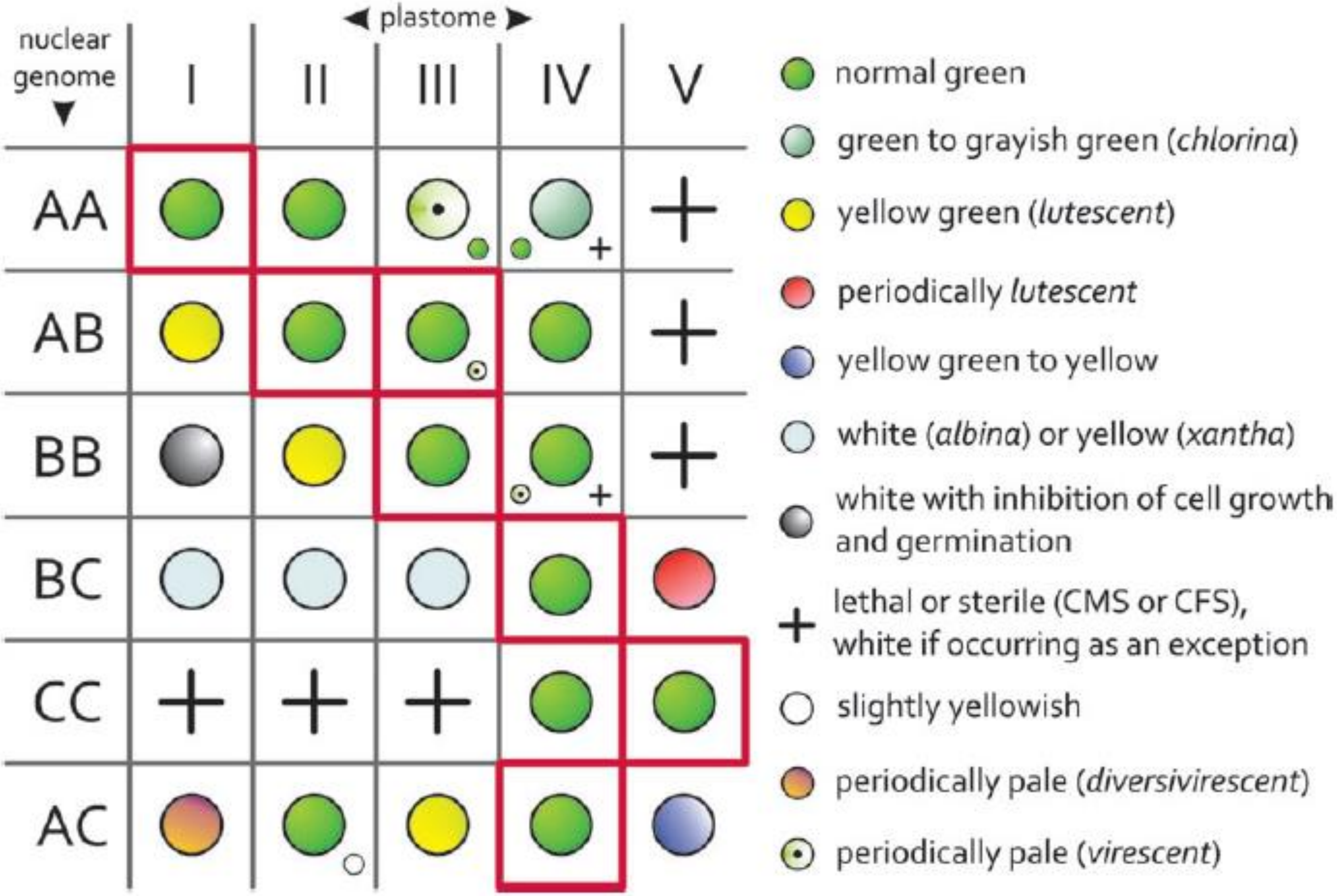


FIG. 1.—Distribution of the 11 North American species of subsection *Oenothera* of the genus *Oenothera*. The map summarizes data presented in Dietrich et al. (1997) and includes information about the 6 basic nuclear genotypes containing the 3 haploid genomes, A, B, and C, and their associated plastome types (I–V) of that subsection. Yellow and red gradations designate the distribution of distinct AA-I and BB-III genotypes. The left map shows the areas populated by homozygous species, the right one that of their hybrids. Note that all genotypes overlap geographically.

