Disomic Polyploidy
(Allopolyploidy; Heterogenomic polyploidy)

Wheat evolution

Dvorak et al 1992; Feldman et al., 1997

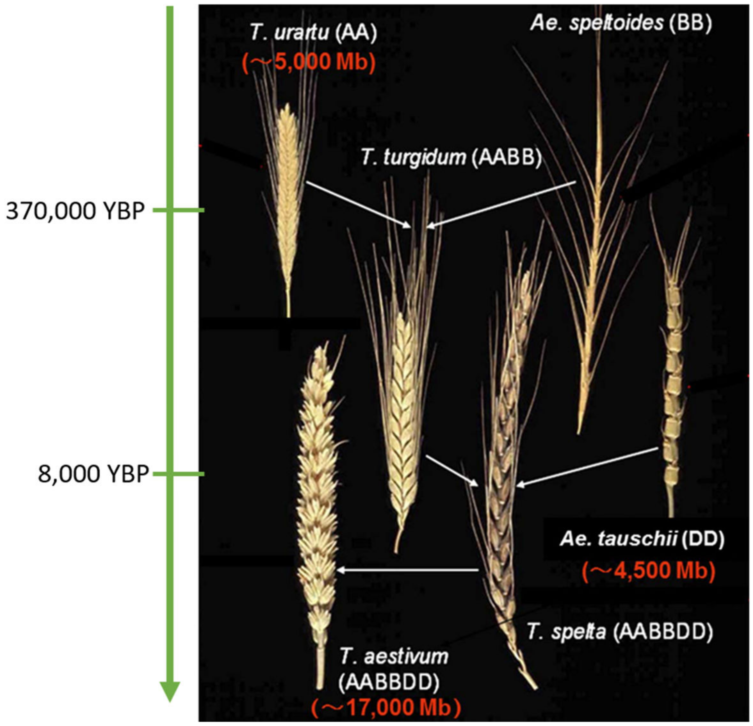
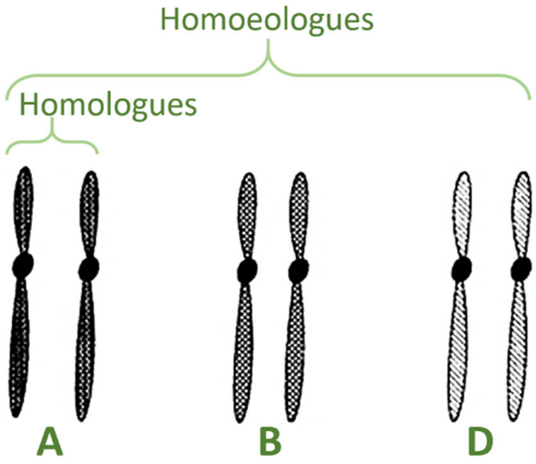


Figure 1. Wheat Genome Consortium

Homoeologous chromosomes

- Homos

- Homoeo
- Logos
- Homologous



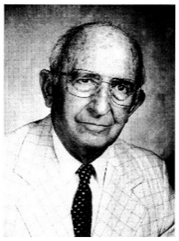
- Autosyndesis
- Allosyndesis

Genetic control of autosyndesis

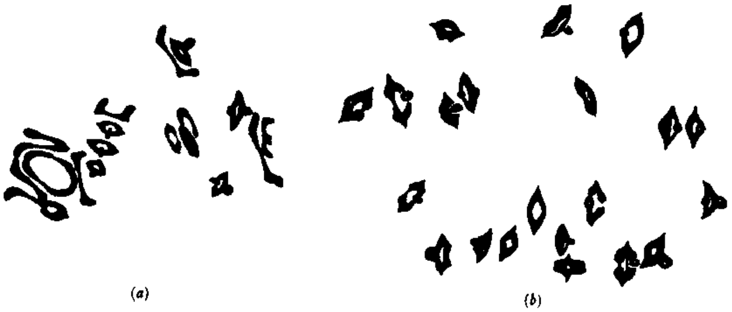
The 5B effect in wheat

Riley and Chapman, 1958; Sears and Okamoto, 1958

Sir Ralph Riley
(1924-1999)



Ernest Robert Sears
(1910-1991)



The *Ph1* locus

Sears, 1977

Aragón-Alcaide et al., 1997 (Moore lab)

	Meiocytes			Tapetum cells			Undifferentiated tissue			N
	sep	V	assoc	sep	V	assoc	sep	V	assoc	
Stage 1	--	--	--	--	--	--	72%	23%	5%	134
Stage 2	10%	88%	2%	31%	61%	8%	--	--	--	41 M 128 T
Stage 3	5%	**2%***	93%	6%	9%	85%	--	--	--	61 M 128 T
ph1ph1 Stage 3	**76%***	7%	0%	55%	37%	8%	--	--	--	29 M 67 T

Greer et al., 2012

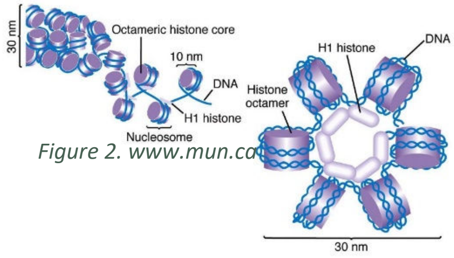


Figure 2. www.mun.ca

Zhang et al., 2014

Martin et al., 2015

Jenczewski and Alix, 2004

- There is good evidence for pairing genes in:
    - *Triticum* spp. (wheat)
    - *Avena sativa* (oat)
    - *Festuca arundinacea* (tall fescue)
    - *Brassica napus* (canola)
    - *Gossypium hirsutum* (cotton)
    - *Gossypium barbadense* (Sea Island cotton)
    - *Lolium multiflorum* (annual ryegrass)
    - *Lolium rigidum*
- The existence of pairing genes can be inferred in:
    - *Aegilops* (wheat grasses)
    - *Hordeum* (barley)
    - *Nicotiana* (tobacco)
    - *Coffea* (coffee)

Doyle and Egan, 2009

Taxonomic definition:	**Autopolyploidy**	**Segmental allopolyploidy**	**Allopolyploidy**
Cytogenetic definition:	**Polysomic**	**Mixosomic**	**Disomic**

Characteristics of disomic polyploids

Genetic duplication

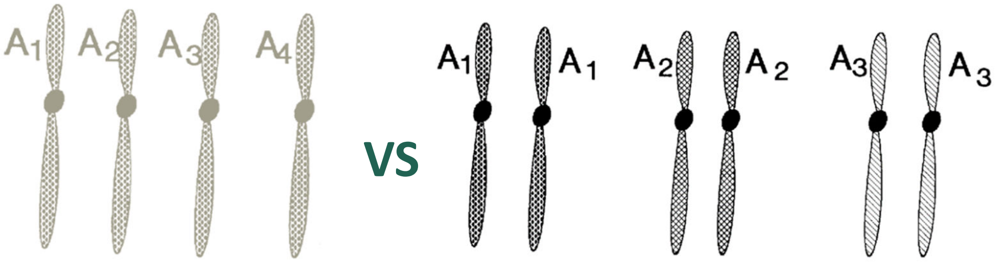
Stadler, 1929

Lewis John Stadler
1896-1954

Induced mutation rate in wheat, per million

2x	4x	6x
10.4	2.0	0.0

Built-in heterozygosity (Intergenomic heterozygosity)



