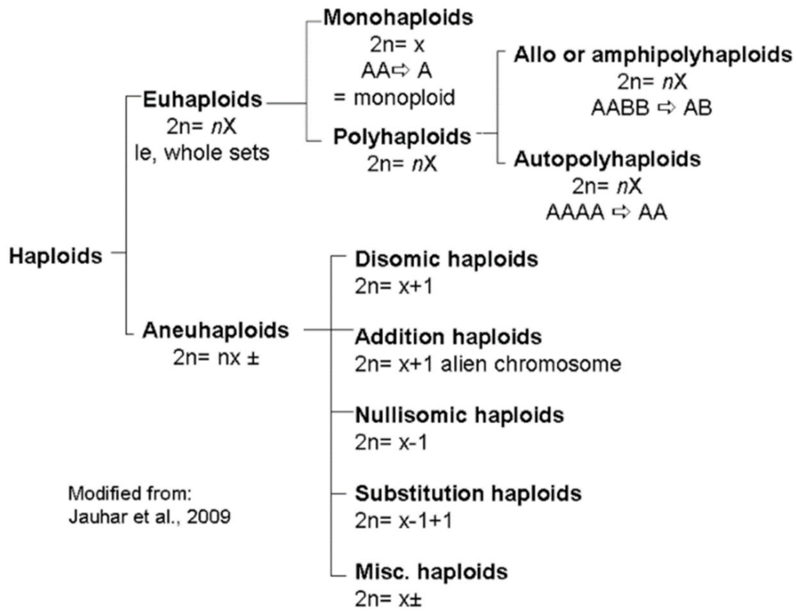
Dermail et al. 2024
Quiroz et al. 2024

Haploidy Terminology

Haploid: A sporophyte with the same chromosome number as the gamete



- Polyhaploids are sometimes called holoploids
- Note: The term "dihaploid" has two distinct definitions
  - in potato AAAA → AA (refers to a haploid from a 4x)
  - in tobacco SSTT → ST → SSTT (a 4x from a 2x from a 4x) = doubled haploid

Haploid history

Strawberry *faux hibrides*

Millardet, 1894

Crossed white fruit x red fruit → plants just like maternal parent

- But with red fruit, which he dismissed as inconsequential
- Also got plants just like the paternal parent

Giard A, 1903

Thought they were like the sea urchin patriclines

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

Manglesdorf & East, 1927

Attributed most to sloppy technique, but agreed that the maternal types might be doubled haploids

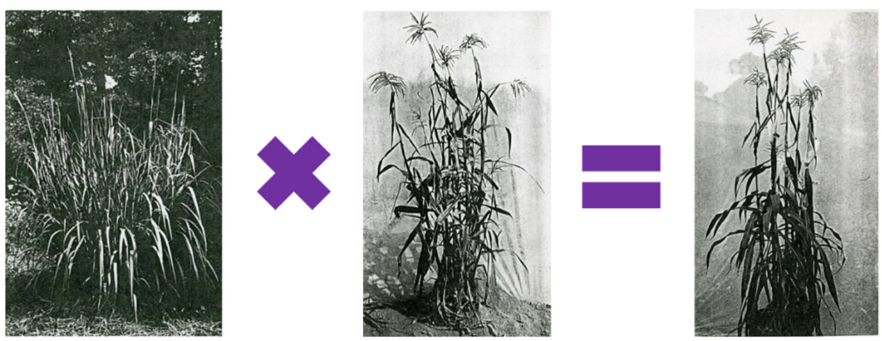
- Maternal types → selfing, pseudogamy
  →doubled haploids or apomicts
- Paternal types → true hybrids with paternal dominance

Gets credit for figuring out they were haploids; credit not really justified

Patrogenesis from *Tripsacum* x *Euchlaena*

Collins & Kempton, 1916

Recovered paternal types in crosses of *Tripsacum* x *Euchlaena*



Grown by English settlers in 1786 on sea islands of Georgia and South Carolina.

'Man Cotton'

Harland 1920/1936

1920 - Man Cotton described

- So called by the workers b/c it bore no cotton
- One per 3-4K plants of Sea Island cotton in Trinidad and St. Vincent
- Smaller, weaker, sterile, stayed green longer

1936 - Recognized as haploids from twin seedlings by Harlan 1936

Recognition

Blakeslee & Belling, 1922

Blakeslee, Belling, Farnham, & Bergner, 1922

1921 - **AD Bergner** recognized that the *Datura stramonium* reported by Blakeslee et al. 1922 were haploids

- Clausen & Mann, 1924 - tobacco haploids
- Gains & Aase, 1926 – *Triticum compactum* haploids
- Manglesdorf & East, 1927 – strawberry false hybrids = haploids
- Das & Rahimulla, 1933 – rice haploids
- Moringa and Fukushima, 1933 - *Brassica napellis* haploids
- Harland, 1936 - ‘Man Cotton’ = 2x haploid of sea island cotton isolated in Trinidad (Harland, 1936), which had come to his attention in 1920 (Harland, 1920).
-

However natural occurrence was too infrequent to be exploited in plant breeding.

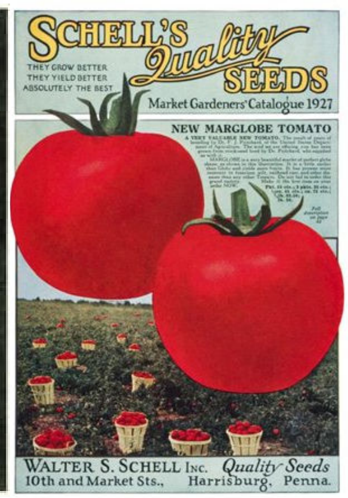
The Marglobe tomato

Morrison 1932

'Marglobe' tomato

- The first crop cultivar developed by doubling a haploid that came from a twin.
- From 1917 cross by FJ Pritchard between Marvel & Globe
- Released in 1925 by USDA, and parent to major varieties since then

FJ Pritchard



Obtaining haploids

Reviews by **Dunwell, 2010** & **Hooghvorst & Nogués, 2021**

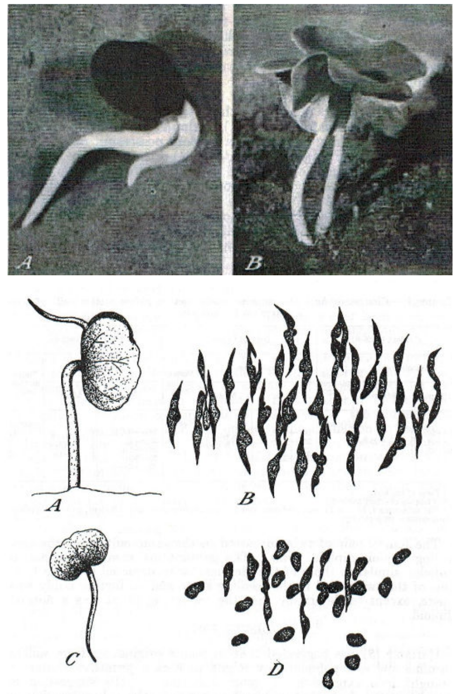
Twin seedlings

Weber, 1938

A synergid develops along with the fertilized egg, leading to twin embryos in the seed