V případě hybridů je také důležitá kompatibility jaderného a cytoplasmatického genomu



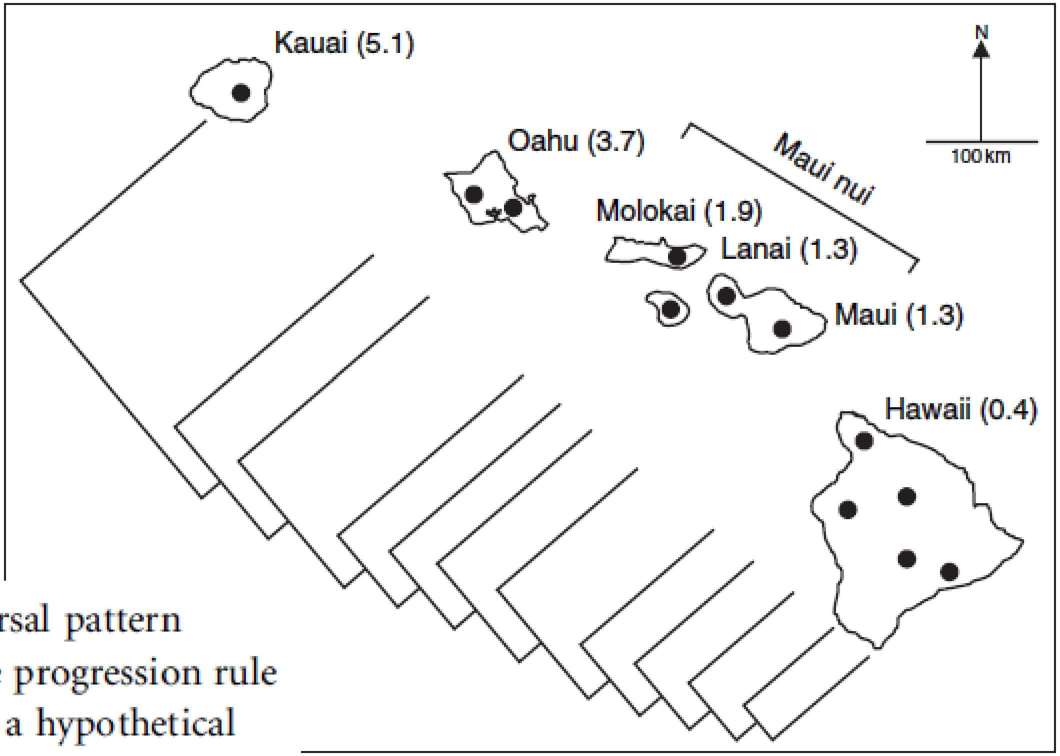


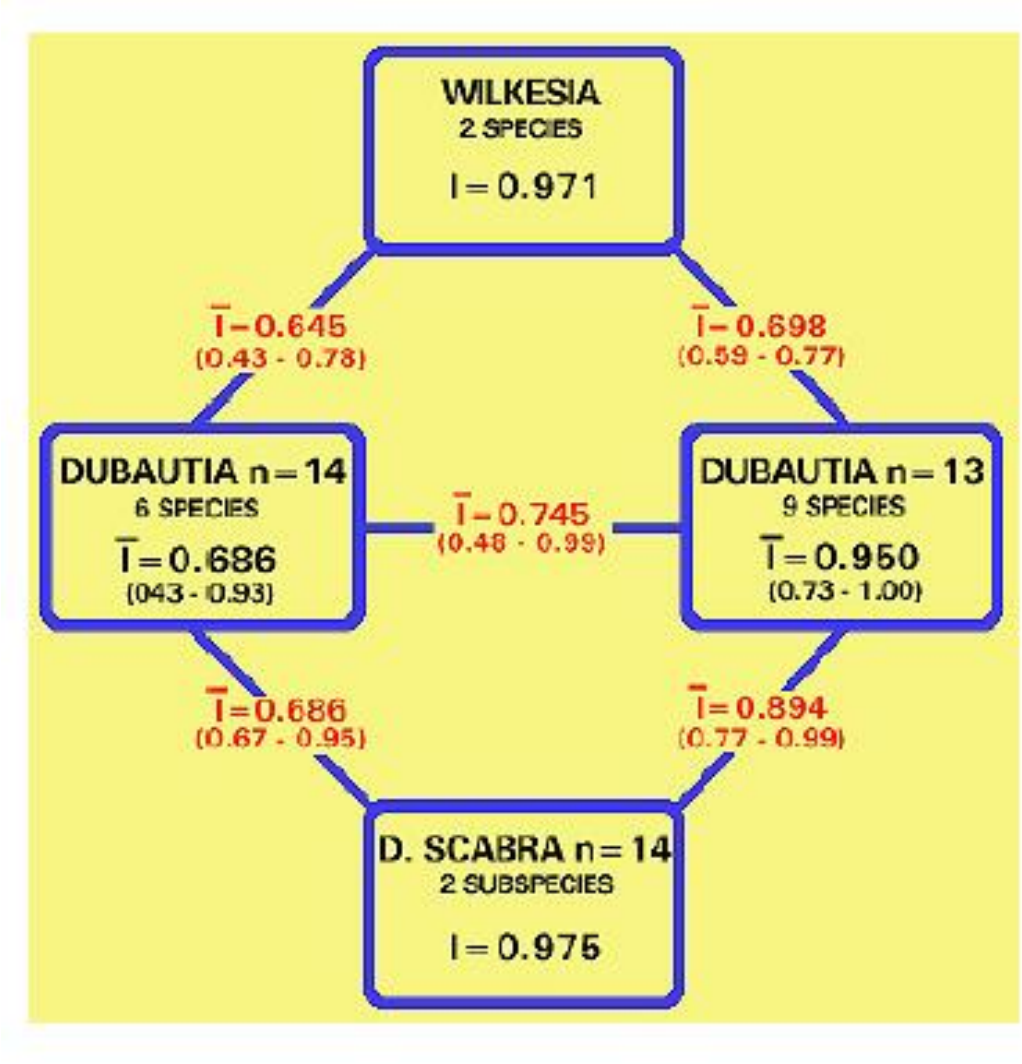
Figure 1 An example of a non-stochastic dispersal pattern observed for many plant and animal lineages, the progression rule pattern of island colonization, here depicted for a hypothetical Hawaiian island lineage. The volcanoes of the six main Hawaiian islands arose over a hot spot in the south-east. As the Pacific plate moves northwestwards it carries with it each sequentially formed island (island ages shown in parentheses, in millions of years). According to the progression rule, the initial colonization event occurs on the oldest island, Kauai, accompanied by subsequent lineage splitting as individuals disperse down the island chain from volcano to volcano (black circles). More complex patterns, involving radiations within islands, back-colonizations and dispersal that passes over an intermediate island, are often superimposed on the basic progression rule pattern.

The Hawaiian Silverswords exhibit enormous phenotypic variation (from herbs to trees to vines)..,

(photos from http://www.botany.hawaii.edu/faculty/carr/silversword.htm)

Argyroxiphium, Dubautia a Wilkesia (Asteraceae)