Eg, **Abel et al., 2005**

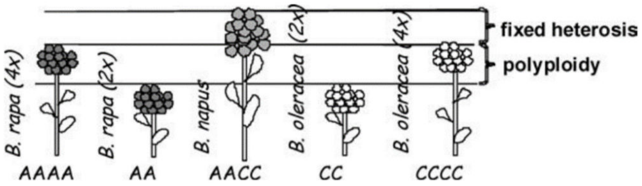


Figure 3. The concept of fixed heterozygosity in alloploids. (WP: Not convinced it is greater than the heterozygosity of autoploids)

Enzymatic diversity

Eg, **Roose & Gottlieb, 1976**

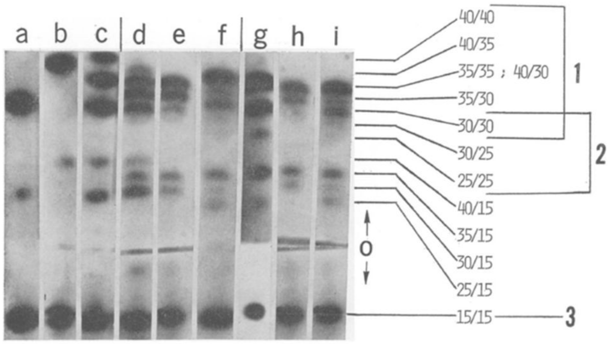
Tragopogon spp.
Salsify

2x *T. dubius*

4x *T. mirus*

2x *T. porrifolius*

Alcohol dehyrogenase

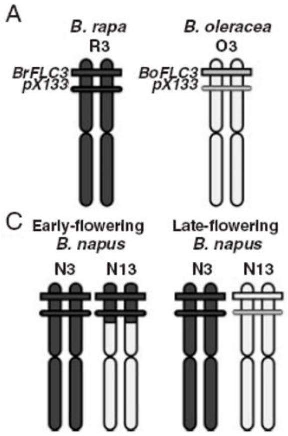


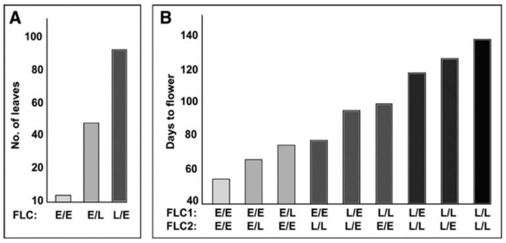
Metabolic richness

Levy & Levin, 1971

Phenotypic diversity

Osborn, 2004

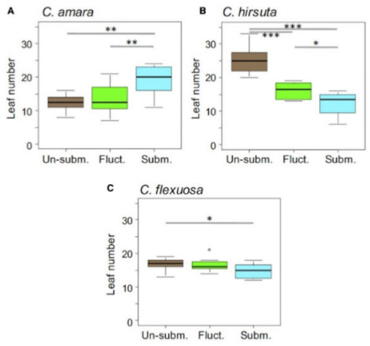


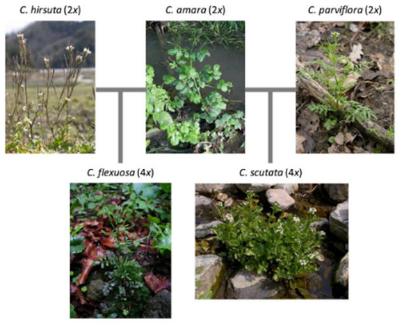


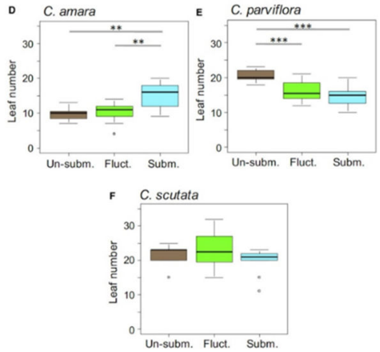
Note for panel: the third bar should be labeled L/L

General purpose genotypes

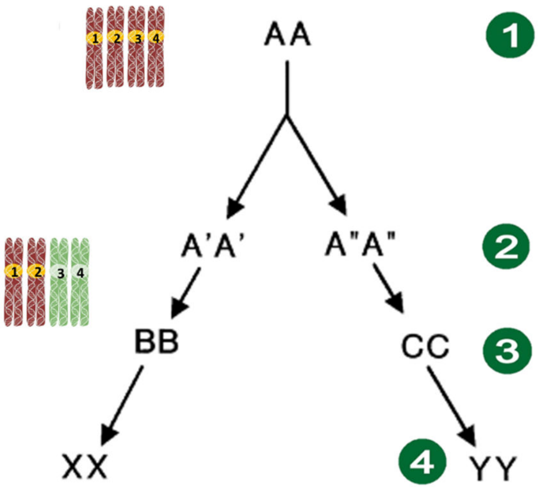
Shimizu-Inatsugi et al, 2017





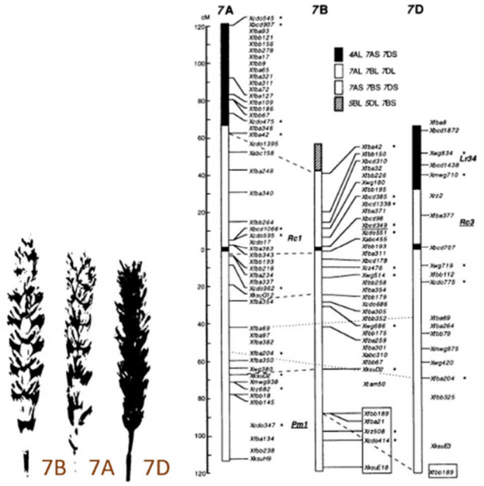


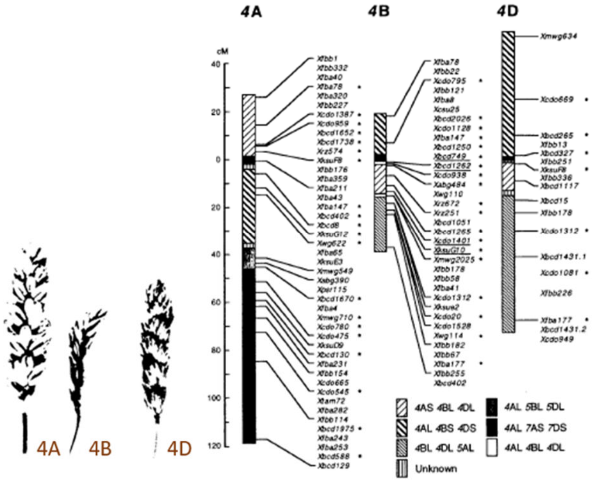
Divergence & polyploidization



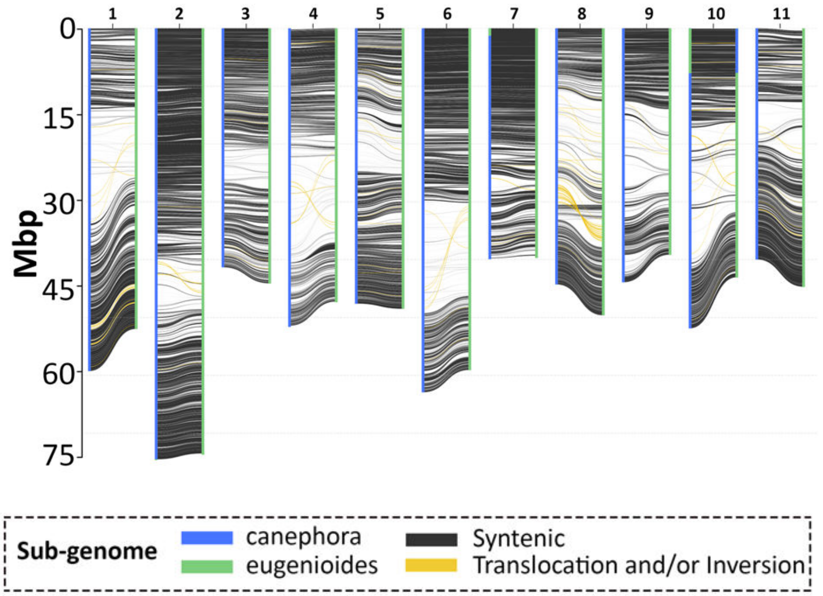
How similar are homoeologous chromosomes

