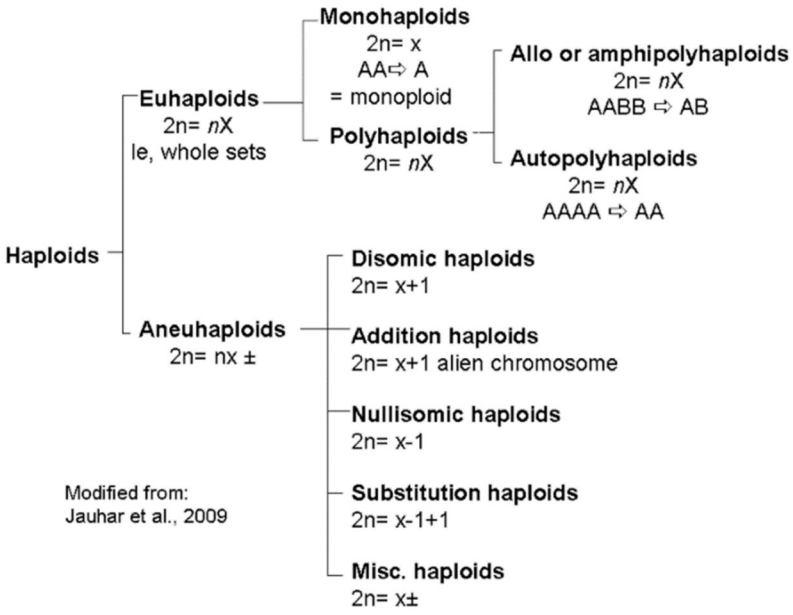
Dermail et al. 2024
Quiroz et al. 2024

Haploidy Terminology



Haploid history

Strawberry *faux hibrides*

Millardet, 1894

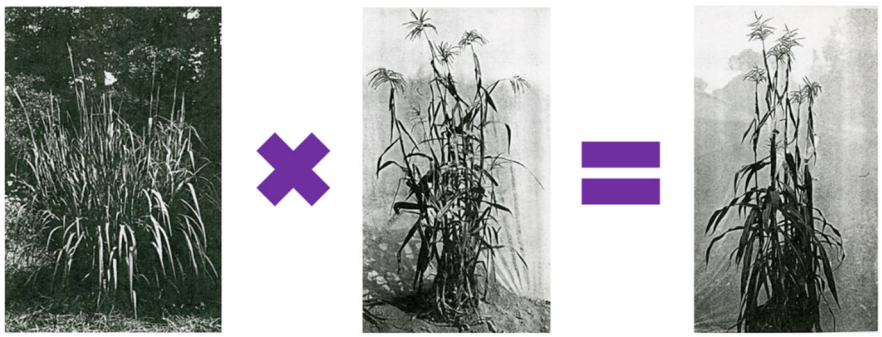
Giard A, 1903

"F. virginiana x F. eliator F1. Practically indistinguishable from F. eliator, but sterile." -- Manglesdorf & East, 1928.

Manglesdorf & East, 1927

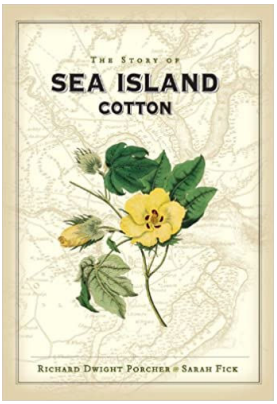
Patrogenesis from *Tripsacum* x *Euchlaena*

Collins & Kempton, 1916



'Man Cotton'

Harland 1920/1936



Recognition

Blakeslee, Belling, Farnham, & Bergner, 1922

Blakeslee & Belling, 1922

- Clausen & Mann, 1924
- Gains & Aase, 1926
- Das & Rahimulla, 1933
- Moringa and Fukushima, 1933
- Harland, 1936

The Marglobe tomato

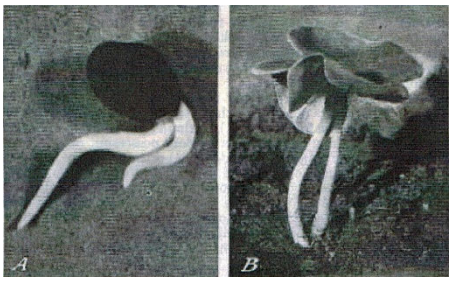
Morrison 1932

Obtaining haploids

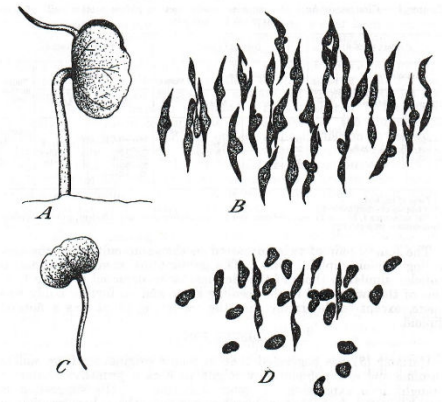
Review by **Dunwell, 2010**

Twin seedlings

Weber, 1938



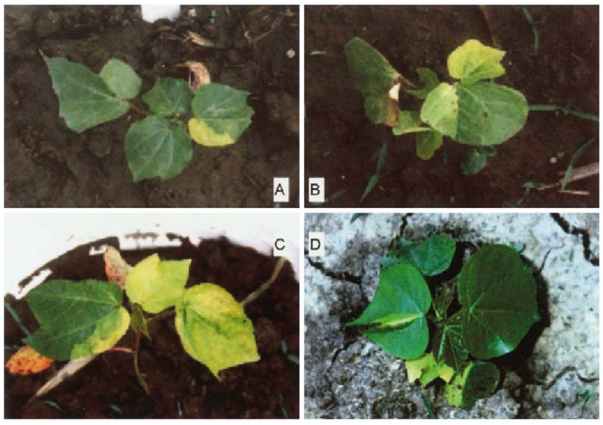
Morgan & Rappleye, 1950



Weber, 1938

Semigamy

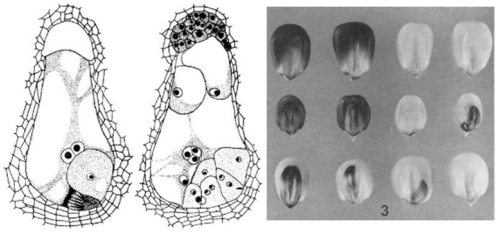
Turcotte & Feaster, 1963



Zhang J, W Guo, and T Zhang. 2002. Molecular linkage map of allotetraploid cotton (Gossypium hirsutum L. × Gossypium barbadense L.) with a haploid population. TAG. DOI:10.1007/s00122-002-1100-4