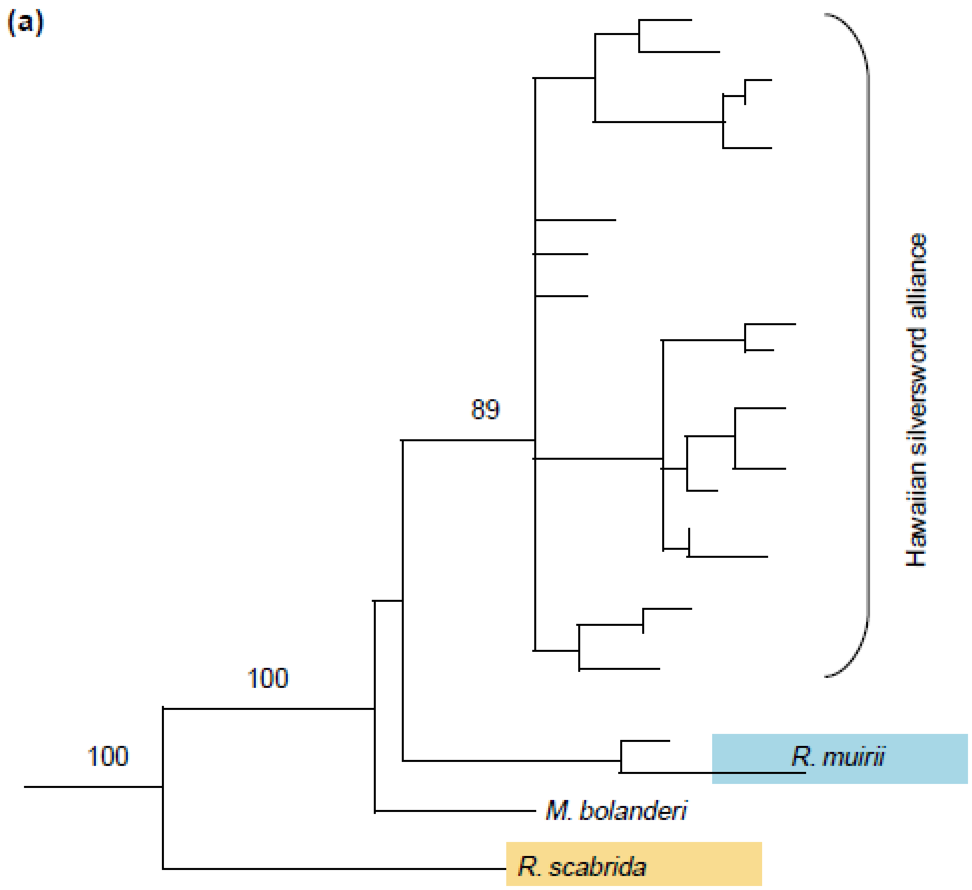
Velká morfologická, ekologická ale nízká genetická variabilita