Nelson et al., 1995



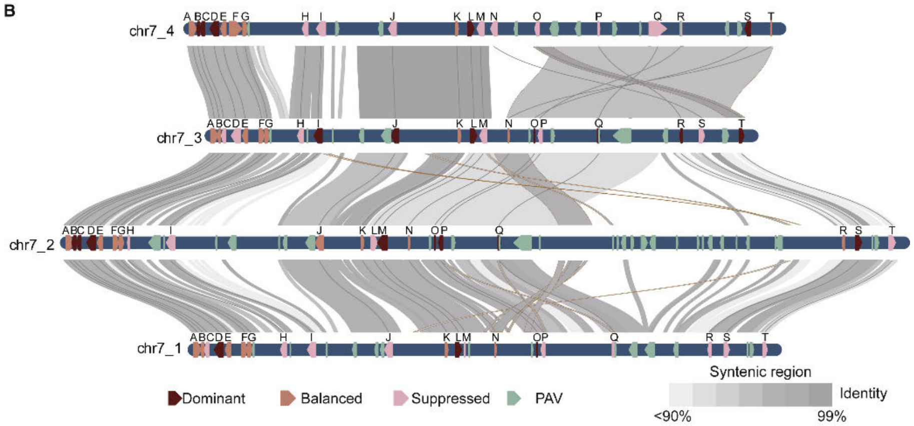


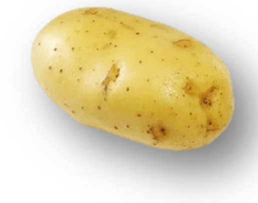
Scalabrin et al. 2024



Compare with homologues from potato

Bao et al. 2022





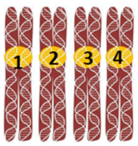
Pairing vs inheritance

Disomic inheritance

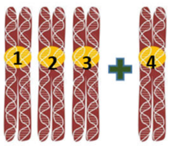
Tetrasomic inheritance

3 possible pairing configurations

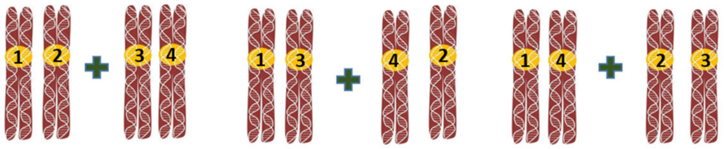
Quadrivalent



Trivalent + Univalent



Two Bivalents– note there are 3 possible combinations



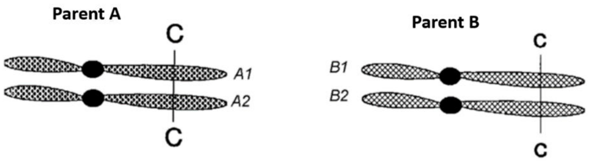
Quantifying allosyndesis vs autosyndesis

Autopolyploidy
- **Polysomic**
- **Random**

Segmental allopolyploidy
- **Mixosomic**

Allopolyploidy
- **Disomic**
- **Autosyndetic**

For a polyploid from these two parents:



There are 3 pairing possibilities:

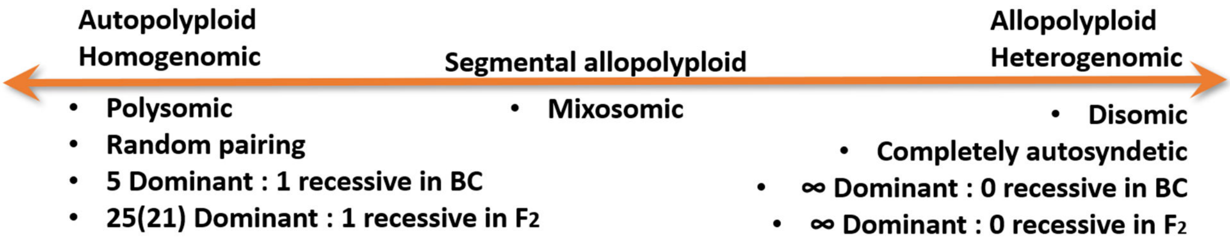
1) All pairing in autosyndetic

		Dominant:recessive ratio	
Type of pairing	Gametes	Backcross	F_2
All autosyndetic	*Cc*	∞:0	∞:0

2) All pairing is completely random

		Dominant:recessive ratio	
Type of pairing	Gametes	Backcross	F_2
No preference	1*CC* + 4*Cc* + 1*cc*	5:1	35:1 (20:1)

3) Autosyndesis occurs preferentially, but not to the exclusion of allosyndesis



Autopolyploid
Homogenomic

- **Polysomic**
- **Random pairing**
- **5 Dominant : 1 recessive in BC**
- **25(21) Dominant : 1 recessive in F2**

Segmental allopolyploid

- **Mixosomic**

Allopolyploid
Heterogenomic

- **Disomic**
- **Completely autosyndetic**
- **∞ Dominant : 0 recessive in BC**
- **∞ Dominant : 0 recessive in F2**

Pelé et al, 2018

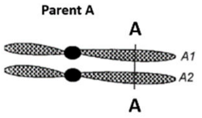
- “Speciation success of polyploid plants closely relates to the regulation of meiotic recombination”

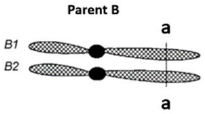
Gerstel 1963

Cross:	Genomes: n = 13	II in F_1:	IV in amphidiploid	BC Ratio: (exp. 5:1)	Comments:	Most like an:
G. arboreum × *G. herbaceum*	$A_2 \times A_1$	$^{12.9}/_{13}$	$^{\sim 8}/_{13}$	4:1	Closest to a 5:1 ratio*	Autoploid
G. thurberi × *G. raimondii*	$D_1 \times D_5$	$^{12.9}/_{13}$	$^{3.9}/_{13}$	13.4:1	Deviates from 5:1 ratio	????
G. arboreum × *G. raimondii*	$A_2 \times D_5$	$^{6}/_{13}$	$^{0.2}/_{13}$	103.5:1	Approaches an ∞:0 ratio	Alloploid
G. arboreum × *G. thurberi*	$A_2 \times D_1$	$^{8}/_{13}$	$^{0.44}/_{13}$	393.0:1	Approaches an ∞:0 ratio	Alloploid

*Figure 4. *Note the high frequency of IV being formed*

Burnham, 1962





- The "theoretical %of recessives in backcross progenies from an F1 duplex for a recessive gene"
  - I.e., a cross of AAaa × aaaa in which various levels of autosyndetic pairing are assumed

Pairing	% allosyndesis	% autosyndesis t_1	% recessives in BC	% of BC progeny that are *Aaaa*	Type of pairing
All allosyndetic	100	0.0	25.0	50.00	AB only
	87.5	12.5	21.88	56.25	
	75	25.0	18.75	62.50	
Random *(autoploid)*	66.66	33.33	16.67	66.67	⅔(AB+AB); ⅓(AA+ BB)
	50	50.00	12.50	75.00	
	33.33	66.66	8.33	83.33	
	25	75.00	6.25	87.50	
	12.5	87.50	3.125	93.75	
All autosyndetic (*alloploid*)	0	100.0	0.00	100.00	AA & BB only

Burnham, 1962 using data from **Emerson, 1929**

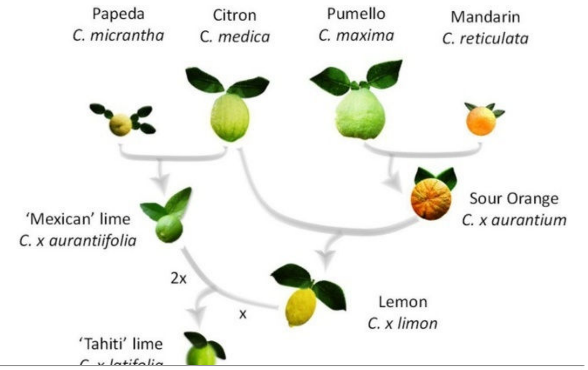
"Data from the 4x hybrid of recessive maize × perennial teosinte backcrossed to the recessive."