Indeterminate gametophyte/Haploid initiator

Kermicle, 1969, 1971; Lin, 1978; Hagberg and Hagberg, 1980



Egg sacs of Ig and ig ig maize – Lin, 1978

Irradiated pollen/stress

Turcotte & Feaster, 1963
Katayama, 1934

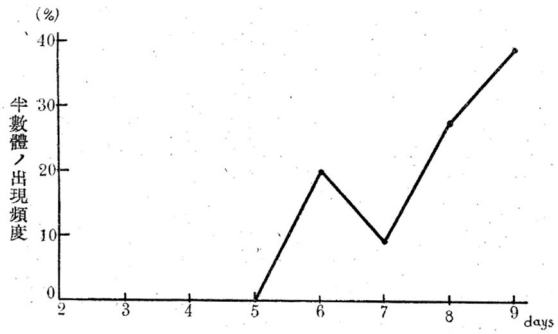
Naers et al., 1998

. A 4x leaf (center) and 2x leaves obtained from 4x blackberry pollinated with 100 and 150 kR irradiated Rubus cuneifolius pollen.

Pollen parent		Dosage	# Surviving	Offspring ploidy % of seedlings in each ploidy category								
Species	Ploidy		seedlings	n[w]	2x	3x	4x	5x	6x	aneu[x]	mixo[y]	χ^{2a}
R. spp[z]	4x	0 kR	432	183	1	1	67	1	7	19	4	
		50 kR	31	31	0	0	26	13	0	55	6	***
		100 kR	34	34	15	0	62	0	0	20	3	***
		150 kR	21	21	24	0	57	0	9	5	5	***

Delayed pollination

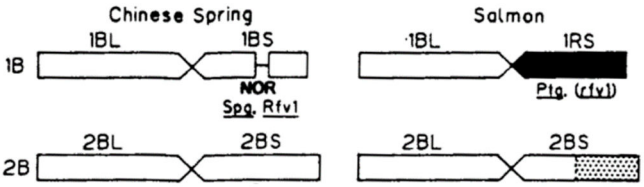
Kihara, 1940



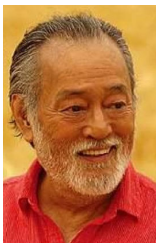
Alien cytoplasm

Reviewed in **Hsam & Zeller, 1993**

Kihara & Mukai, 1962; Tsunewaki & Mukai, 1990

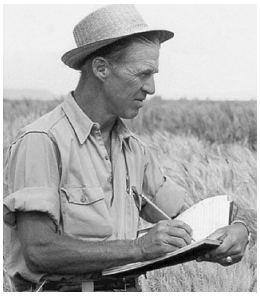


Gonjirô Inazuka, Cecil Salmon & Norin 10



Gonjirô Inazuka

Orville Vogel



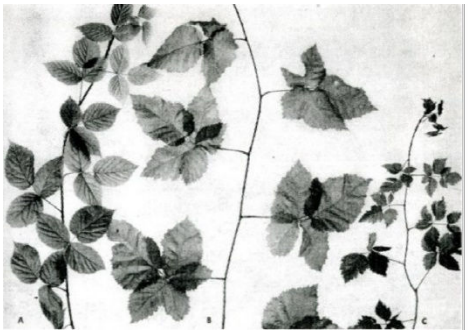
Norman Borlaug

Sennedjem and Iineferti in the Fields of Iaru A.D. 1922; original ca. 1295–1213 BCE

Somatic reduction

Britton & Hull, 1957

Leaves showing unstable sectors.



3 primocanes from somaclonal sectors

Super reduction, double reduction

Eg, **Thompson, 1962**

Androgenesis

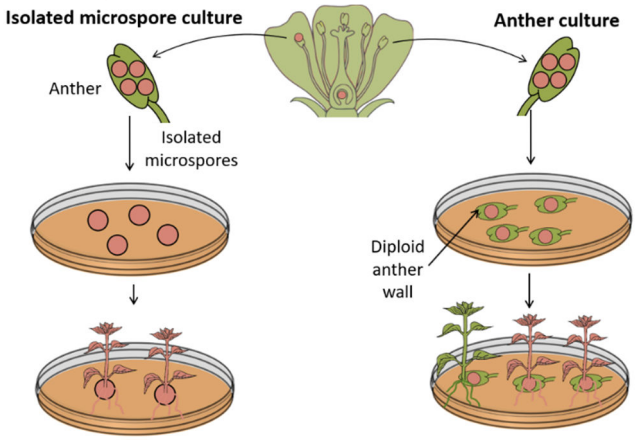


Diagram by course alum, Gurjot Singh

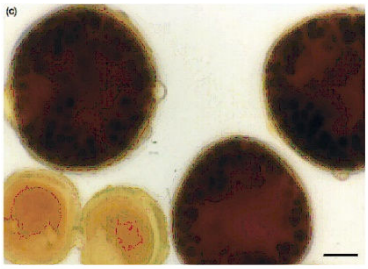
Shipra Guha Mukherjee

Satish Chandra Maheshwari

Dunwell, 2010

Vegetative cell division

Dimorphic pollen



Dimorphic pollen of poppy.