- Source of the greatest number of 'natural' haploids

Morgan & Rappleye, 1950



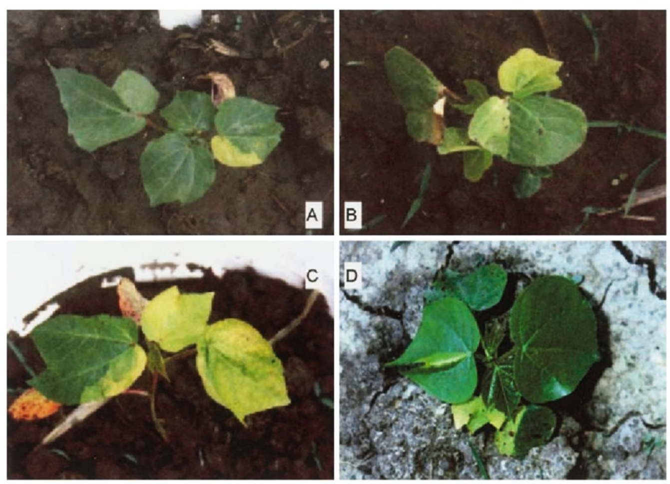
Weber, 1938

Semigamy

Turcotte & Feaster, 1963

The ♀ and ♂ nuclei do not always fuse at fertilization

- Tissues are binucleate
- Eventually, sectors with only one nucleus appear

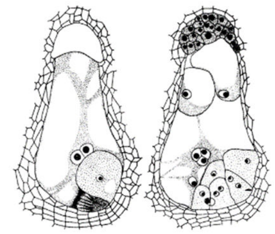


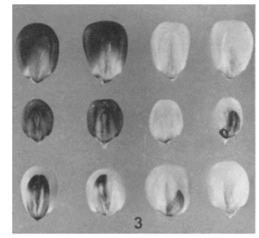
Zhang J, W Guo, and T Zhang. 2002. Molecular linkage map of allotetraploid cotton (Gossypium hirsutum L. × Gossypium barbadense L.) with a haploid population. TAG. DOI:10.1007/s00122-002-1100-4

Indeterminate gametophyte/Haploid initiator

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

The *ig* mutation in maize leads to up to 4 mitoses during megagametophyte development, so can end up with 0 to 5 egg cells





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

- Can give maternal or paternal haploids
- After pollination, the ♂ nucleus develops in the cytoplasm of the egg, resulting in a paternal haploid
- This is a rapid method of changing cytoplasm
- Similar to haploid initiator gene in barley

Irradiated pollen/stress

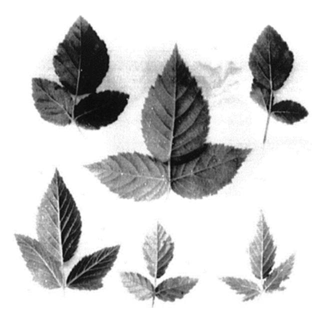
Turcotte & Feaster, 1963
Katayama, 1934

Katayama - Got 16/91 seedlings with X-rayed pollen in *T. monococcum*

- Got none if X-rayed the styles

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	***

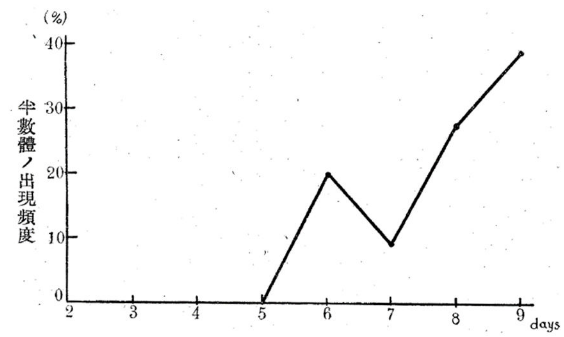
Also: heat, toluidine blue, maleic hydrazide, brassinolide (refs in Dunwell, 2010)

Delayed pollination

Kihara, 1940

Found a *T. monococcum* genotype that spontaneously gave 0.5% haploids

- Frequency increased to 13.66% if used X-rayed pollen
- Frequency of ~40% obtained by delaying pollination for 9 days
- Frequency of twins also increased



Alien cytoplasm

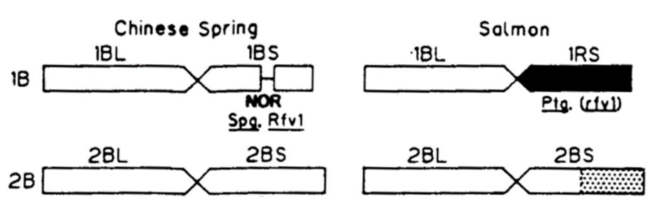
Reviewed in **Hsam & Zeller, 1993**
Kihara & Mukai, 1962; Tsunewaki & Mukai, 1990

Wheat cv Salmon with cytoplasm from *Aegilops caudata* → 30%, haploids

- Cytoplasms C, C^u, M^u, M^t, S^1, and S^v → 70% haploids in Salmon
- Of these, S^v from *Ae. variabilis* and M^u from *Ae. uniaristata* or *Ae. kotschyi* do not produce deleterious effects

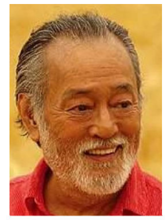
Due to an interaction between the cytoplasm and a 1BL/1RS translocation present in Salmon

- 1RS has *Ptg* gene for parthenogenesis → must be present
- 2BS has *Spg* gene for suppression of parthenogenesis → must be absent



Gonjirô Inazuka, Cecil Salmon, Orville Vogel & Norin 10

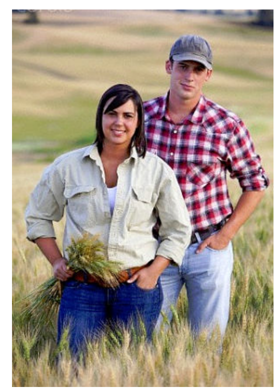
- ‘Norin 10’, bred by **Gonjirô Inazuka**, 1938
  - From ‘Daruma’ landrace
  - In turn, derived from centuries-old Korean landraces
- Cecil Salmon
  - USDA Agronomist in Kansas
  - Attached to occupying forces in Japan under McArthur
  - Came across Norin 10
  - Sent to USDA Small Grains Collection
- Orville Vogel, Washington State
  - Used Norin 10 to breed ‘Gaines’ in 1962
  - 1st variety to surpass 100 bu/ac
- Norman Borlaug
  - Obtained in 1952
  - Used by Borlaug at CIMMYT
  - Triggered the Green Revolution


Gonjirô Inazuka


Orville Vogel


Norman Borlaug


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



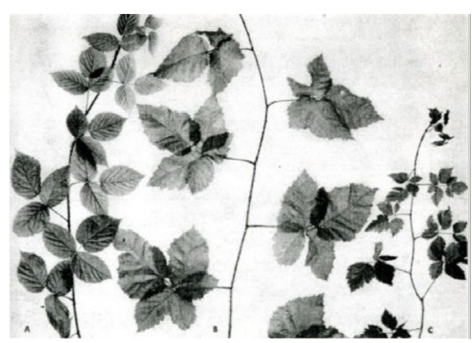
Somatic reduction

Britton & Hull, 1957
Sorghum, *Rubus*

In *Rubus*, somatic reduction takes place in various sectors.


Leaves showing unstable sectors.

- If a node is involved, can plant the node to get a plant with fewer chromosomes.


Three primocanes from somaclonal sectors

Super reduction, double reduction

Eg, **Thompson, 1962**

As above, but there is a flower in the sector where reduction took place.