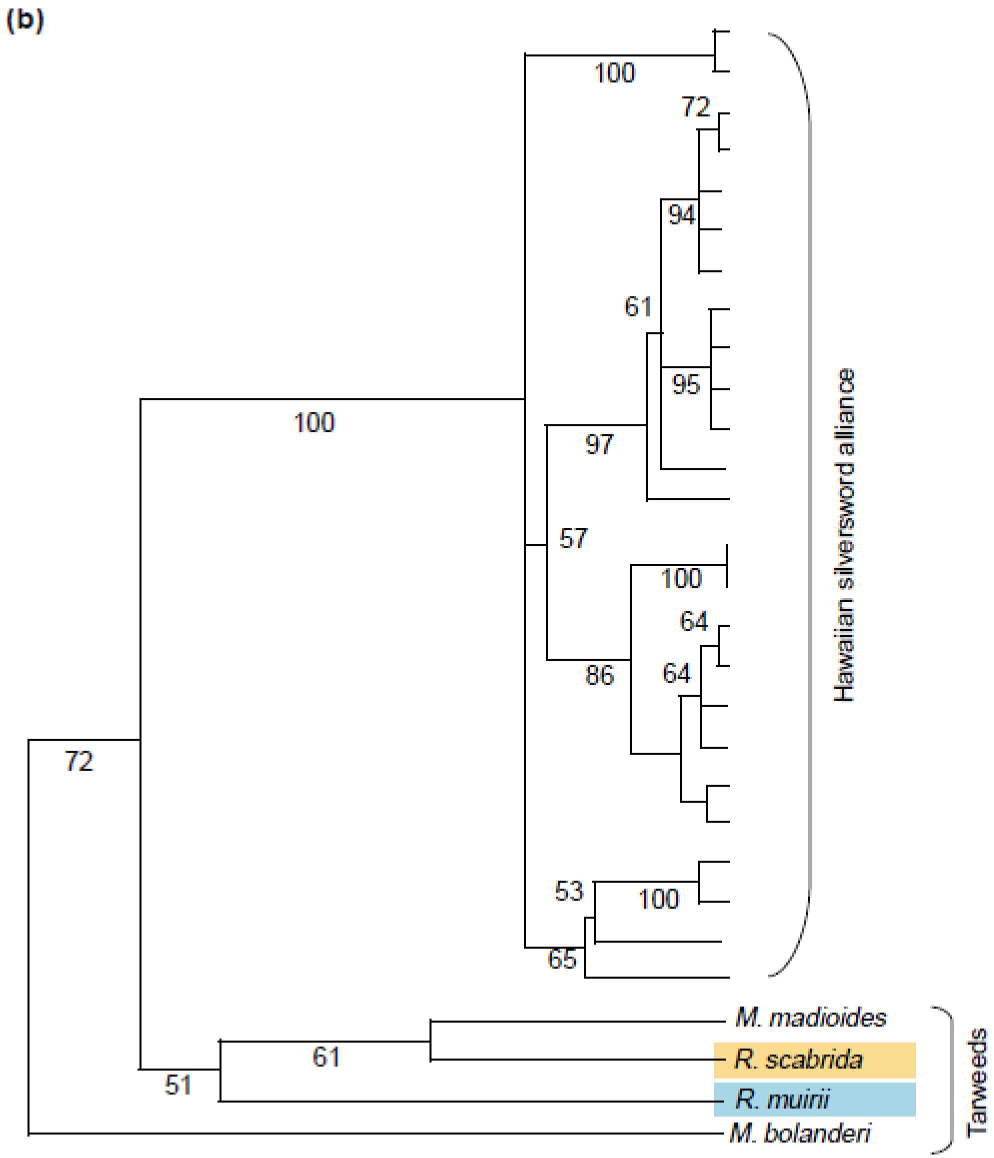
srovnatelná se vzdálenostmi mezi populacemi jednoho druhu na kontinentě