Fusion of vegetative and generative cell

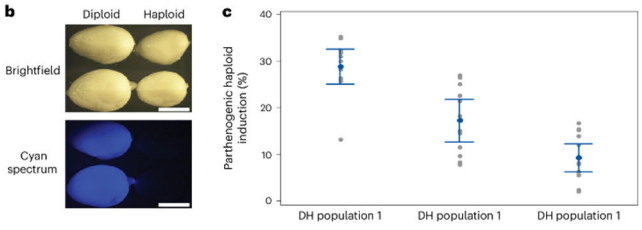
Dunwell, 2010

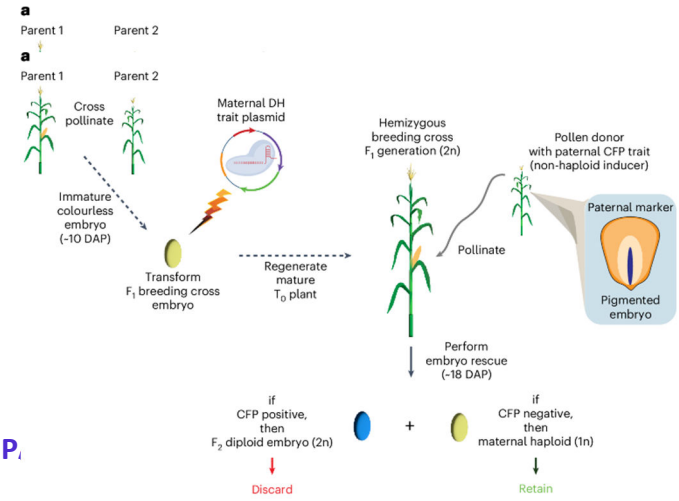
Petolino et al., 1988

TF-mediated parthenogenesis

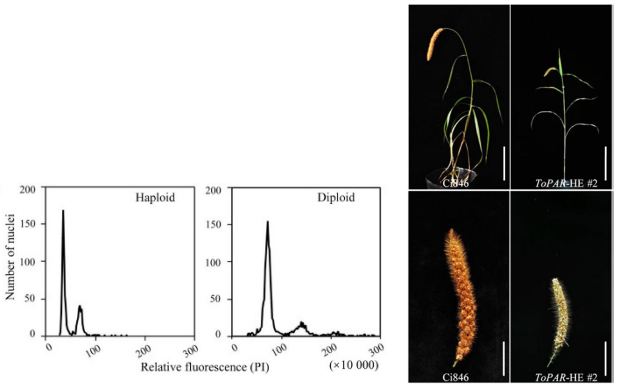
Bbm-

Ye et al. 2024





Huang et al 2024

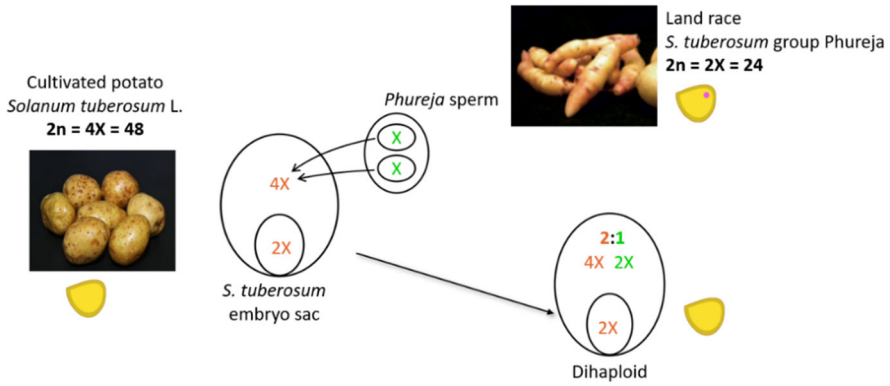


Chromosome-elimination based systems

4x-2x crosses in potato and alfalfa

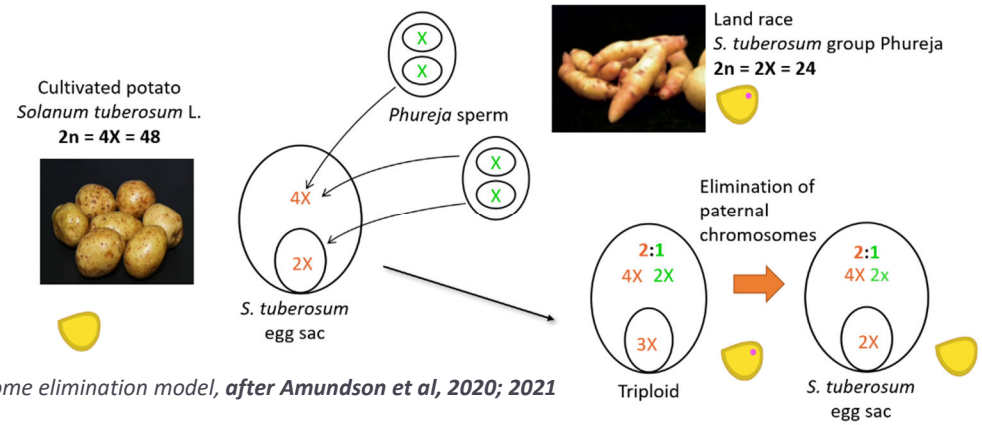
Hougas et al, 1963; Hermsen & Verdenius 1973; Peloquin et al, 1996
Ercolano et al, 2004

Montelongo-Escobedo & Rowe, 1969



The Montelongo-Escobedo & Rowe 1969 model, from Amundson et al, 2020

Reviewed in **Ercolano et al, 2004**



Chromosome elimination model, ***after Amundson et al, 2020; 2021***

Patrogenesis

Millardet 1894/Manglesdorf & East, 1927

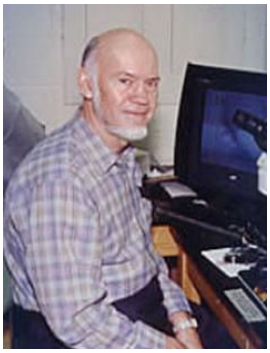
- Strawberry faux hibrides

Collins & Kempton, 1916

- Patrogenesis from *Tripsacum* x *Euchlaena*

Chromosome elimination

Subrahmayan and Kasha, 1973



https://www.plant.uoguelph.ca/kkasha

Age (days)	Cells with chromosome # of:								Ave. # of cells/ embryo
	7	8	9	10	11	12	13	14	
3	3		1		2		1		37
4		3		2	2	1	2	1	75
5	10	6	4	4	1	1	1	1	199
6	26	14	5	3			1	1	370
7	68	16	10	3	1				772
8	160	11	2	2		1			1178
9	177	41	11						2306
10	218	13	7	2	1				4710
11	431	22	7						7430

Bennett et al., 1976

Haploid metaphase cell in an embryo of barely x bulbosum.

