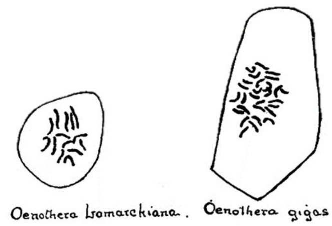
Polyploidy

Discovery

DeVries 1900

https://www.hugodevriesfonds.nl



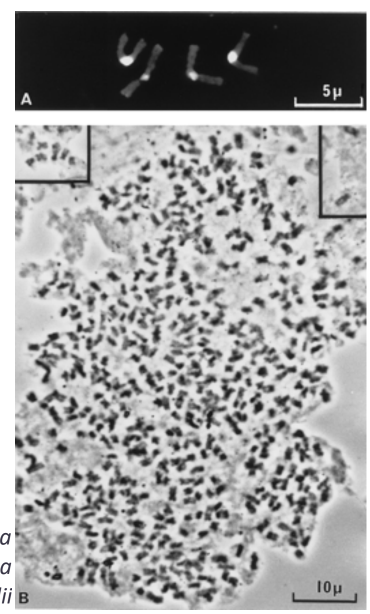
Lutz 1907

Anne Mae Lutz
1871-1938

Lutz 1907; Gates 1909

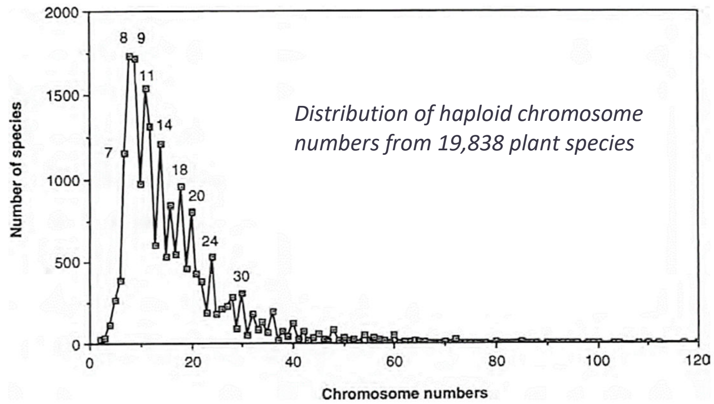
Winker 1916

Chromosome number range



A) Chromosomes of Zingeria bierbersteriana; B) Voanicola gerardii

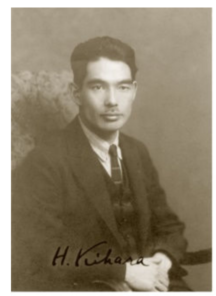
Masterson, 1994



Polyploidy types (Neopolyploidy)

Blakeslee et al, 1923

Kihara and Ono, 1926



Hitoshi Kihara
(1893-1986)

Incidence

Barker et al, 2016

Clausen et al, 1945

"Fairly safe examples of true autoploids can be recognized only in essentially monotypic genera and sections, and in those groups that have been thoroughly investigated cytogenetically"

Autopolyploidy

2x & 4x alfalfa

Tetrasomic inheritance vs disomic (diploid) inheritance

5 possible allelic compositions at a locus

AAAA	- quadriplex
AAAa	- triplex
AAaa	- duplex
Aaaa	- simplex
aaaa	- nulliplex

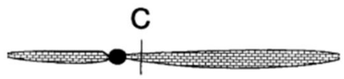
>2 alleles are possible at a locus

- monoallelic	$A_1A_1A_1A_1$	(homozygous)
- unbalanced diallelic	$A_1A_1A_1A_2$	(heterozygous)
- balanced diallelic	$A_1A_1A_2A_2$	"
- triallelic	$A_1A_1A_2A_3$	"
- tetraallelic	$A_1A_2A_3A_4$	"

Gametes can be heterozygous

- A_1A_1	homoallelic
- A_1A_2	heteroallelic

Genetic ratios are complex



Cc --> *CCcc*
↓⊗ ↓⊗

	C	*c*
C		
c		¼ *cc*

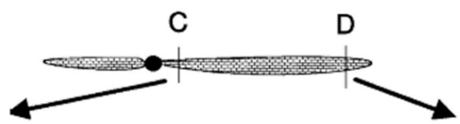
	1 *CC*	4 *Cc*	1 *cc*
1 *CC*			
4 *Cc*			
1 *cc*			$^{1}/_{36}$ *cccc*

Random chromosome segregation

1-2	1'-2				
1-2'	1'-2'				
1-3	1'-3	2-3	2'-3		
1-3'	1'-3'	2-3'	2'-3'		
1-4	1'-4	2-4	2'-4	3-4	3'-4
1-4'	1'-4'	2-4'	2'-4'	3-4'	3'-4'