- Thus gametes produced by a sector where somatic reduction has taken place.

Androgenesis

Anther or microspore culture- only works for gramineae, solanaceae, crucifereae, and a few others, such as asparagus and *Betula*

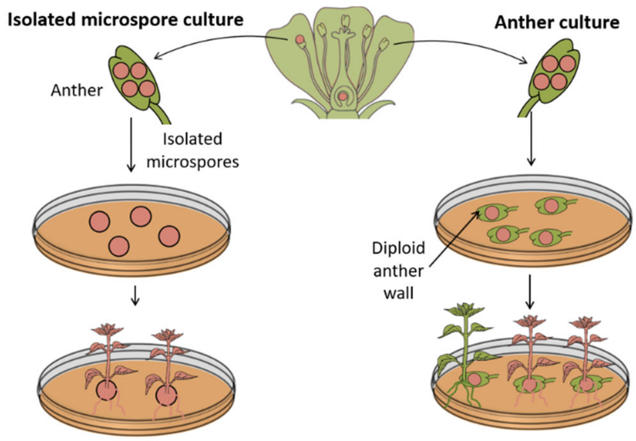
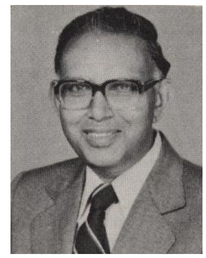


Diagram by course alum, Gurjot Singh

Shipra Guha Mukherjee



Satish Chandra Maheshwari

Dunwell, 2010 -

3 pathways

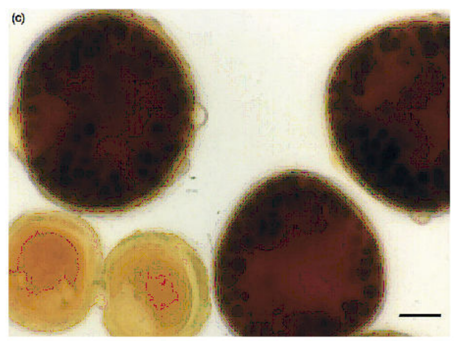
Vegetative cell division

The vegetative cell in the pollen divides to form an embryo

Dimorphic pollen

Some species can produce dimorphic pollen

- 1st pollen division is symmetric rather than asymmetric
- If cultured, will go ahead and produce an embryo



Dimorphic pollen of poppy.

Fusion of vegetative and generative cells

- After the 1st mitotic division in the microspore

Dunwell, 2010

Merits

- >200 species
- Rice – South East Asia

Drawbacks

- High genotype dependency
- Leguminous and woody plants – recalcitrant
- Arabidopsis thaliana - recalcitrant
- Regeneration from somatic tissue – confused with doubled haploids

Petolino et al., 1988
Worked with anther culture of a 3-way hybrid of maize

- Two plants (3.5% regenerated)
- Crossed those 2 plants to get an F1, then got the S1
    - Regeneration frequency was 23.4%

Chromosome-elimination based systems

4x-2x crosses in potato and alfalfa

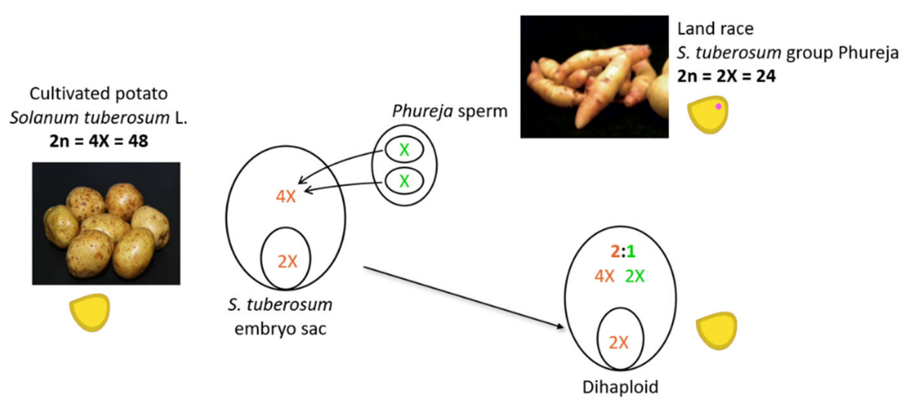
Hougas et al, 1963; Hermsen & Verdenius 1973; Peloquin et al, 1996

Alfalfa: 4x × 2x → 1 in 1000 is 2x
Potato: 4x × Phureja pollinator in potato (*S. tuberosum* Group *Phureja,* 2n = 2x = 24), genotype IVP 101

Approximately 1 haploid seed per 10 pollinations
Montelongo-Escobedo & Rowe, 1969
Proposed a model whereby the two sperm nuclei fertilize the endosperm.

- The unfertilized egg develops anyway

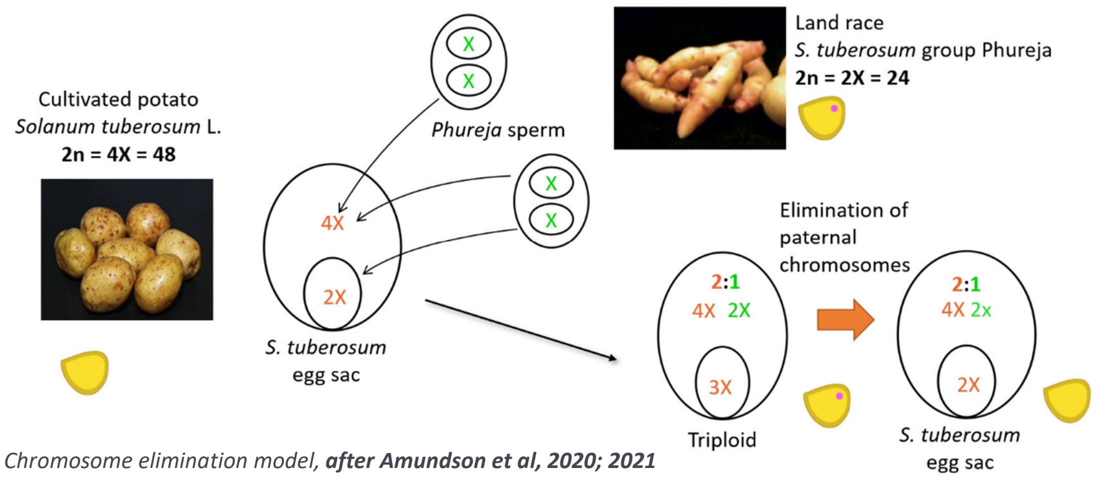
Endosperm is 6x. Note that fertilization of the central cell by two monoploid sperm is equivalent to being fertilized by one diploid sperm cell, as would normally happen when two tetraploids are crossed with each other.



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

Reviewed in **Ercolano et al, 2004**

- Tuberosum haploids have *phureja* DNA in them
- How does *phureja* DNA get into the embryo?
- Thought now is that a 3x embryo is formed, and the *phureja* chromosomes get eliminated. Heterofertilization required.