Role of ploidy

Kasha, 1974

♀	♂	F_1
VV	BB	V
BB	VV	V
VV	BBBB	VBB
BBBB	VV	VBB
VVVV	BB	VV
VVVV	BBBB	VV
BBBB	VVVV	VV

Studies with trisomics

Ho and Kasha, 1988

VV + chromosome 1 × BBBB	→	stable
VV + chromosome 2 × BBBB	→	elimination
VV + chromosome 3 × BBBB	→	elimination
VV + chromosome 4 × BBBB	→	stable
VV + chromosome 5 × BBBB	→	stable
VV + chromosome 6 × BBBB	→	stable
VV + chromosome 7 × BBBB	→	stable

Wide crosses → patrogenesis

Laurie and Bennett, 1986

Ishii et al. 2016

Monocots	Dicots
74	35
Embryo rescue	Not required

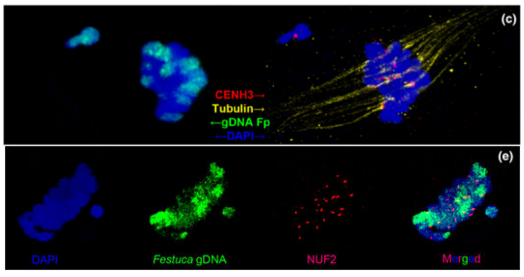
Nicotiana tabacum x N. africana

Rye

Secale cereale X *Zea mays*

Supporting evidence

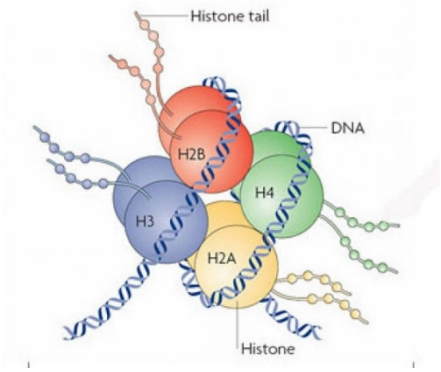
Majka et al, 2023



In situ hybridizations showing Top: fescue univalent without the spindle attached to it, and Bottom, more NUF2 localized to ryegrass metaphase chromosomes than to fescue ones

CENH3-mediated chromosome elimination

Ravi & Chan, 2010



FreeStockImages

https://www.ucdavis.edu/news/obituary-simon-chan-made-breakthroughs-plant-breeding

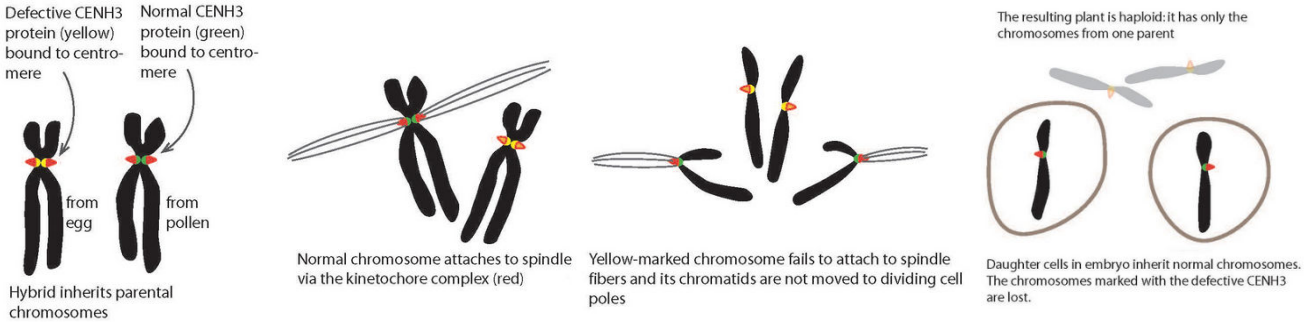
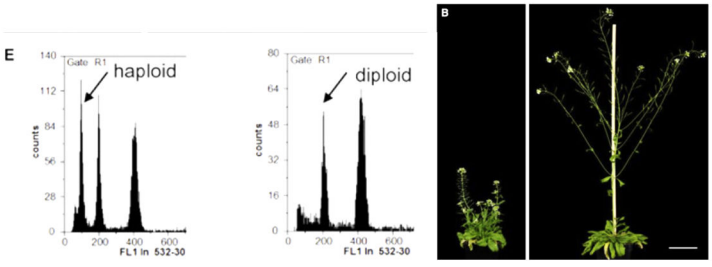


Figure 1. http://www.plb.ucdavis.edu/simonchan/about/research.html

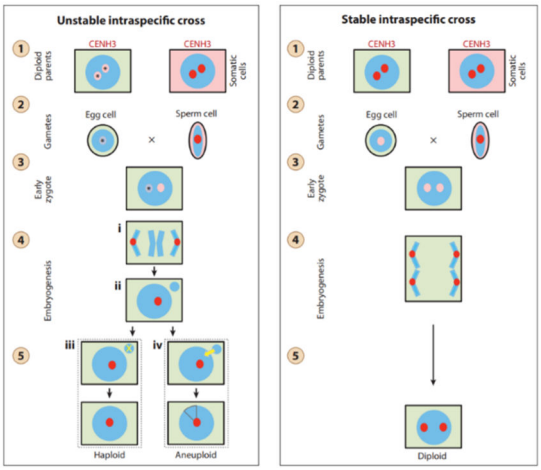
CenH3 loading factor Kinetochore Null2

Ahmadli et al, 2022



Chromosome elimination – over-arching principle

Ishii et al., 2016

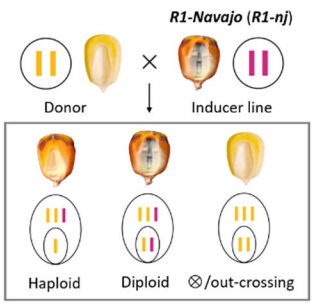


Fertilization-dependent systems

- NLD/MTL/ZmPLA1
  - NOT-LIKE-DAD/MATRILINEAL/ZmPHOSPHOLIPASE-A1
  - Lipid homeostasis
- DMP
  - DOMAIN OF UNKNOWN FUNCTION 679 MEMBRANE PROTEIN
  - Defective fertilization
- PHOSPHOLIPASE D3 (ZmPLD3)
  - Lipid homeostasis