Otázka původu

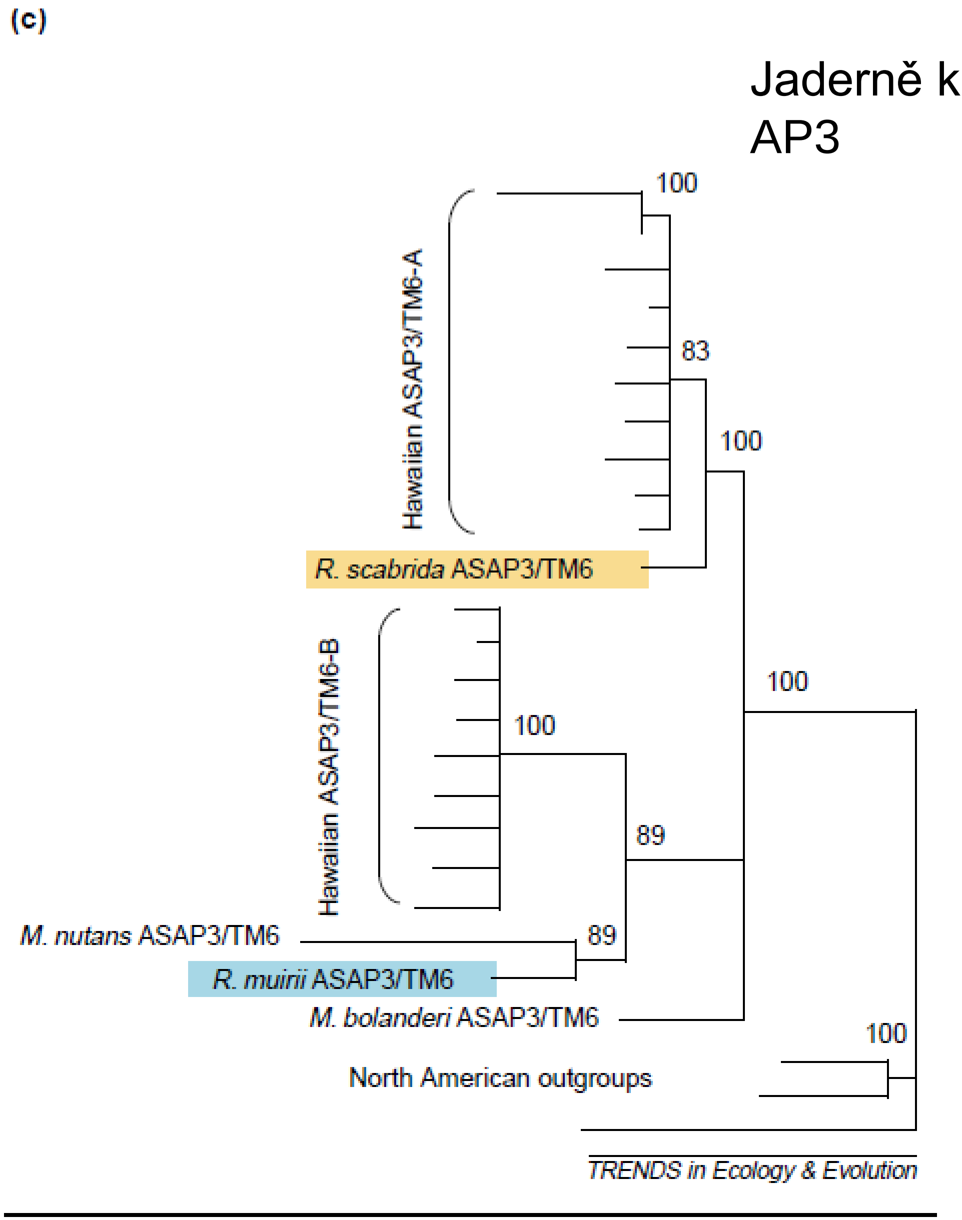
Chloroplastová DNA



Jaderně kódovaný ITS



Jaderně kódovaný květní homeopatický gen AP3



TRENDS in Ecology & Evolution

Nejbližší příbuzné druhy

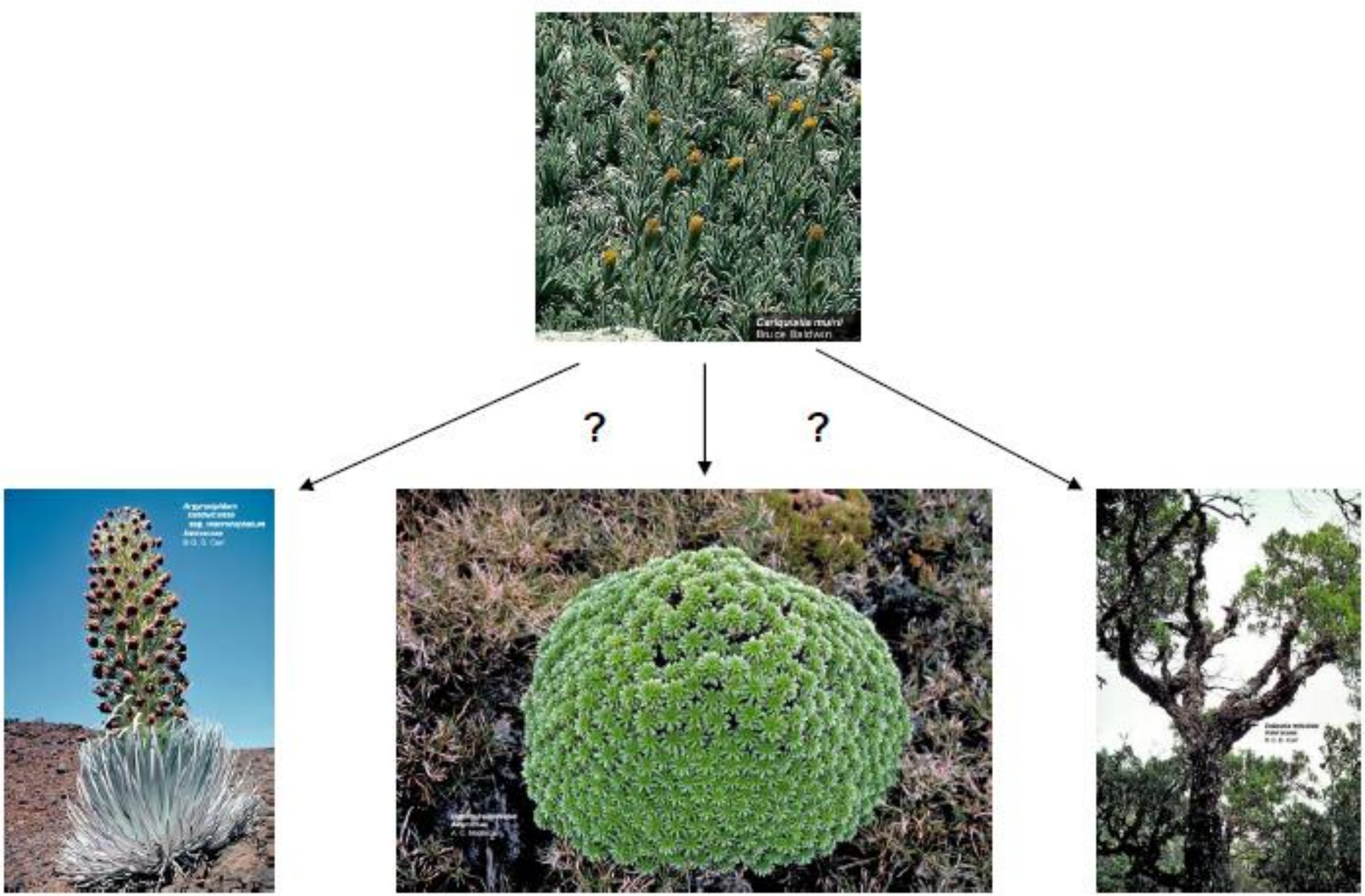
Malé byliny postrádající variabilitu havajských

North American Tarweeds