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

Patrogenesis

Millardet 1894/Manglesdorf & East, 1927

- Strawberry faux hibrides

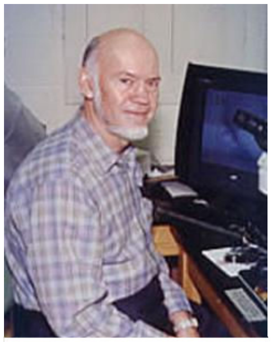
Collins & Kempton, 1916

- Patrogenesis from *Tripsacum* x *Euchlaena*

Barley

Subrahmayan and Kasha, 1973

Hybrid embryos of barley × *H. bulbosum* lose the *bulbosum* chromosomes (both are 2n = 2× = 14)



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

Results differ in interploidy crosses

Only 1V:2B ratios are stable

♀	♂	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

- Factors on both arms of chromosome 2 and short arm of chromosome 3 control chromosome elimination

Wide crosses ➔ Patrogenesis

Laurie and Bennett, 1986

The barley × bulbosum example is an example of a wide hybrid.

The original haploid and *Euchlacna* haploids described in the history section came from wide crosses.

- Following an interspecific cross, maternal chromosomes are lost
- All chromosomes come from male
- Source of first report of a haploid in *Fragaria*
- First bona fide documentation of a haploid
    - Recovery of *Euchlacna* genotype following cross of *Tripsacum* × *Euchlacna*
- Probably due to a chromosome elimination mechanism

Ishii et al, 2016

Nicotiana tabacum x N. africana

Rye
Secale cereale × *Zea mays*

Monocots	Dicots
74	35
Embryo rescue	Not required

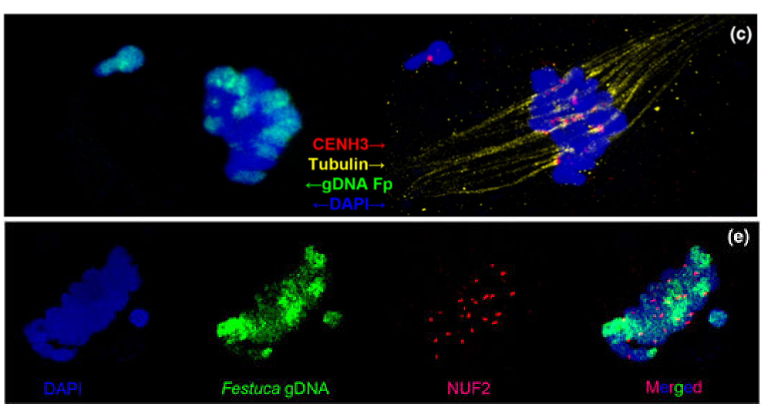
Probably works by spindles from 1 spp not recognizing kinetochores from another spp. in the zygote & developing embryo

Some supporting evidence

Majka et al, 2023

In *Festuca* × *Lolium* crosses, fescue chromosomes get eliminated

- There are non-synonymous SNPs between the fescue & ryegrass genes for kinetochore proteins NDC80 and NNF1
    - Follow with antibodies to NUF2, a component of the NDC80 outer kinetochore complex
- The fescue alleles get silenced in the hybrids
    - Perhaps affecting the ability of the fescue chromosomes to attach to the spindle, leading to their elimination

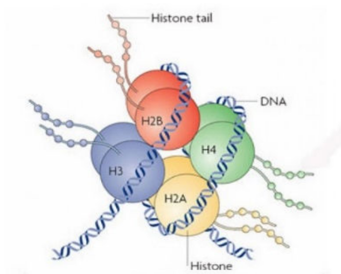


In situ hybridizations showing Top: fescue univalent without the spindle attached to it, and Bottom, more NUF2 localized to ryegrass metaphase chromosomes than to fescue ones

CENH3-mediated chromosome elimination

Ravi & Chan, 2010

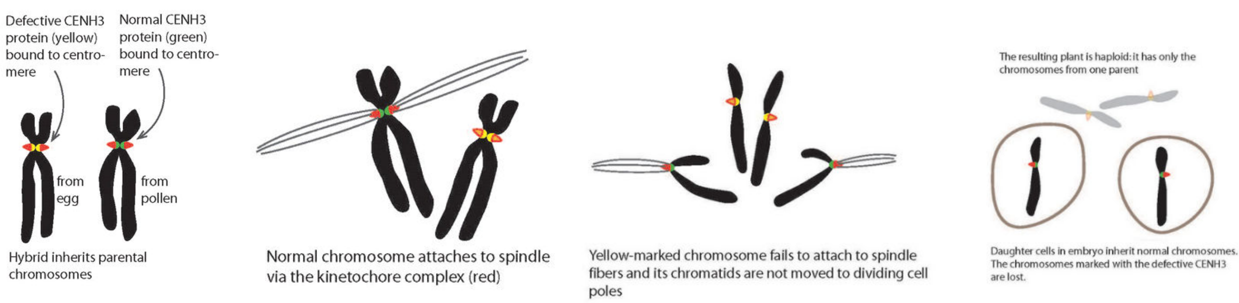
Chimeric gene of CENH3 with the tail domain of H3 in a recessive for cenh3 (null is embryo lethal)



FreeStockImages

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

Crossing mutant × WT → mutant chromosomes get eliminated, presumably due to issues of spindle fiber attachment to the centromere



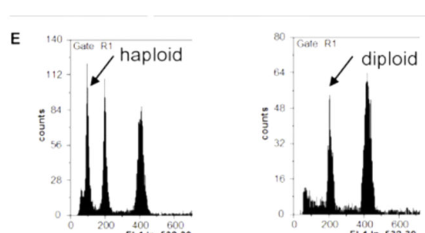
http://www.plb.ucdavis.edu/simonchan/about/research.html

CenH3 loading factor Kinetochore Null2

Ahmadli et al, 2022

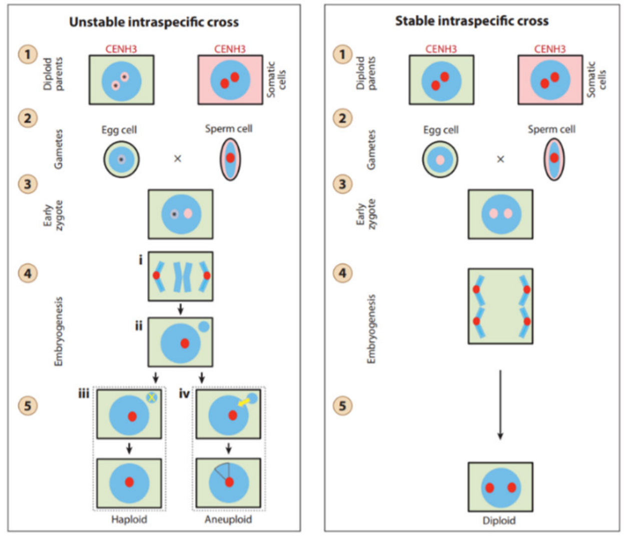
Knockouts for Null2 have reduced amounts of CenH3

- Knl2 → *knl2 knl2* × WT → F1
- Haploid frequency = 1% @ 25°C
    - 10% @ 30°C



Chromosome elimination – over-arching principle

Ishii et al., 2016



Solidifies chromosome elimination as a common phenomenon

- Probably works by spindles from 1 spp not recognizing kinetochores from another spp. in the zygote