Stock 6 in maize

Coe, 1959

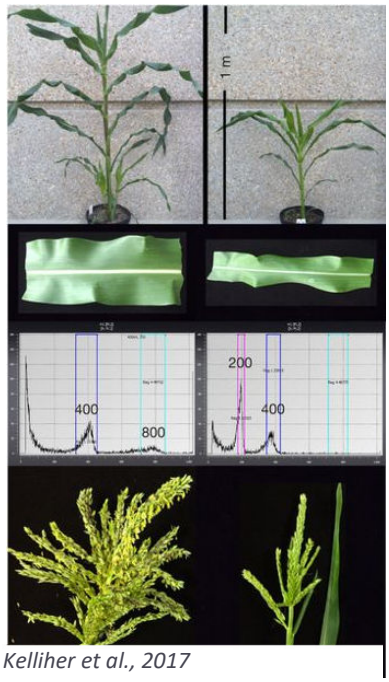


https://ipg.missouri.edu/faculty/coe.cfm

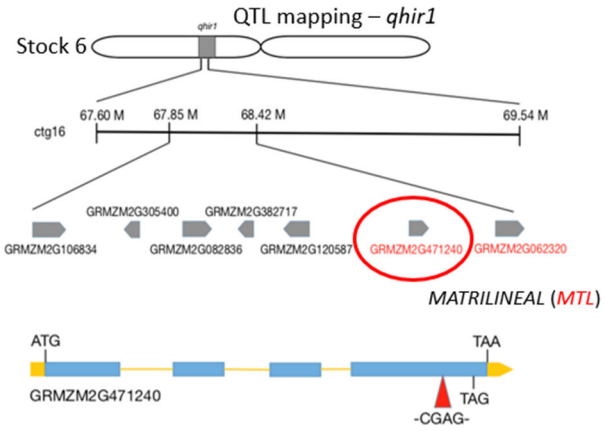
Chase, 1969

Zhao et al, 2013

Kelliher et al., 2017



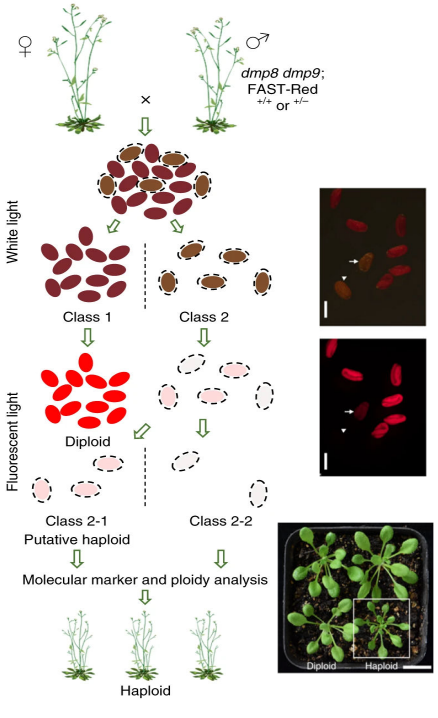
Kelliher et al., 2017



Gilles et al., 2017

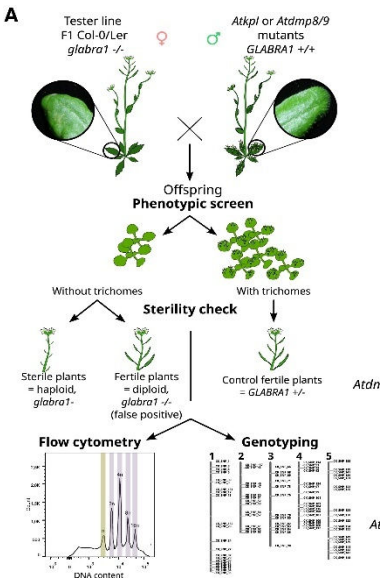
MTL substitutes in dicots

Zhong et al, 2020



Jacquier et al, 2023

Kokopelli mutants

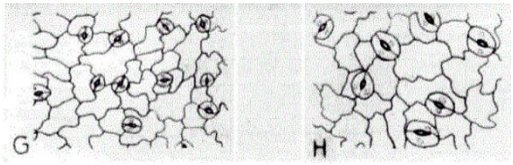


Mao et al., 2023

ECS1 & ECS2

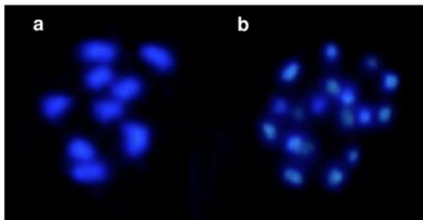
Identification of haploids

Guard cell size



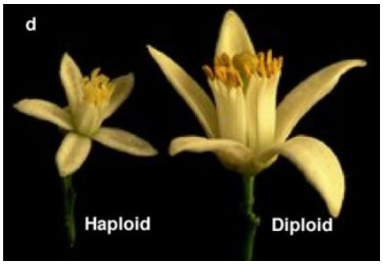
Eg from Christensen & Bamford, 1943. J. Hered. 34(4): 99-104