Gametic products	Genotype	
	AAAa	*AAaa*
AA	12	4
Aa	12	16
aa	0	4
Total:	24	24

Gene-centromere ratios distance affects segregation



Random chromosome segregation

CCcc

↓⊗

1/36 *cccc*

a) Maximal equational segregation, or
b) Random chromatid segregation

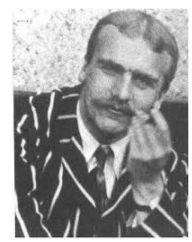
DDdd

↓⊗

ME:1/20.25;
RC: 1/21.8 *dddd*

Random chromosome segregation

Haldane, 1929



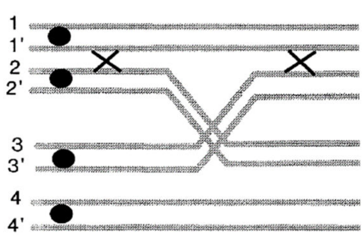
John Burdon Sanderson Haldane
(1892-1920)

Now can recover in one gamete:

- sister alleles → probability = α
- non-sister alleles → probability = 1-α

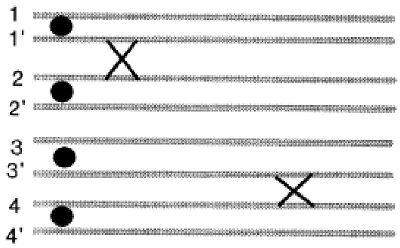
1-1'		2-2'		3-3'		4-4'	α
1-2	1'-2						
1-2'	1'-2'						
1-3	1'-3	2-3	2'-3				
1-3'	1'-3'	2-3'	2'-3'				1-α
1-4	1'-4	2-4	2'-4	3-4	3'-4		
1-4'	1'-4'	2-4'	2'-4'	3-4'	3'-4'		

Gametic products	Genotype				
	BBBb			*BBbb*	
	α = 0	α = $^1/_7$		α = 0	α = $^1/_7$
BB	12	15		4	6
Bb	12	12		16	16
bb	0	1		4	6
Total:	24	28		24	28



Maximum equational segregation

Mather, 1935



Sir Kenneth Mather
(1911-1990)

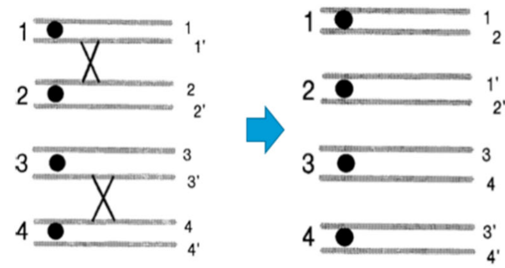
1-1'		2-2'		3-3'		4-4'	α
~~1-2~~	1'-2						
1-2'	~~1'-2'~~						
1-3	1'-3	2-3	2'-3				
1-3'	1'-3'	2-3'	2'-3'				1-α
1-4	1'-4	2-4	2'-4	~~3-4~~	3'-4		
1-4'	1'-4'	2-4'	2'-4'	3-4'	~~3'-4'~~		

Gametic products	Genotype					
	BBBb			*BBbb*		
	α = 0	α = $^1/_7$	α = $^1/_6$	α = 0	α = $^1/_7$	α = $^1/_6$
BB	12 (1)	15	13	4 (1)	6 (3)	5.33 (2)
Bb	12 (1)	12	10	16 (4)	16 (8)	13.33 (5)
bb	0	1	1	4 (1)	6 (3)	5.33 (2)
Total:	24	28	24	24	28	24

Summary

Gametic products	Genotype							
	BBBb				*BBbb*			
	α = 0	α = $^1/_7$	α = $^1/_6$	Formulae	α = 0	α = $^1/_7$	α = $^1/_6$	Formulae
BB	12 (1)	15	13	$^1/_2 + ^1/_4\ \alpha$	4 (1)	6 (3)	5.33 (2)	$^1/_6 + ^1/_3\ \alpha$
Bb	12 (1)	12	10	$^1/_2 - ^2/_4\ \alpha$	16 (4)	16 (8)	13.33 (5)	$^4/_6 - ^2/_3\ \alpha$
bb	0	1	1	$+ ^1/_4\ \alpha$	4 (1)	6 (3)	5.33 (2)	$^1/_6 + ^1/_3\ \alpha$
Total:	24	28	24		24	28	24	