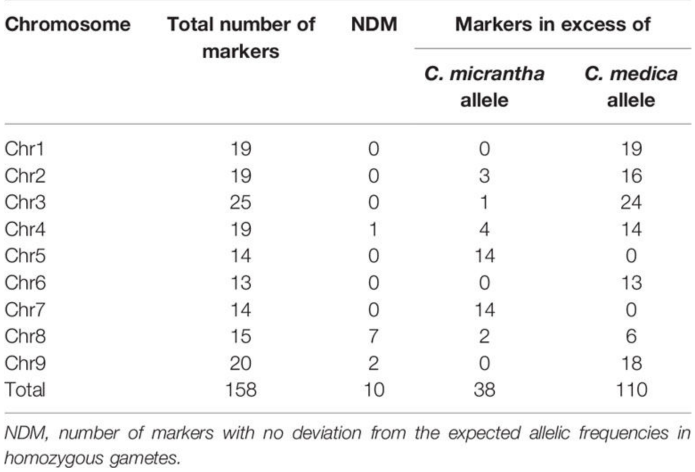
Gene:	Total seeds or plants	Observed recessives		t_1 values (autosyndesis)
		#	%	
g	208	12	5.8	.77
lg	25	1	4.0	.84
su	58	5	8.6	.66
wx	113	11	9.7	.61
TOTAL	404	29	7.2	.71
Expected if pairing is random (*autoploid*):			16.7	.33
Expected if pairing is all autosyndetic (*alloploid*):			0.0	1.00

	t_1	% autosyndesis MM + TT	% allosyndesis MT + MT
Observed	.71	71	29
Expected for autosyndesis	.33	33	67
Expected for allosyndesis	1.00	100	0

Tau statistic

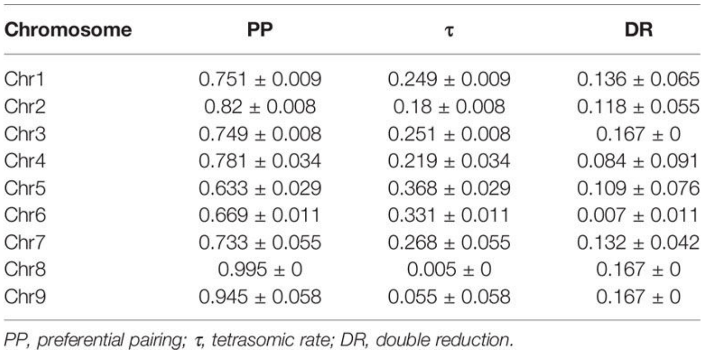
Ahmed et al, 2020





Chromosome	Total number of markers	NDM	Markers in excess of	
			***C. micrantha* allele**	***C. medica* allele**
Chr1	19	0	0	19
Chr2	19	0	3	16
Chr3	25	0	1	24
Chr4	19	1	4	14
Chr5	14	0	14	0
Chr6	13	0	0	13
Chr7	14	0	14	0
Chr8	15	7	2	6
Chr9	20	2	0	18
Total	158	10	38	110

NDM, number of markers with no deviation from the expected allelic frequencies in homozygous gametes.



Chromosome	PP	τ	DR
Chr1	0.751 ± 0.009	0.249 ± 0.009	0.136 ± 0.065
Chr2	0.82 ± 0.008	0.18 ± 0.008	0.118 ± 0.055
Chr3	0.749 ± 0.008	0.251 ± 0.008	0.167 ± 0
Chr4	0.781 ± 0.034	0.219 ± 0.034	0.084 ± 0.091
Chr5	0.633 ± 0.029	0.368 ± 0.029	0.109 ± 0.076
Chr6	0.669 ± 0.011	0.331 ± 0.011	0.007 ± 0.011
Chr7	0.733 ± 0.055	0.268 ± 0.055	0.132 ± 0.042
Chr8	0.995 ± 0	0.005 ± 0	0.167 ± 0
Chr9	0.945 ± 0.058	0.055 ± 0.058	0.167 ± 0

PP, preferential pairing; τ, tetrasomic rate; DR, double reduction.

Distinguishing allo from autotetraploids

Segregation ratios

If tetrasomic, the "2" alleles can pair with the "1" alleles

	1AA	*4Aa*	*1aa*
1AA			
4Aa			
1aa			$^1/_{20-36}$ *aaaa*

If an allo, the "2" & "1" alleles do not pair, they behave as 2 independent loci ➔ **Digenic** inheritance, ie, a 2-gene ratio

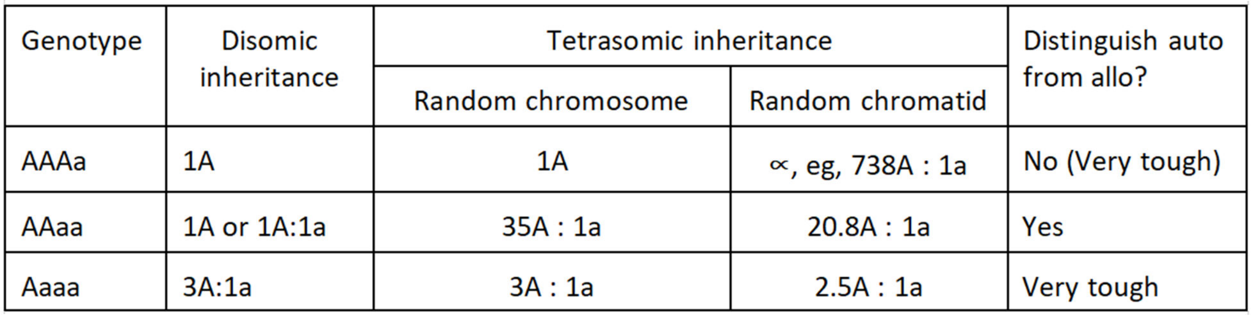
	A_1A_2	A_1a_2	a_1A_2	a_1a_2
A_1A_2				
A_1a_2				
a_1A_2				
a_1a_2				$^1/_{16}$ $a_1a_1a_2a_2$

Segregation ratios vs sample size

$AAaa \xrightarrow{\otimes}$

Expected ratios after selfing an autotetraploid

Barone et al., 2002



Genotype	Disomic inheritance	Tetrasomic inheritance		Distinguish auto from allo?
		Random chromosome	Random chromatid	
AAAa	1A	1A	∝, eg, 738A : 1a	No (Very tough)
AAaa	1A or 1A:1a	35A : 1a	20.8A : 1a	Yes
Aaaa	3A:1a	3A : 1a	2.5A : 1a	Very tough