(http://www.botany.hawaii.edu/faculty/carr/silversword.htm)

Carlquistia *Anisocarpus* *Myhosia*

Jak se vyvinuly rozrůzněné havajské druhy



Evidence genomové duplikace

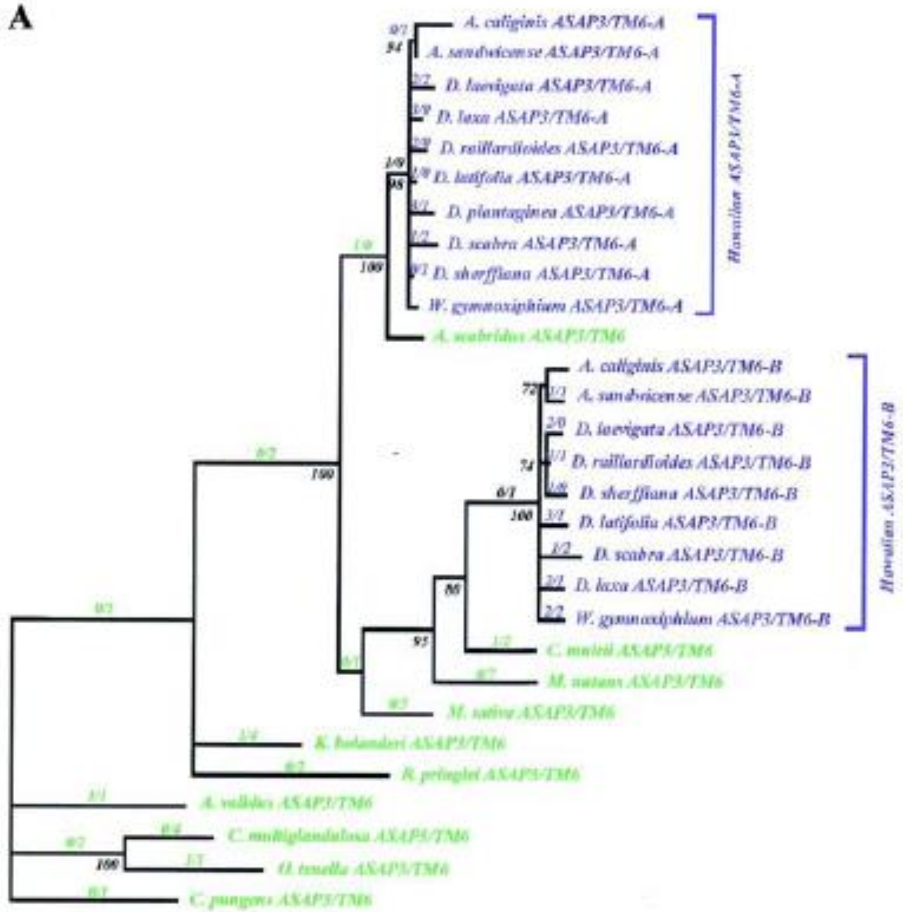
- **Twice the Chromosomes:**
  http://www.botany.hawaii.edu/faculty/carr/silversword.htm
  - Silverswords have roughly twice the chromosome number as Tarweeds, which suggests they're tetraploids
- **Duplicate Genes:**
  (Barrier et al 1999, 2001)
  - Two regulatory genes, *ASAP3/TM*6 and *ASAP1*, and one structural gene, *ASCAB9*, exist as single copies in the Tarweeds, but as duplicate copies in the Silverswords.