Cytologically

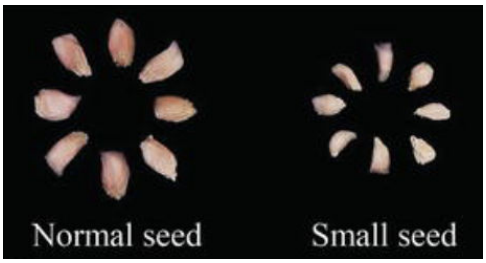


Aleza et al, 2009

Size

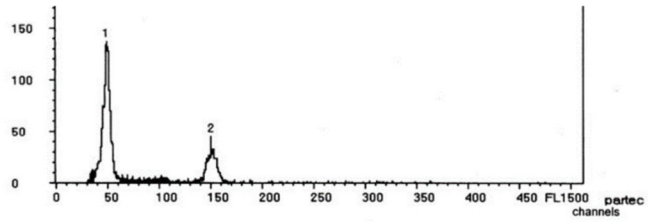


Aleza et al, 2009



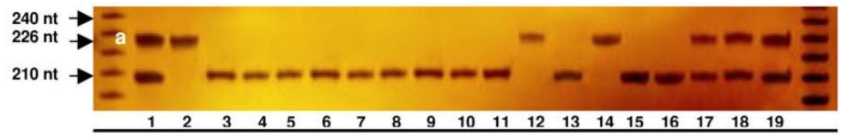
Yahata & Kunitake, 2019

Cytometry



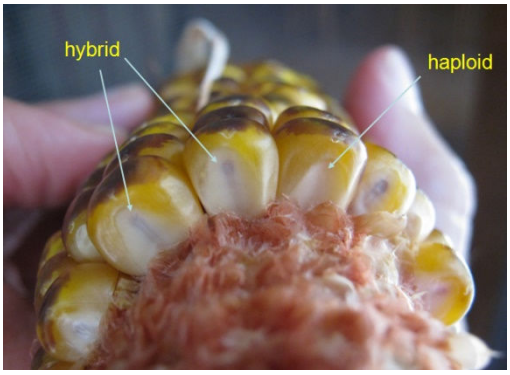
Aleza et al, 2009

Molecular markers

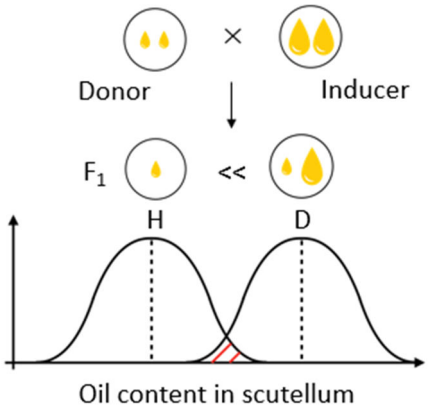


Aleza et al, 2009

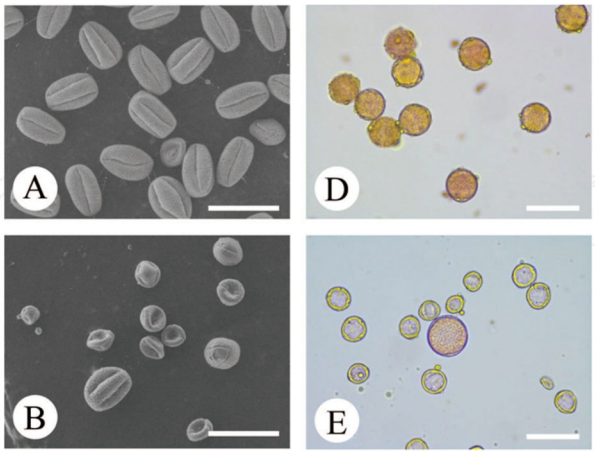
Phenotypic markers/metabolite levels



http://www.plantbreeding.iastate.edu/DHF/Service.asp



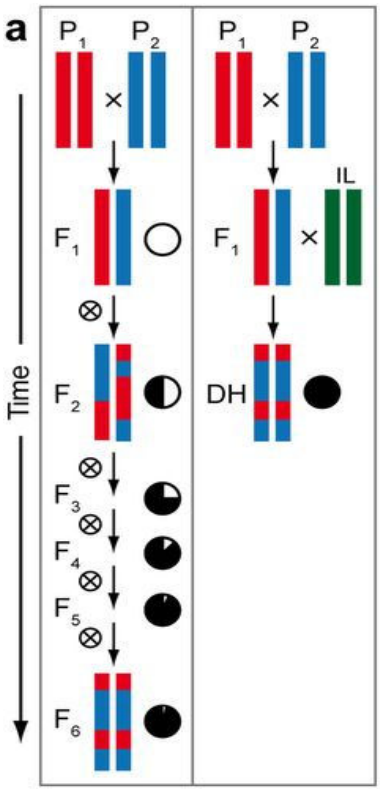
Pollen fertility



Yahata & Kunitake, 2019. Flowering and fruiting haploid and doubled haploid pummelo. DOI: 10.5772/intechopen.79180

Uses of haploids

Instant inbreds



Melchinger et al., 2013

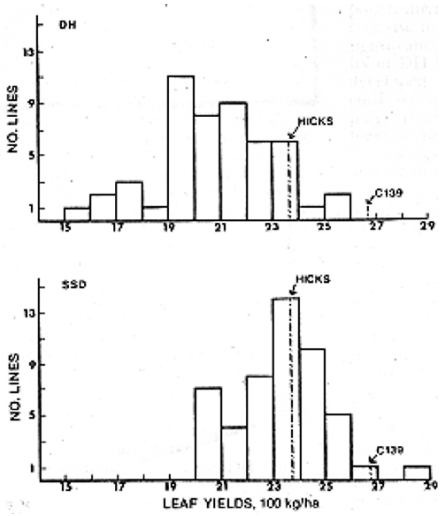
MINGO BARLEY

Mingo, a six-rowed spring feed barley (*Hordeum vulgare* L.), is the first barley cultivar developed by the doubled haploid method. It has a high yield, high test weight and good threshability. It took only 5 yr from the time when the parental lines were crossed to the time when Mingo was licenced on 28 March 1979. Breeder seed of Mingo is maintained by CIBA-GEIGY Seeds Ltd., Ailsa Craig, Ontario.