Chromosome pairing

Jackson, 1982

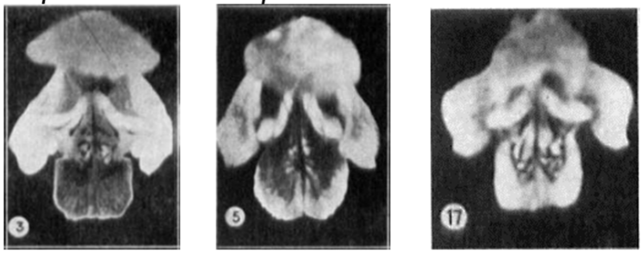
Clausen et al., 1945

Chromosome number

Resynthesizing hybrid from ancestral species

First done by **Müntzing, 1932**

Galeopsis pubescens x *G. speciosa* → Artificial tetrahit



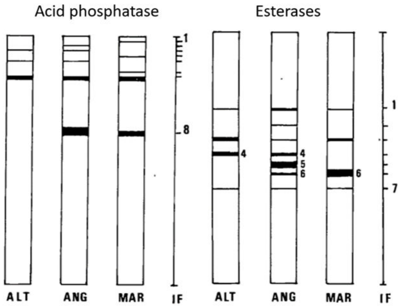
Karyotype

Karyotype of Milium montianum. Bennett & Bennett, 1992. Allopolyploid derived from M. vernale x unknown spp.

Morphology

Biochemical traits

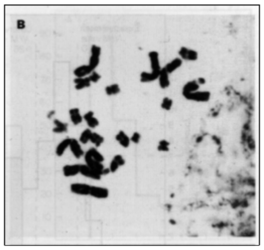
Eg, Guénégou et al., 1988



Breeding behavior

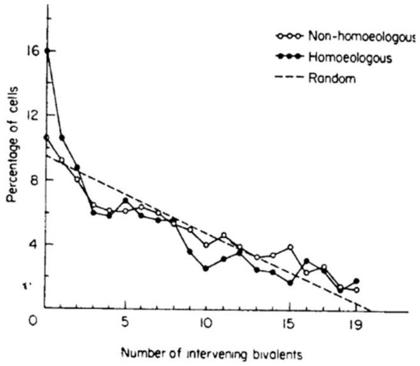
Barrington, 2007

Nuclear architecture & 2^o associations

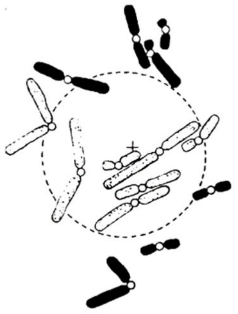


Secondary associations visible in Milium montianum. Bennet & Bennett, 19920

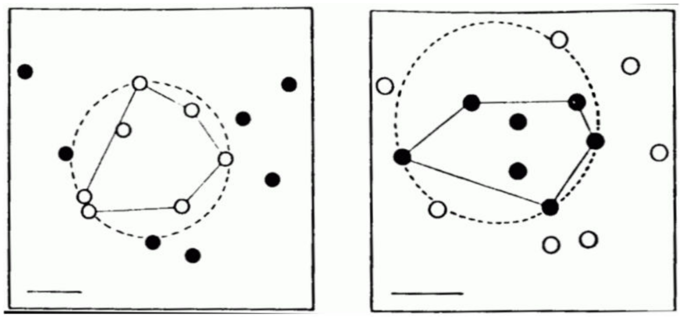
Kempanna and Riley, 1964



Bennett, 1984; 1987

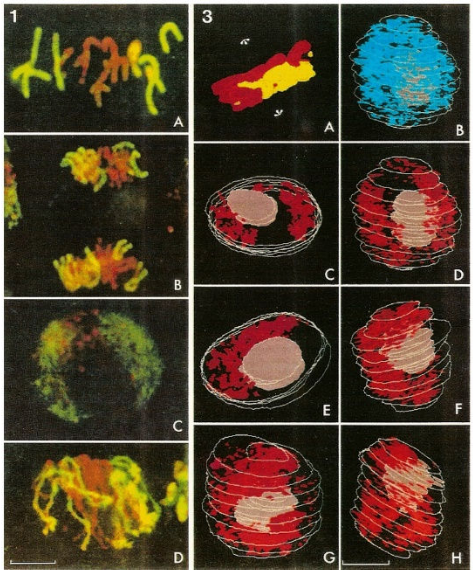


Root tip chromosomes of an F1 between barley (stippled) and H. bulbosum (solid). Bennett, 1984

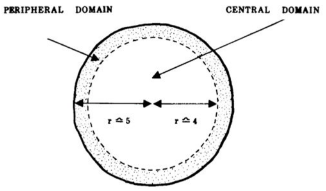


Hordeum (white circle) & Secale (black circle) centromeres R: H. vulgare x S. africanum L: H. chilense x S. africanum (Bennett, 1987)

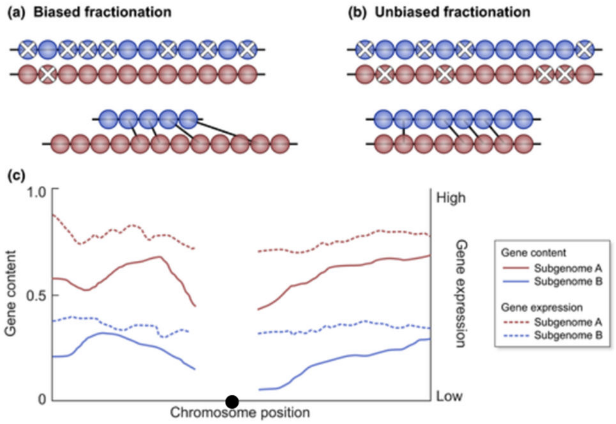
Swarzachter, Leitch, Bennett, & Heslop-Harrison, 1989



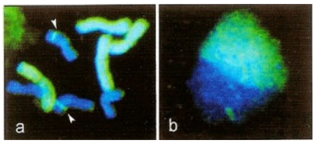
Bennett, 1987



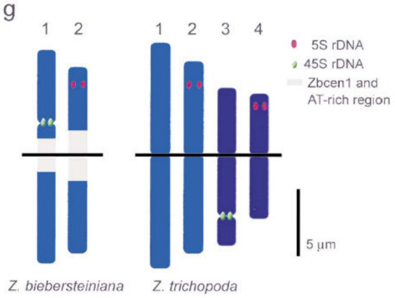
Bird et al (Edger lab), 2018



Kotseruba et al., 2003



- *Zingeria bierbersteiniana* → 2n = 2x = 4
- *Z. trichopoda* → 2n = 4x = 8, an alloploid between *Z. bierbersteiniana* and an unknown sp.



The 45S loci from Z. bierbersteiniana have been lost in the allotetraploid.