Fertilization-dependent systems

All interfere with double fertilization

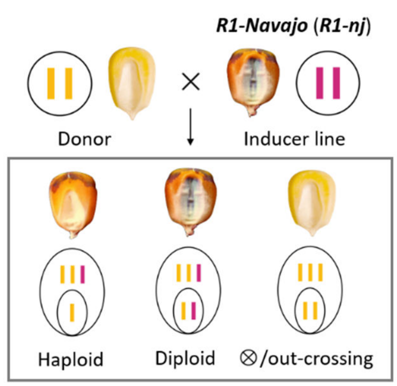
- NLD/MTL/ZmPLA1
  - NOT-LIKE-DAD/MATRILINEAL/ZmPHOSPHOLIPASE-A1
  - Lipid homeostasis
- DMP
  - DOMAIN OF UNKNOWN FUNCTION 679 MEMBRANE PROTEIN
  - Defective fertilization
- PHOSPHOLIPASE D3 (ZmPLD3)
  - Lipid homeostasis

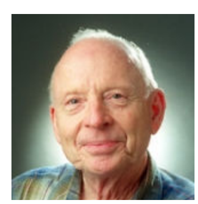
Stock 6 in maize

Coe, 1959

Found Stock 6

- Induced 1-2% haploids when used as a pollen parent
- Ancestor to current inducer lines





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

Chase, 1969

Was a plant breeder with DeKalb (today part of Bayer)

- ♀genotypes varied 10-20x in frequency of haploid production
    - from 2/10,000 to 3/1000
- Pollen parents differed ten-fold in their effectiveness, from 0.17/1000 to 1.7/1000
- Haploids from doubled haploids had increased frequency of haploid production:
    - Parent stock = 1/1000
    - Doubled haploids = 8/1000
- Best frequency obtained was 3% haploids
- Today get ~10% induction frequency

$^{1}/_{20}$ of DeKalb’s research effort in inbred development was geared towards haploid product

- yet, incorporated into ¼ of DeKalb's hybrids by the 1980's

Zhao et al, 2013

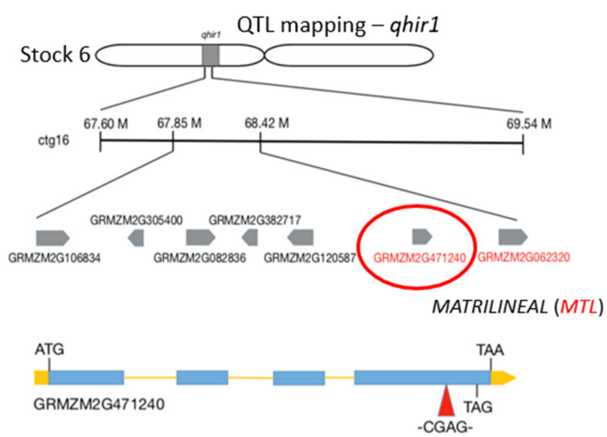
Mechanism is chromosome elimination

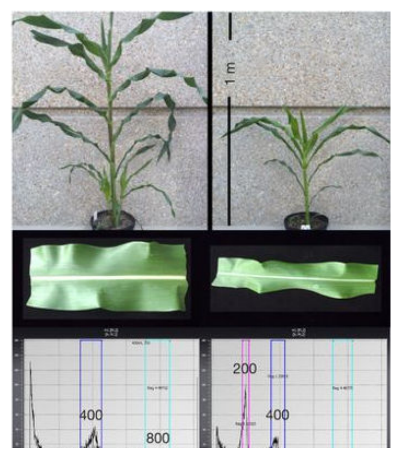
- *need to question this conclusion now that the gene has been cloned*
- *Paternal DNA is found in embryo, supporting chromosome elimination*

Kelliher et al, 2017

Matrilineal is the gene responsible for Stock 6

- A 4-bp insertion leads to frame shift mutation in a *pollen-specific phospholipase = qhir1*
- A new deletion via editing gives 6.7% haploids!





Kelliher et al., 2017

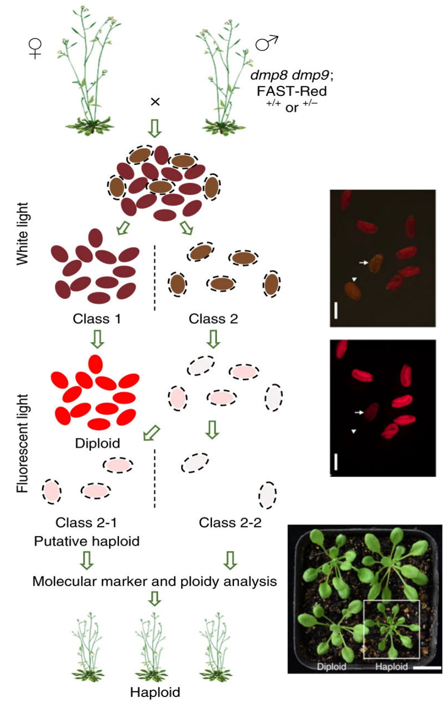
Paternal DNA can be present, again pointing to paternal chromosome elimination as the mechanism

Gilles et al., 2017

Independently cloned the same gene, but named it *Not Like Dad*

MTL substitutes for dicots

Zhong et al, 2020



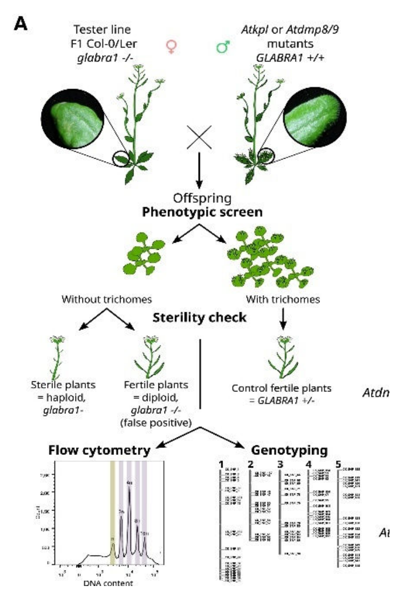
MTL (*qhir1*) has no orthologs in dicots

- But there is *qhir8*
- DMP (DOMAIN OF UNKNOWN FUNCTION 679 membrane protein)
- Found arabidopsis orthologs, *AtDMP8* and *AtDMP*
- Knocking them out leads to ~2% haploid formation
- Combine with RFP as a marker

Jacquier et al, 2023

Kokopelli mutants

- Defects in double fertilization
- Up to 0.3% haploids



Mao et al., 2023

ECS1 & ECS2

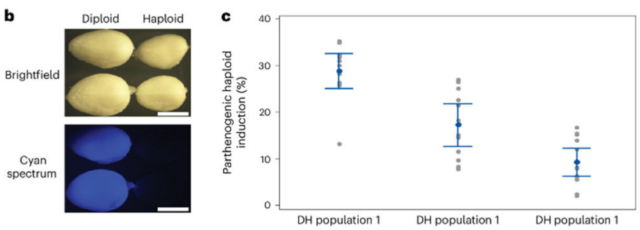
- These play a role in double fertilization
- When defective, double fertilization does not always take place, leading to haploids