Evidence alotetraploidního hybridního původu

C. murii a C. scabrida
se ve fylogenetických studiích vyskytují mezi nejbližšími příbuznými havajských druhů

Evidence alotetraploidního hybridního původu

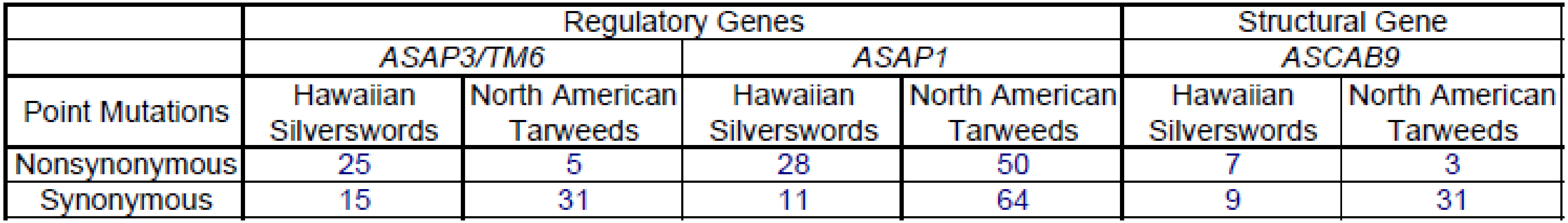
(Barrier et al 1999, 2001)



- One Silversword copy of regulatory gene, *ASAP3/TM6-A*, shows *R.scabrida* to be the nearest Tarweed relative to the Silverswords.
- The other copy, *ASAP3/TM6-B*, shows *R.muirii* to be the nearest Tarweed relative to the Silverswords

Havajské druhy se vyvíjejí rychleji než severoamerické

(Barrier et al 2001)



	Regulatory Genes				Structural Gene	
	ASAP3/TM6		*ASAP1*		*ASCAB9*	
Point Mutations	Hawaiian Silverswords	North American Tarweeds	Hawaiian Silverswords	North American Tarweeds	Hawaiian Silverswords	North American Tarweeds
Nonsynonymous	25	5	28	50	7	3
Synonymous	15	31	11	64	9	31

- Hawaiian Silverswords vs North American Tarweeds
  - All 3 genes accumulated relatively more nonsynonymous point mutations in the Silverswords than in the Tarweeds
- Regulatory vs Structural Genes
  - Within the Silverswords, the Regulatory Genes accumulated relatively more nonsynonymous point mutations than the Structural Gene