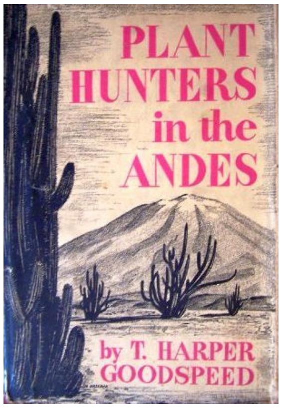
Identification of progenitor species

Chromosome pairing

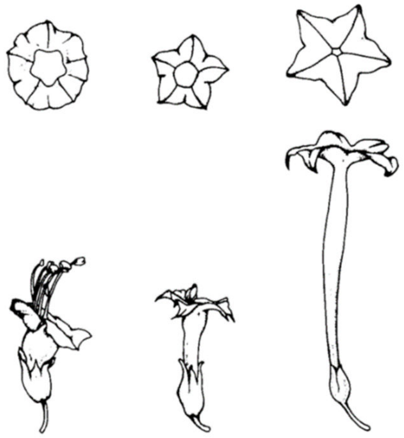
Goodspeed & Clausen, 1927; 1928
Clausen 1932

Roy Elwood Clausen
(1891-1956)

Thomas Harper Goodspeed
(1887-1967)

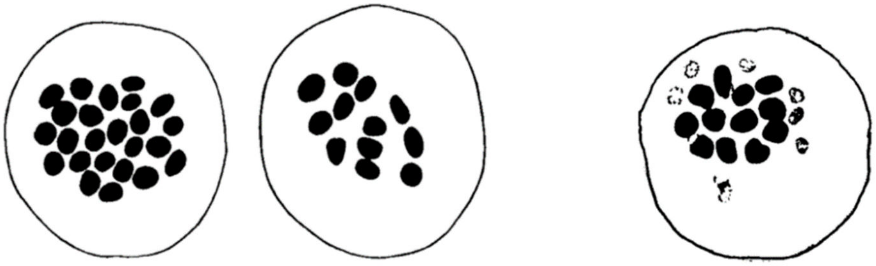


PLANT HUNTERS in the ANDES
by T. HARPER GOODSPEED



Tobacco and its putative ancestors. *Nicotiana tomentosa* (2x = 24); *N. tabacum* (4x = 48); *N. sylvestris* (2x = 24) Goodspeed, 1954.

N. tabacum	×	*N. sylvestris*	⇒	F_1 =
n = 24		n = 12		n =
TTSS		SS		



N. tabacum (24 II) and N. sylvestris (12 II). Right: N. sylvestris × N. tabacum (12 II + 12 I)

N. tabacum	×	*N. tomentosa*	⇒	F_1 =
n = 24		n = 12		n =
TTSS		T'T'		

Figure 5. Left: N. tabacum (24 II); Right: N. tabacum x N. tomentosa (12 II + 12 I).

N. sylvestris	×	*N. tomentosa*	⇒	F_1 =	$\overset{\text{doubling}}{\Rightarrow}$
n = 12		n = 12		n =	
SS		T'T'			

N. tabacum	×	*amphiploid*	⇒	F_1 =	⇒
n = 24		n = 24		n =	
TTSS		T'T'SS			

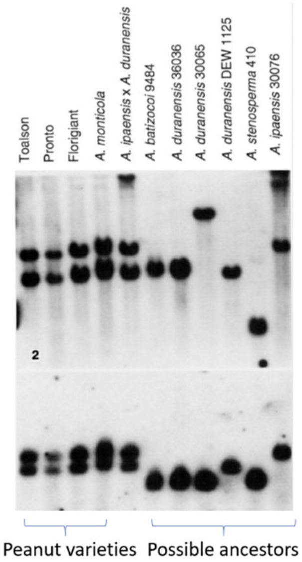
N. tabacum	×	amphidiploid	⇒	F_1 = 24 II

Gerstel, 1963

- Made hybrids between tobacco and *N. tomentosa*, *N. otophora*, and *N. tomentosiformis*, all of which are T'T'
- This gave him TT'S hybrids → doubled to get TTT'T'SS → ⊗

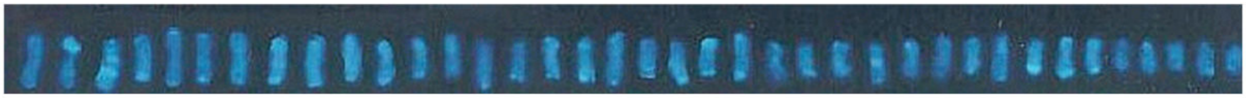
Molecular markers

Kochert et al., 1996



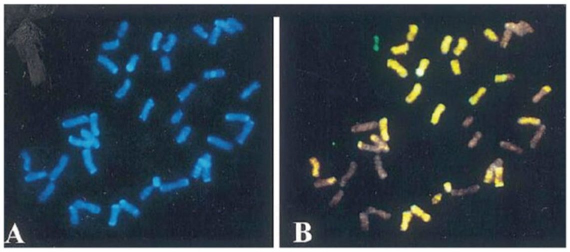
Genomic In Situ Hybridization (GISH)

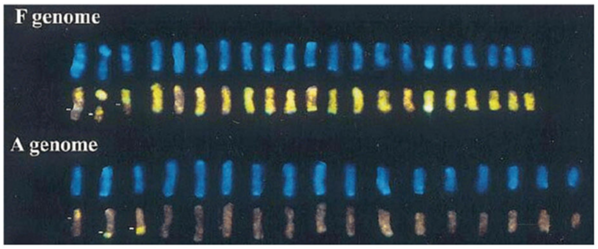
Brysting et al., 2000



Karyotype of Poa jemtlandica, 2n = 38, ¿allopolyploid between P. alpina & P. flexuosa?

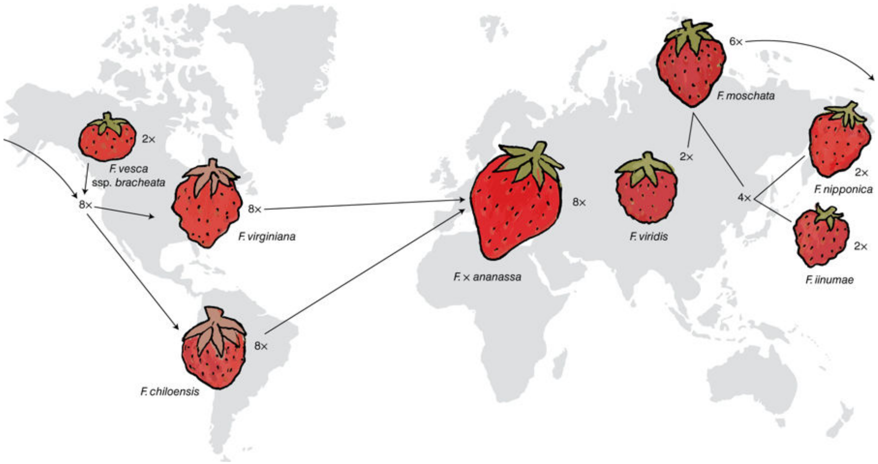
Poa jemtlandica *Poa jemtlandica + P. flexuosa DNA*





Genome sequencing

Eg., Edger et al, 2019



https://www.nature.com/articles/s41588-019-0365-3/figures/1

2x *F. nipponica* × 2x *F. iinumae* → 4x sp. × 2x *F. viridis* → 6x *F. moschata* × 2x *F. vesca* → *8x F. virginiana* & 8x *F. chiloense* which crosses to get *F.* × *ananassa* in the 1740's

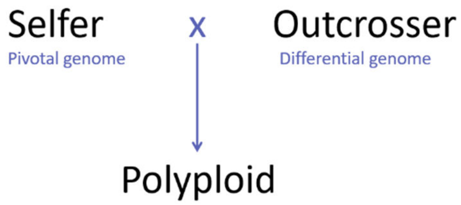
Determining the maternal parent

What happens during allopolyploidization?