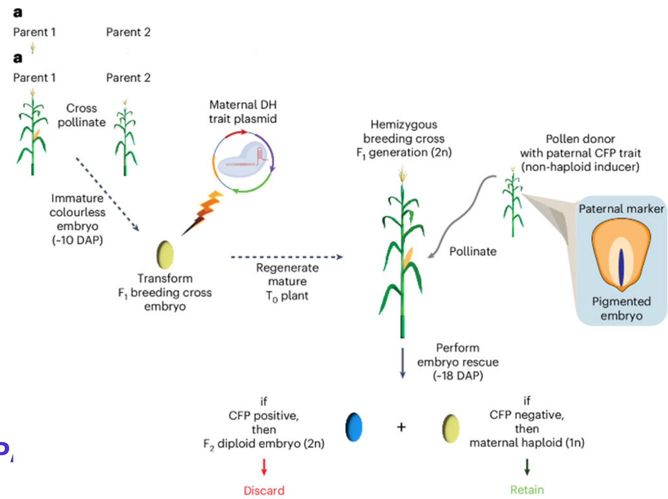
TF-mediated parthenogenesis

Bbm-

Ye et al. 2024

- Fertilization independent system based on TFs





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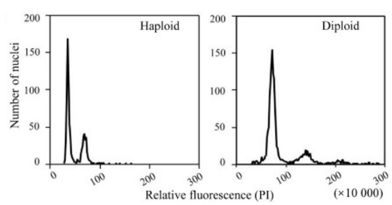
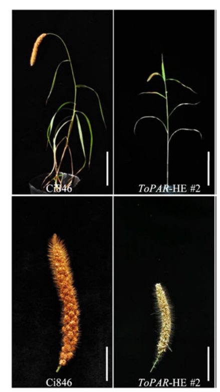
Huang et al 2024

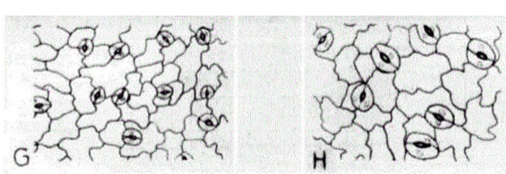
- Dandelion PAR functions in foxtail millet





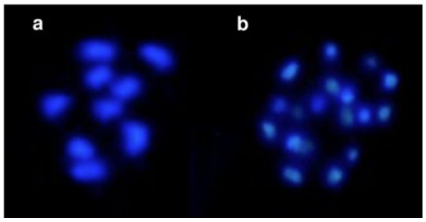
Identification of haploids

Guard cell size



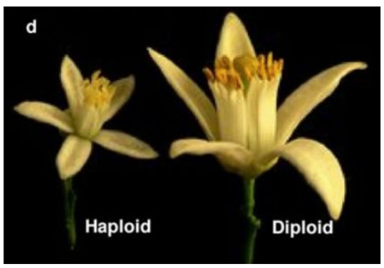
Eg from Christensen & Bamford, 1943. J. Hered. 34(4): 99-104

Cytologically

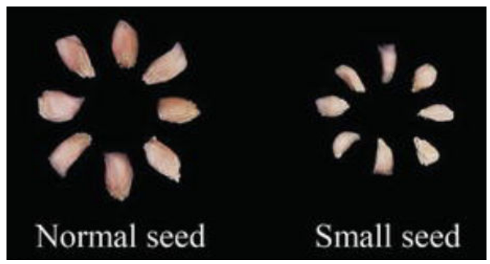


Aleza et al, 2009

Size

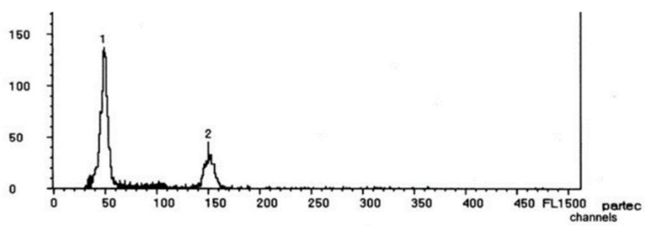


Aleza et al, 2009



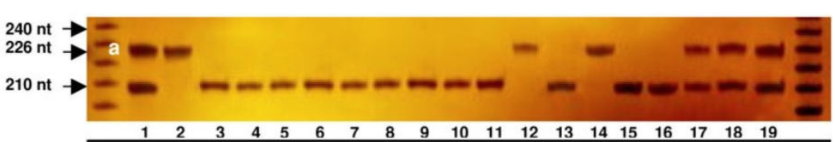
Yahata & Kunitake, 2019

Cytometry



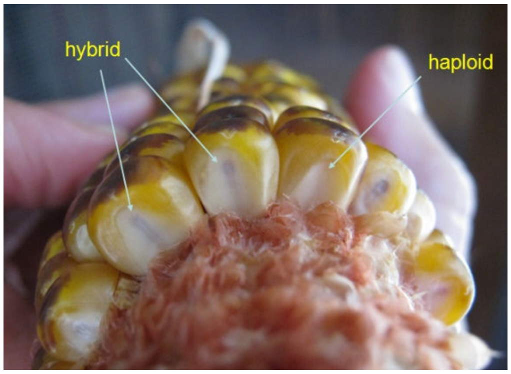
Aleza et al, 2009

Molecular markers

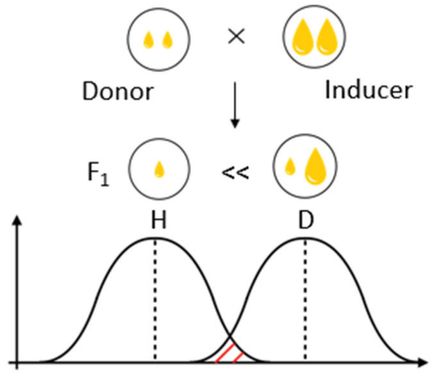


Aleza et al, 2009

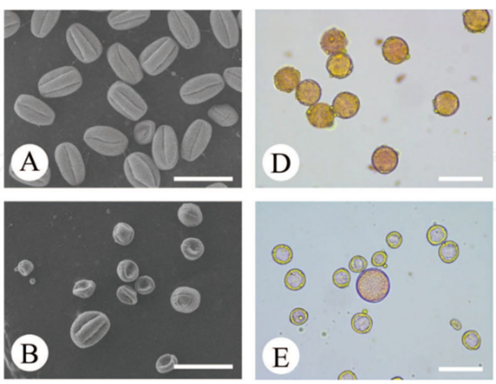
Phenotypic markers/metabolite levels



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

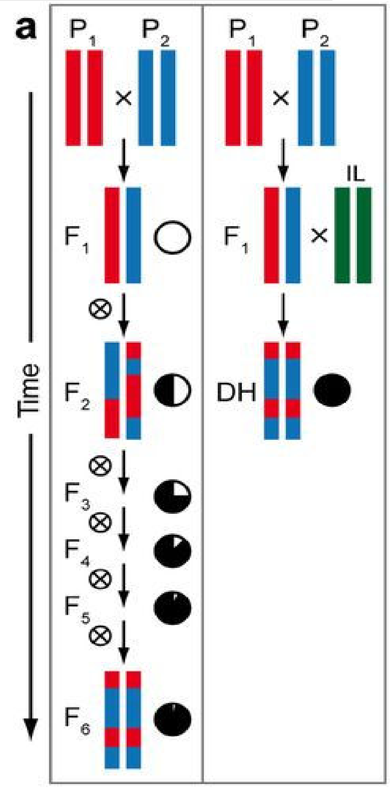
Instant inbreds

1925: Marglobe from a twin seedling
1952: Chase – 1st to use haploidy inbreeding

- Requires 1 generation instead of 7 or 8
- Reduces field expenses
- Increases efficiency of MAS
- Used in over 200 spp

1978/9: 'Mingo' barley - the highest-yielding Canadian barley cultivar of its time