Maximum equational

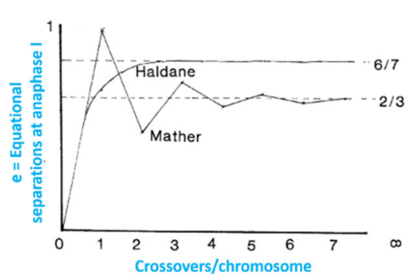


Haldane

Crossovers per chromosome	Total arrangements	Anaphase I separations		
		Reductional	Equational	Proportion equational
0	4	4	0	0.0
0.5	96	48	48	0.5
1.0	2,304	672	1,632	0.708
1.5	55,296	11,328	43,968	0.795
2.0	1,327,104	223,872	1,103,232	0.8313
2.5	31,850,496	4,892,928	26,957,568	0.84638
3.0	764,411,904	112,630,272	651,781,632	0.85266
3.5	18,345,885,696	2,655,126,528	15,690,759,168	0.85527
∞	∞	$^1/_7$	$^6/_7$	$^6/_7$ = 0.85714
n	4×24^{2n}	$(4 \times 24^{2n}) \times [^1/_7\{1+6(^5/_{12})^{2n}\}]$	$(4 \times 24^{2n}) \times [^6/_7\{1-(^5/_{12})^{2n}\}]$	$^6/_7[1-(^5/_{12})^{2n}]$

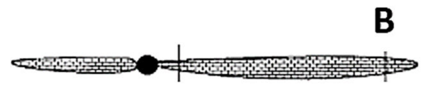
Mather

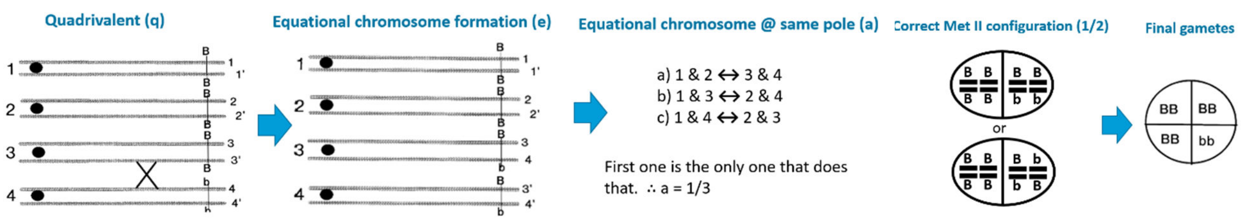
Crossovers per chromosome	Anaphase I separations		
	Reductional	Equational	Proportion equational
0	1	0	0
1	0	1	1
2	$^1/_2$	$^1/_2$	0.5
3	$^1/_4$	$^3/_4$	0.75
4	$^3/_8$	$^5/_8$	0.625
5	$^5/_{16}$	$^{11}/_{16}$	0.688
6	$^{11}/_{32}$	$^{21}/_{32}$	0.656
7	$^{21}/_{64}$	$^{43}/_{64}$	0.672
8	$^{43}/_{128}$	$^{85}/_{128}$	0.6641
∞	$^1/_3$	$^2/_3$	0.6667
n	$1-^2/_3[1-(-^1/_2)^{n/2}]$		$^2/_3[1-(-^1/_2)^{n/2}]$



Double reduction

Blakeslee, Belling, & Farnham, 1923





Burnham, 1962

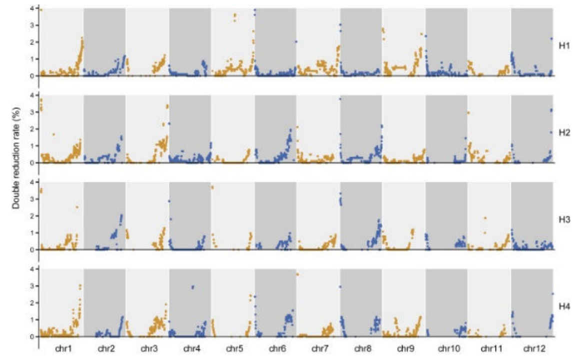
Summary

α	=	q	×	e	×	a	×	½		
Mather	=	1		1		$^1/_3$		½	=	$^1/_6$
Haldane	=	1		$^6/_7$		$^1/_3$		½	=	$^1/_7$

Haynes & Douches, 1993

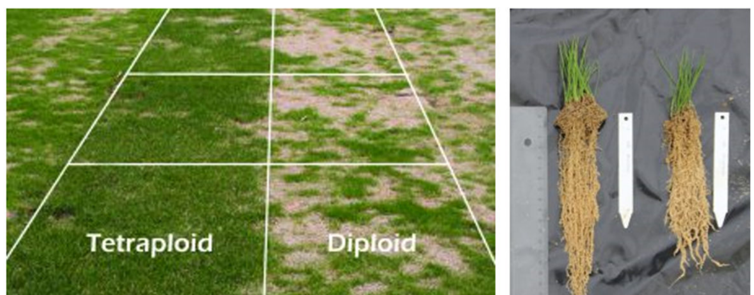
Locus	Total progeny	Double reduction products	α	±SE	Gene-centromere distance (cM)
Mdh-1	283	7	0.099*	0.037	33.5
6-Pgdh-3	214	7	0.131*	0.049	30.1
Pgi-1	122	3	0.098ns	0.057	26.0
Idh-1	314	2	0.025ns	0.018	18.4
Mdh-2	144	1	0.063ns	0.044	n/a

Bao et al, 2022



Why autotetraploids?