Concept of the pivotal genome

MacKay, 1970

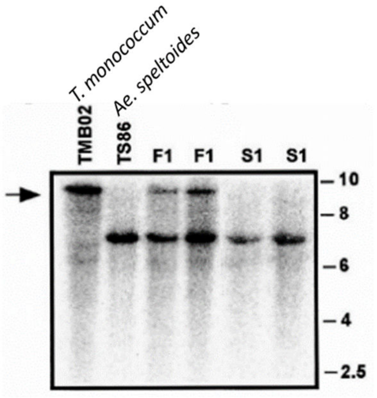
Mirzaghaderi & Mason, 2017



Rapid effects of allopolyploidization

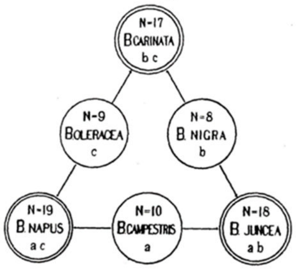
Loss/ gain of AFLP or RFLP fragments in polyploid relative to parents

Ozkan et al., 2001

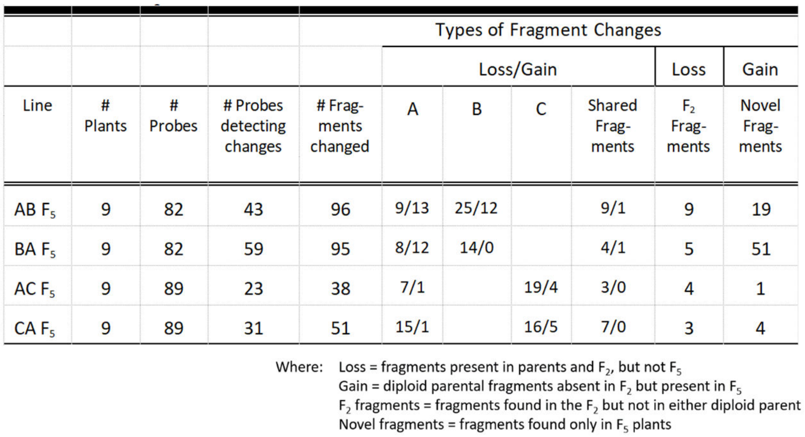


U, 1935

U triangle



Song et al., 1995 (Osborn lab)



					Types of Fragment Changes					
					Loss/Gain				Loss	Gain
Line	# Plants	# Probes	# Probes detecting changes	# Fragments changed	A	B	C	Shared Fragments	F_2 Fragments	Novel Fragments
AB F_5	9	82	43	96	9/13	25/12		9/1	9	19
BA F_5	9	82	59	95	8/12	14/0		4/1	5	51
AC F_5	9	89	23	38	7/1		19/4	3/0	4	1
CA F_5	9	89	31	51	15/1		16/5	7/0	3	4

Where: Loss = fragments present in parents and F_2, but not F_5
Gain = diploid parental fragments absent in F_2 but present in F_5
F_2 fragments = fragments found in the F_2 but not in either diploid parent
Novel fragments = fragments found only in F_5 plants

Liu et al, 1998

Amphiploid	Generation	# seqs. studied # polymorphic	# seqs. changed	Loss	Loss + gain of new band
SSAA	S_6	9/6	6	5	1
SSDD	S_3	9/7	7	4	3
AABBDD	S_5	9/7	7	6	1
AABBDD	S_5	9/8	8	7	1
AABBDDSS	S_3	9/8	8	8	0

Loss/gain of DNA after allopolyploidization is

Rapid

Levy & Feldman, 2004

Extensive

Nonrandom & repeatable

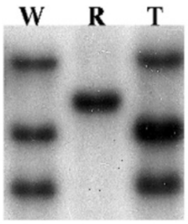
Blanc & Wolfe, 2004

Retrotransposon activation

Gu et al., 2004

Preferential loss of DNA from one parental genome

Jones & Flavell, 1982
Ma et al., 2004



Silencing

Comai et al., 2000, 2003

Wang et al., 2004

He et al., 2003

	Origin		
	DD	AABB	Total
Bands Scored	1650	1750	2800
Bands polymorphic between two parents	1050	1150	2200
Bands reduced or missing in hexaploid	122 (11.6%)	38 (3.3%)	160 (7.3%)
Bands induced in hexaploid		8 (0.4%)	

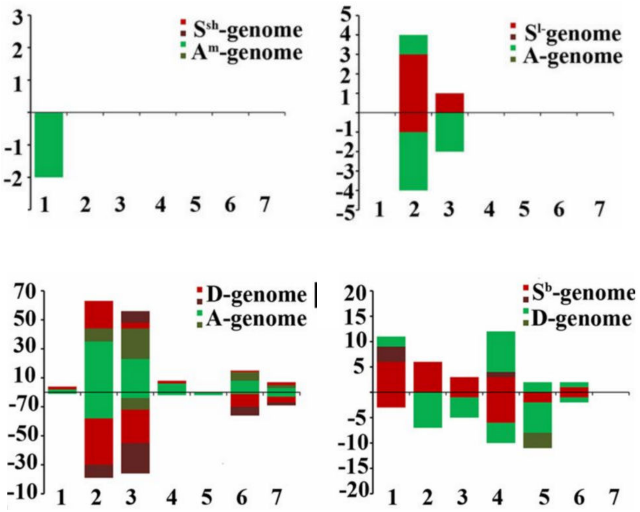
Expression differences between synthetic 6x wheat and the parental Aegilops tauschii & Triticum turgidum

Involves nucleolar dominance

Plant	**Reference**	**Effect**
allotetraploid *Arabidopsis suecica* Genome is AACC: • AA from *A. thaliana* • CC from *A. arenosa*	**Chen et al., 1998**	In the AACC tetraploid • rDNA from *A. thaliana* silenced When backcrossed to both parents to get ACCC or AAAC • The rDNA from *A. arenosa* is silenced
Solanum allopolyploids from tomato × potato	**Komarova et al., 2004**	• Tomato (*S. lycopersicon*) provides 95-100% rRNA relative to potato (*S. tuberosum*)
allotetraploid cotton	**Adams et al., 2004**	• Twice as many genes from paternal subgenome silenced relative to maternal subgenome

Some genomes are > compatible than others

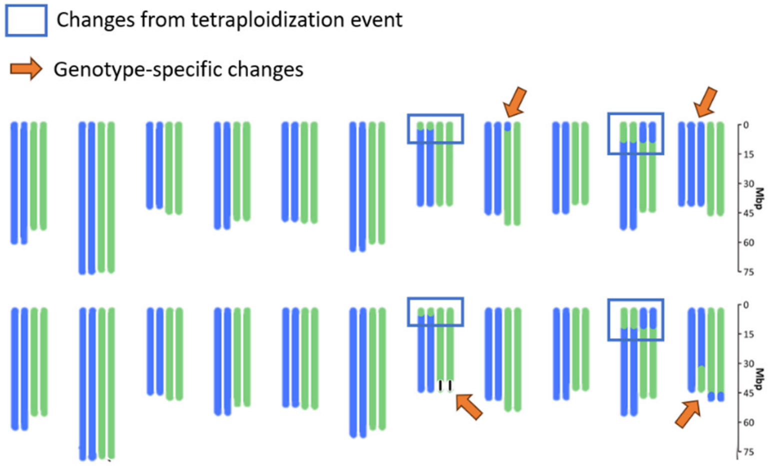
Zhang et al, 2013



“Therefore, it is likely that the survived and eventually established nascent polyploids are those that are able to fine-tune the balance of mutability and karyotype stability.”