- Derived via chromosome elimination
- Ciba-Geigy [became Novartis became Syngenta] saw this technique as a fast way to enter the market and start a program from scratch



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

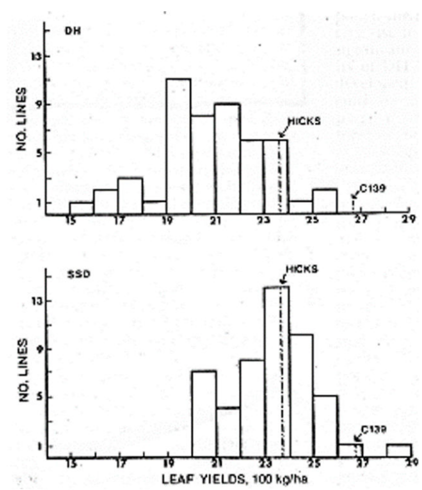
2007: 3 of top 5 red spring wheat varieties are doubled haploids (ref = Dunwell 2010)

- 99% of acreage of soft white spring wheat is from anther culture: 'AC Andrew'

2017: 298 cultivars/inbreds listed

Have no opportunity to select during the selfing process

- Need to evaluate huge numbers of doubled haploids to compensate for this
- Linkage drag is present
- Requires very skilled labor and special facilities



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

In tobacco, most doubled haploids are inferior to conventional inbreds

- Depends on genotype and doubling technique
- Paternal haploids (from anther culture) are inferior to maternal haploids (from chromosome elimination following crosses with *N. africana*)

Overcome limitations with large numbers– ***it just takes 1 superior genotype***

Geiger and Gordillo, 2009

Anther culture is too genotype specific, and needs tissue culture

Maternal haploids (ie, chromosome elimination) is most frequent and dependable method

- Thought to work by elimination of paternal chromosomes in the developing embryo
    - Find micronuclei in embryo cells first 20 days
    - Indicates paternal chromosomes are not in nucleus and get excluded
- Can complete a DH cycle + two test crosses in 3-4 years
- But, must maintain a minimal effective population size to prevent drift and loss of genetic variance

YY "supermale" asparagus


Heirloom varieties 'Mary Washington' & 'Martha Washington'

'Jersey Knight' - a supermale variety

Chee-Kok Chin

Asparagus is normally diecious

Howard Ellison & Chee-kok Chin

Howard Ellison found a male asparagus plant with hermaphrodite tendencies

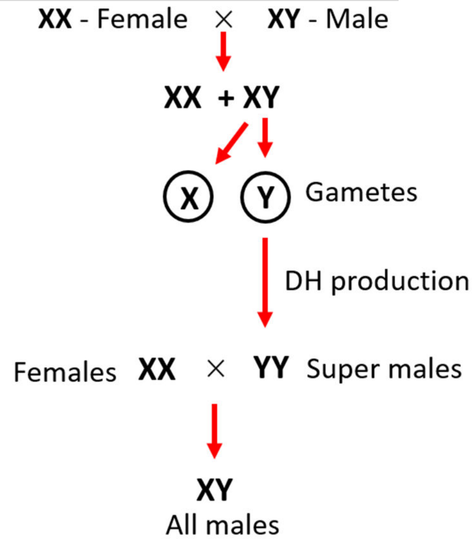
- Could be selfed to produce all males

Males (XY) are 15-25% higher yielding than females (XX)

- Males do not produce seeds, so less likely to lodge, and also avoid volunteer seeds competing with the plant
- Also, their longevity and tolerance to diseases are higher
  - But,if normal males are used to produce hybrid seed, only ½ of the progeny is male

- Chee-kok Chin figured out the anther culture
  - Get female (XX) and supermale (XY) plants

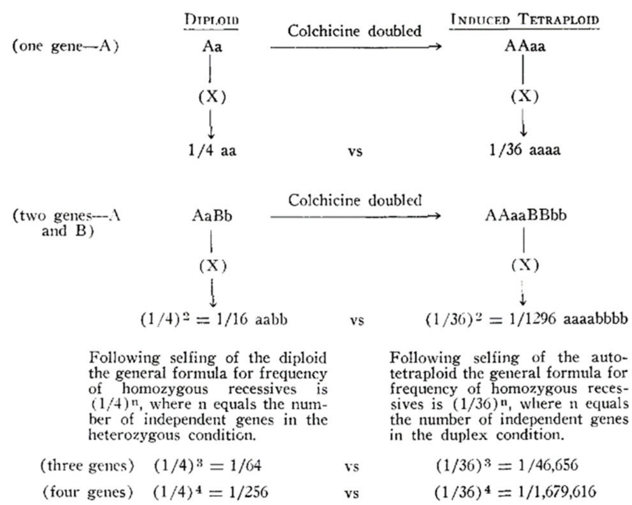
When supermales (YY) are used to produce hybrid seed, all the progeny are male



Genetic analysis of qualitative and quantitative traits

Hougas & Peloquin, 1958

- Monoploids have no dominance effects, just additive
- Have simpler genetic ratios



Differentiate between allo & autotetraploids

- Haploids from alloploids should have univalents
- Haploids from autoploids should form bivalents

NOTE: Pairing mutants can give misleading results! E.g. Originally thought that potato was an allotetraploid because the first haploid examined for pairing had univalents. It later turned out to be a synaptic mutant.

Diploidize autotetraploids

Easier to breed a 2x than a 4x

- Then cross with 2x relatives to introgress germplasm

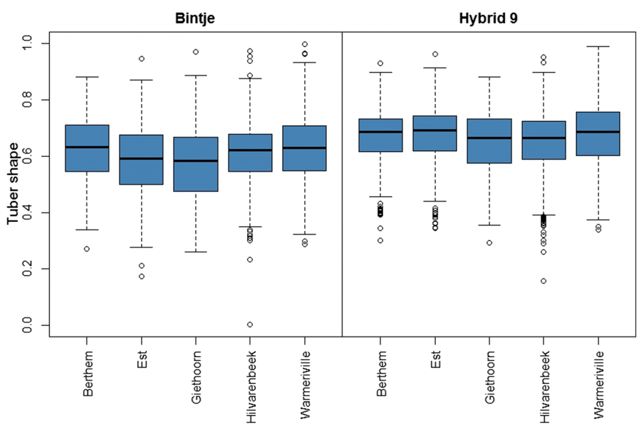
Jansky et al., 2016

Inbreeding comes from heavy genetic load.

May be possible to get inbred or hybrid 2x plants as productive as the auto4x.