Ho & Jones. 1980. Mingo barley. Can J Plant Sci 60: 1-4.

Pros and cons

Dunwell 2010



*Average yields of dihaploid plants (top) compared with plants derived via single-seed descent. [**Schell et al., 1980**. Crop Sci 20:619-622]*

Geiger and Gordillo, 2009

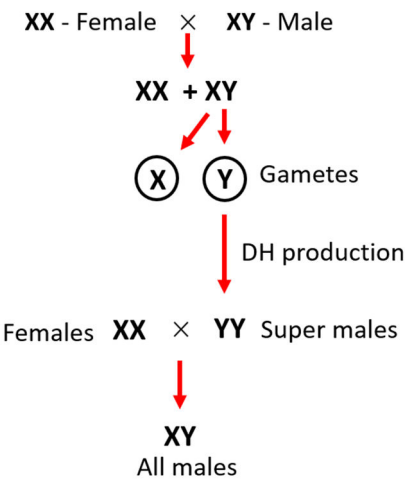
YY "supermale" asparagus

Heirloom varieties 'Mary Washington' & 'Martha Washington'

'Jersey Knight' - a supermale variety

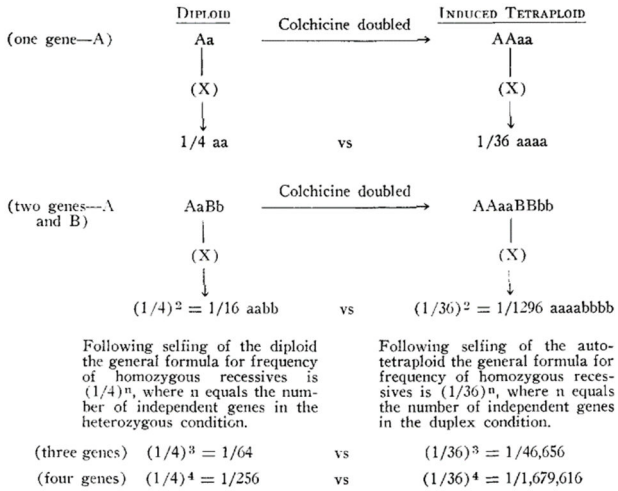
Chee-Kok Chin

Howard Ellison & Chee-kok Chin



Genetic analysis of qualitative and quantitative traits

Hougas & Peloquin, 1958

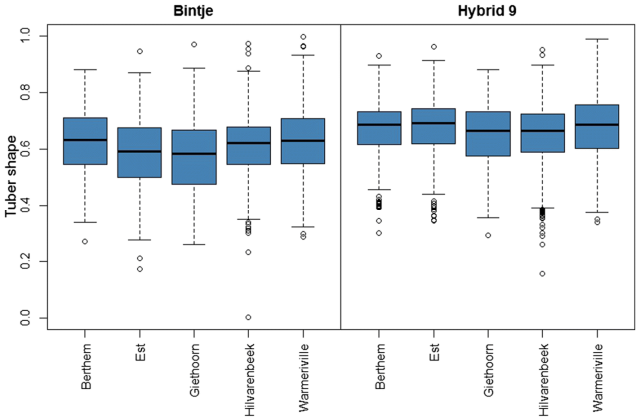


Differentiate between allo & autotetraploids

Diploidize autotetraploids

Jansky et al., 2016

https://janskylab.horticulture.wisc.edu/



Comparative yields in NW Europe of 4x Bintje can a 2x hybrid. Stockem J, M de Vries, E van Nieuwenhuizen, P Lindhout & PC Struik. 2020. Potato Research, 63: 345-366.

Novel ornamentals

Dunwell, 2010

Uncover recessive traits

Maluszynski & Kasha, 2002

Selection at gamete level

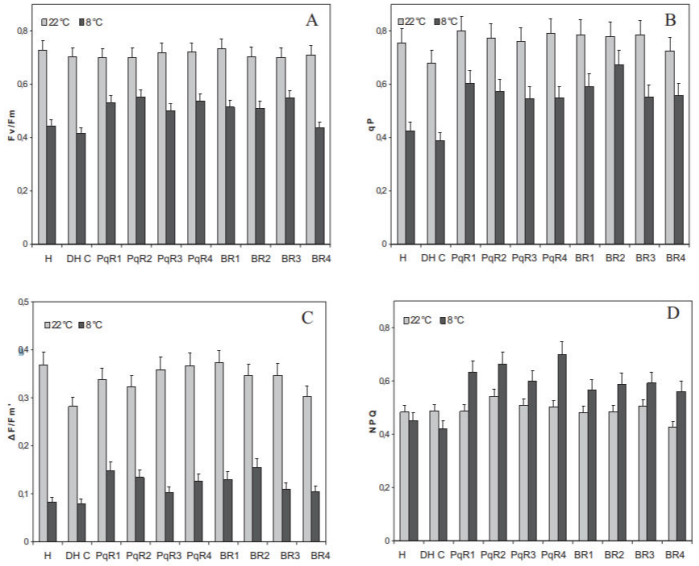
Ambrus et al., 2006; Darkó et al., 2011

Figure 2. Haploid Pelargonium 'Kleine Liebling'. Scale bar is 5 cm.