Instability remains in alloploids

Scalabrin et al. 2024

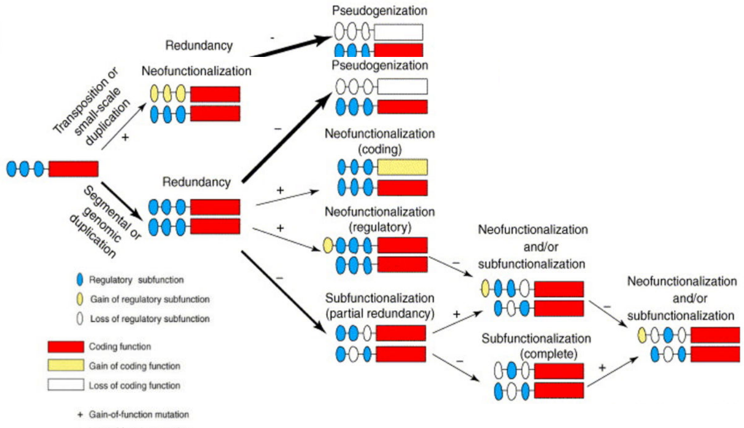


Fate of duplicated genes

Review by Birchler & Yang 2022

Blanc and Wolfe, 2004

Moore & Purugganan, 2005



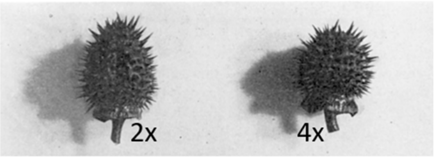
Blanc and Wolfe, 2004

Summary

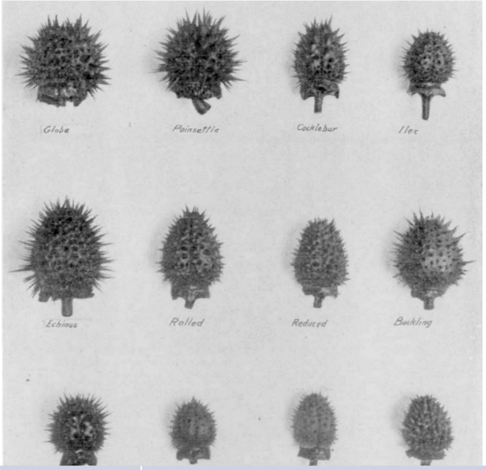
Modified from **Cheng et al, 2018**

	Needed mutations	
Phase 1: Pre-allo and continuing	- Genome differences pre-exist between progenitors	- Transposons being silenced
Phase 2: The new polyploid	- New epigenetic subgenome differences	- Permanent heterozygosity - Gene dominance - Homoeologue interference

Gene dosage & balance in plants



Blakeslee, 1922

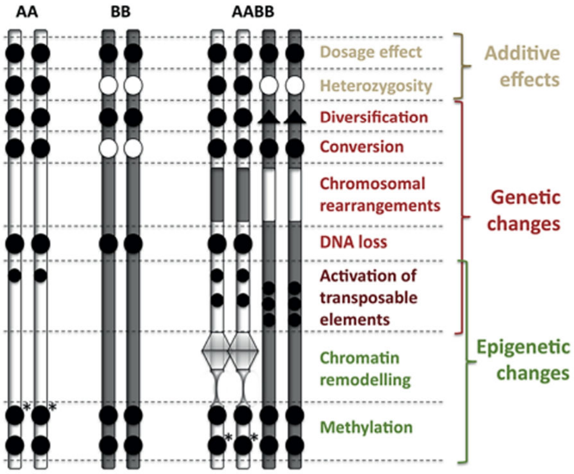


Blakeslee & Belling, 1922

Phase 3: Moderate time post-allo and continuing	- Expression fine-tuning - Chromosomal breaks and reunions	- Dosage rebalancing by fractionation - Continued RdDM-dependent transposon and gene silencing
	- Fractionation of genes/cis-sites - Canonical mutations (SNPs and INDELs) begin	- Mutation under non-functionality - Subfunctionalization, (duplication, degeneration, complementation) - Continued homoeologue interference - Innovation, amplification and divergence
	- Neofunctionalization (rare and multiple mutations)	- Gene product neofunctionalization - Expression/regulatory neofunctionalization

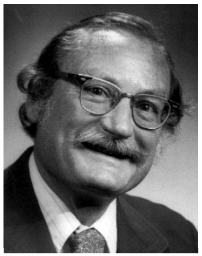
Phase 4: Establishment of polyploids	- Evolution of new gene networks. - Very rare, multiple mutation combinations	- Unstable environment - Ecological niches - Adaptive radiation - Novel physiological diversifying selection

Tayalé & Parisod, 2013



Origin of neopolyploidy

Harlan and deWet, 1975



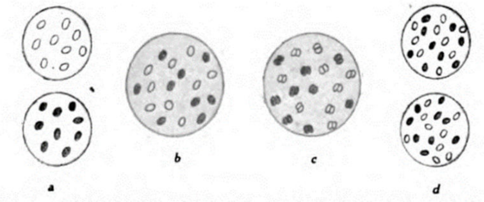
Jack Rodney Harlan
(1917-1998)

Artificial

Somatic doubling

Winge, 1917

Öjving Winge
(1886-1964)



Occurrence of doubled chromosome numbers through hybridization

2n gametes

Mendiburo & Peloquin, 1976; Soltis et al, 2010

Stanley J. Peloquin
(1921-2008)

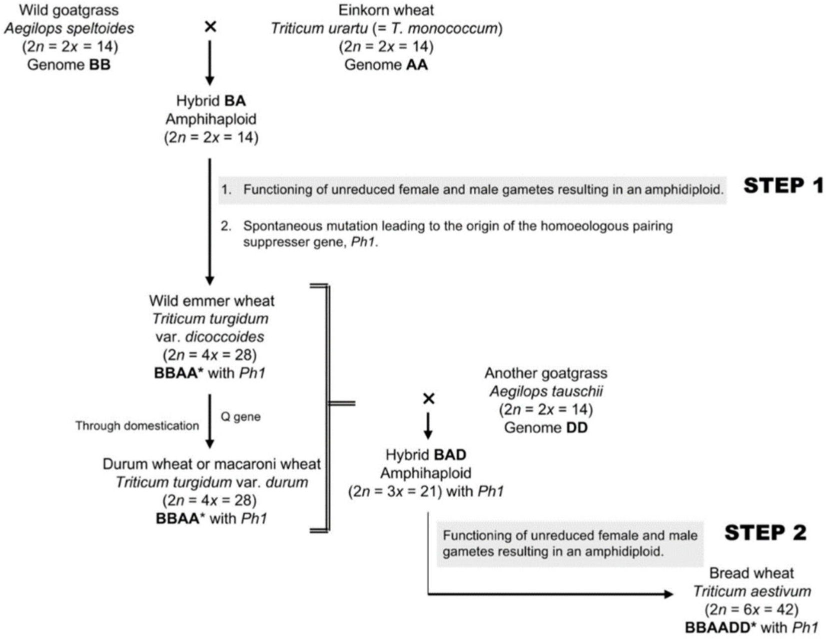
Bilateral sexual tetraploidization
One-step

Triploid bridge
Two-step

Unilateral sexual tetraploidization

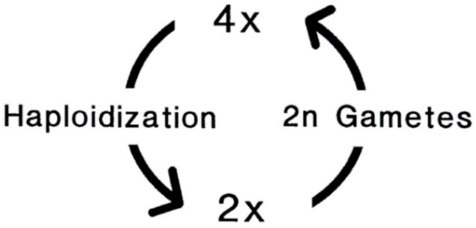
Steps in the evolution of bread wheat

Jauhar,2007



Repeated neopolyploidization

Raven & Thompson, 1965



Soltis, 2005

Hybridization without polyploidization

Pesakinskiené et al., 1996

2x *Lolium multiflorum* × 6x *Festuca arundinacea*
⇓
4x hybrids
⇓
8x × 8x
⇓
3-5 % 2x plants