Prediction has been proven true:

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

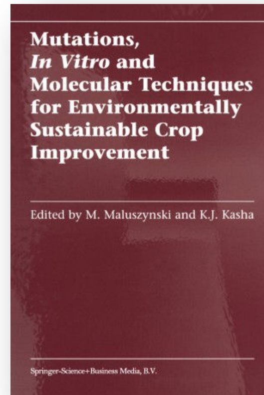
Dunwell, 2010

Are miniature in size

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

Uncover recessive traits/isolation of mutants

Maluszynski & Kasha, 2002



Bioassay for mutagens

Pohlheim et al., 1977
Christianson & Chiscon, 1978

Spontaneous mutation rate = 3×10^{-8}

Takes advantage of the fact that mutations in a haploid can be lethal

Selection at gamete level

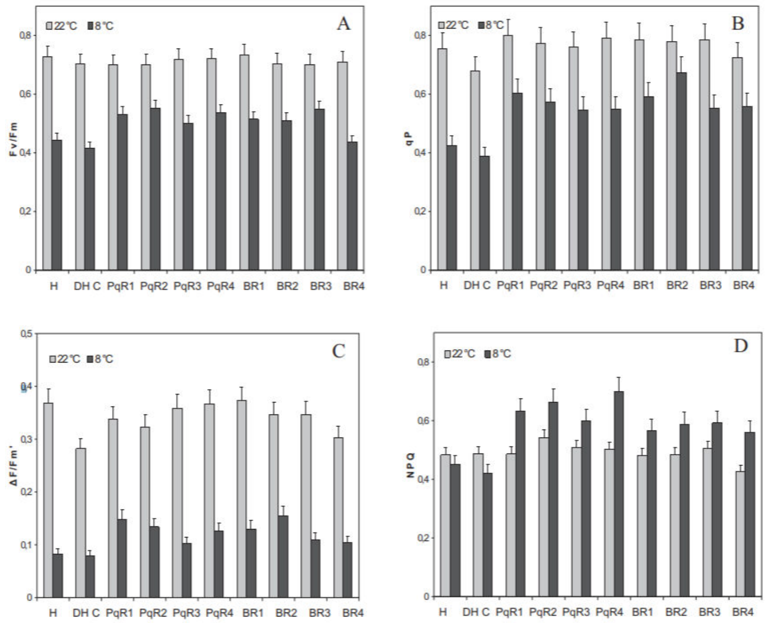
Ambrus et al., 2006; Darkó et al., 2011

Takes advantage of the fact that recessive traits are expressed

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"



Triploidy

Are highly sterile E.g.,

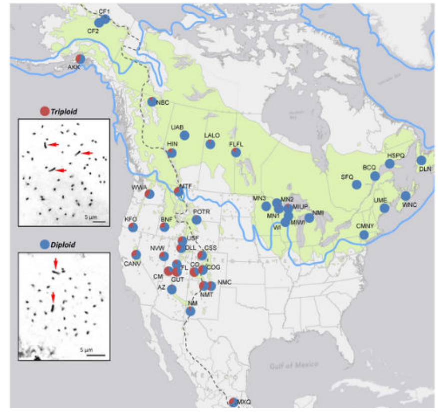
- Seedless orange, lime, etc
- Seedless watermelon
- Banana
- Extra yielding sugar beet
- Ornamentals
    - Don't set seed, so flowers last longer
    - Safeguard against invasiveness

They are found in low frequencies in natural populations. Origin:

- 2x-2x crosses via 2n gametes
- 4x-2x crosses

Triploids are difficult to obtain, giving the perception that there is something wrong with them

- That is not the case



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

Widespread triploidy in aspens

Mock et al, 2012

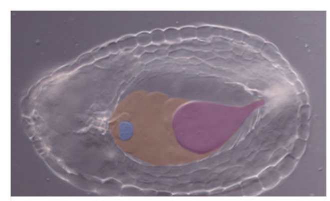
Prevalent in the West where climate is rougher, while those growing on land that was previously under ice are mostly 2x

World's largest organism

- 106 acres
- 13 million lbs
- 47,000 trunks
- > 12,000 years old

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

Triploid block



doi:10.1111/nph.18438

Triploids are prevented by the presence of endosperm barriers (i.e., the 'triploid block').

In those species with rudimentary endosperms, triploids are much more frequent

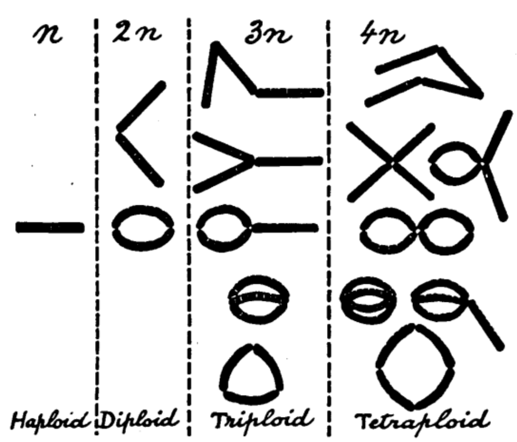
- E.g., watermelon & sugar beet, of which most commercial hybrids are triploid.

Meiotic behavior

Belling & Blakeslee, 1927

Each individual chromosome behaves as though it were a trisome

- Can either get a III or a II + I
- Longer chromosomes are more likely to form a III, as they are better able to handle the increased number of crossovers necessary to keep the III together



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

Disjunction – Ana I

Frequency of III formation in 3 species of 2n = 3x = 36

Lilies have the longest chromosomes, and accordingly, the largest frequency of III formation

	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**

3x plants can form gametes that are 1x, 1x+1 or 2, or 2x, 2x-1 or 2

To predict meiosis in a 3x plant:

- Will always have II ← → I or I ← → II disjunction at anaphase I
- ∴ p (II) = a = .5 and p (I) = b = .5
- The chromosome number for a given spore produced by a 3x plant can be predicted as $(a+b)^x$

E.g., for petunia, 2n = 3x = 21:

Begin by adding the exponents, $(a+b)^7 = a^7b^0 + a^6b^1 + a^5b^2 + a^4b^3 + a^3b^4 + a^2b^5 + a^1b^6 + a^0b^7$

Then get the coefficients from Pascal's triangle

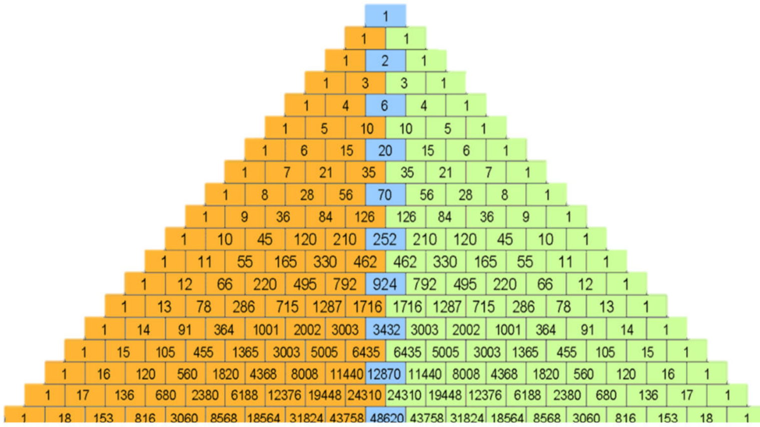


Image World-Mysteries.com

End up with $(a+b)^7 = a^7 + 7a^6b + 21a^5b^2 + 35a^4b^3 + 35a^3b^4 + 21a^2b^5 + 7ab^6 + b^7$

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

In this case, the expected frequency = the observed frequency

Datura case study

Satina and Blakeslee, 1937

Datura, 2n = 3x = 36; $(a+b)^{12}$

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

Notice

- Significant deviations from expected. Perhaps due to lagging univalents
- ♂ ≠ ♀

Other cases of binomial disjunction

Binomial distributions can be used to predict chromosome disjunctions

- Cases where 0 ← → I or I ← → 0 disjunction is expected
  - Monoploids
  - Allohaploids
  - Synaptic mutants

- Cases where II ← → 1 or I ← → II disjunction is expected
  - Triploids

As gametes can usually tolerate an extra chromosome

- Triploids can be a good source of trisomics