Treatment	Concn.	Nr. of anthers plated	% anthers responding	MDS/100 plated anthers	% MDS developed into plantlets	Nr. of plants grown to maturity	Nr. (%) of fertile DH plants grown to maturity	Nr. of seeds from DH plants (range)
Control		8000	50	124	14	[140][a]	[28] (20)	50–120
Paraquat (μM)	0.5	7000	20.8	40.2	10.1	154	10 (6.5)	8–95
	1.0	7000	13	22.3	3.45	43	5 (11.6)	3–167
Methionine plus riboflavin (μM)	10	5000	30	73	3.8	69	10 (14.8)	1–146
Menadione (μM)	100	5000	19.6	62	1.8	29	3 (10.3)	2–56
t-BHP (mM)	1	5000	28	49	5.4	54	8 (14.8)	1–120
	10	5000	18	32	4.4	21	2 (9.5)	7–28

[a] In the control, only a limited number of healthy plantlets were grown to maturity

"The optimal, Fv/Fm (A) and effective, F/Fm'(C) quantum yield of PS II, and the photochemical, qP (B) and non-photochemical, NPQ (D) quenching parameters in leaves of different DH maize lines and hybrid plants after cold treatment (at 8°C for 5 days). For control measurements, the plants were kept at 22°C"



Bioassay for mutagens

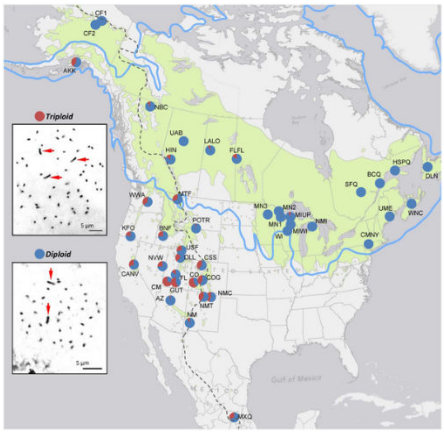
Pohlheim et al., 1977
Christianson & Chiscon, 1978

- Spontaneous mutation rate = 3×10^{-8}

Triploidy

Widespread triploidy in aspens

Mock et al, 2012



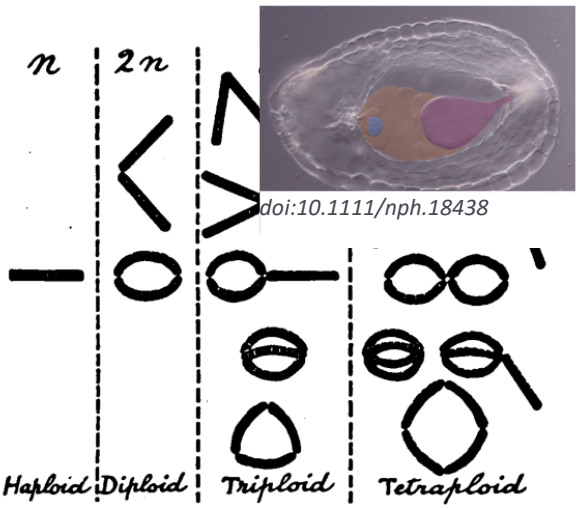
World's largest organism

https://catalystmagazine.net/can-save-pando/

Triploid block

Meiotic behavior

Belling & Blakeslee, 1927



doi:10.1111/nph.18438

Belling & Blakeslee, 1923. Note that the use of n to denote ploidy has since changed.

Disjunction – Ana I

	0	1	2	3	4	5	6	7	8	9	10	11	12	# cells	III/cell
Tomato				5	13	17	10	5						50	4.9
Lily								5	10	25	27	29	2	98	9.7
S. chaucha			1		1	2	3		7	2	6	2		25	7.1

Anaphase I and Binomial distribution

Concept from **Belling & Blakeslee, 1927**

$$(a+b)^7 = a^7b^0 + a^6b^1 + a^5b^2 + a^4b^3 + a^3b^4 + a^2b^5 + a^1b^6 + a^0b^7$$

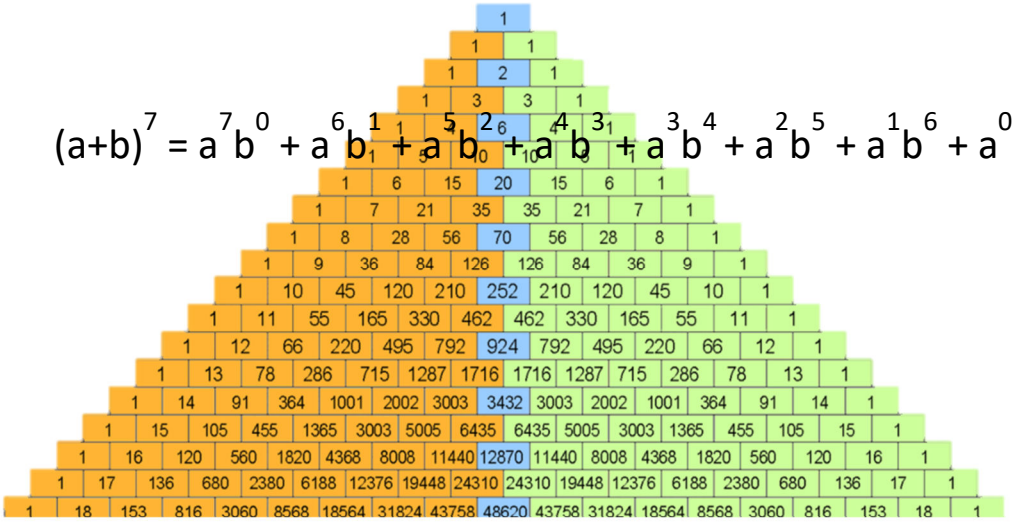


Image World-Mysteries.com

Gametic chromosome #	7 (n)	8	9	10	11	12	13	14 (2n)
Expected	b^7	$7ab^6$	$21a^2b^5$	$35a^3b^4$	$35a^4b^3$	$21a^5b^2$	$7a^6b$	a^7
Expected freq.	0	0.1	0.164	0.273	0.273	0.164	0.06	0
Expected (%)	0.8	5.5	16.4	27.3	27.3	16.4	5.5	0.8
Observed (%)	0.7	7.9	21.1	26.3	27.0	13.2	3.3	0.7

Datura case study

Satina and Blakeslee, 1937

Gametic chromosome #	12	13	14	15	16	17	18	19	20	21	22	23	24
Expected (%)	.025	.3	1.6	5.4	12.1	19.3	22.6	19.3	12.1	5.4	1.6	.3	.025
Observed (♂)	2.6	4.0	7.2	11.0	16.4	16.0	11.2	10.8	9.2	5.0	3.8	2.6	1.2
Observed (♀)	7.0	9.0	5.0	13.0	17.0	14.0	13.0	11.0	4.0	3.0	2.0	1.0	1.0

Other cases of binomial disjunction