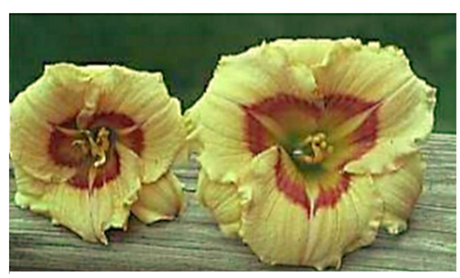
Auto4x and 2x perennial ryegrass (*Lolium perenne*)



http://www.greenkeepingeu.com/greenkeeping-feature-tetraploid-perennial-ryegrass-technology-explained/

Which diploids make good autotetraploids?

Levan, 1942; Åkerberg et al., 1961



2x and auto4x daylilies. https://plantlet.org/autopolyploidy-multiplying-same-genome/

Inbreeding at the tetrasomic level

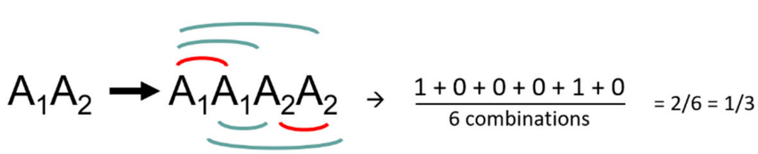
F = the coefficient of inbreeding, and is defined as the probability that two alleles are identical by descent. For example, for $A_1A_1A_2A_2$, obtained by doubling A_1A_2, both copies of A_1 are descended from the same allele, making them identical by descent.

- When there is random mating in a 2x population: F = $\frac{3\alpha}{2+\alpha}$
- Selfing a 2x: F = $\frac{1}{2}(1+F')$
- Selfing an auto4x: F = $\frac{1}{6}[1+2\propto(5-2\propto)F']$
  - Where FT(L) = current level of inbreeding and
  - F' = the previous level of inbreeding

Thus 1 generation of selfing gives 50% in breeding in a 2x plant (F = ½), but only 17% inbreeding (F=1/6) for an autotetraploid (if α = 0)

Somatic chromosome doubling

Note that somatic chromosome doubling leads to an inbreeding of F = $^1/_3$:



In the above examples, there are 6 possible pairs of alleles. Out of these 6 possible pairs, two (indicated in red) are pairs of alleles that consist of alleles that are identical by descent. The resulting F = $^1/_3$ is what one would obtain with a little more than 2 generations of selfing.

Analytic breeding

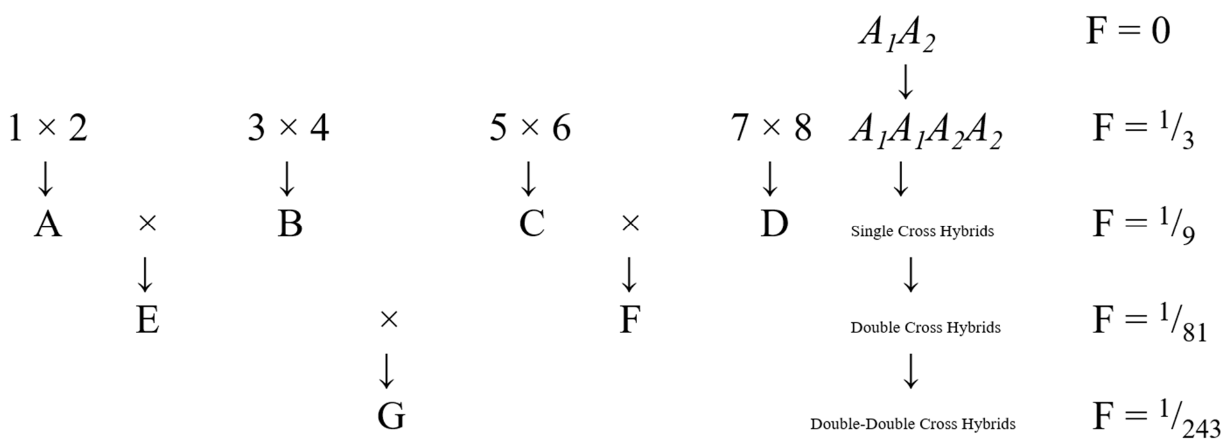
Sherrett Spaulding Chase 1918 - 2021

Chase 1962

Designed a breeding scheme to maximize heterozygosity, called it **analytic breeding**

Chase 1963

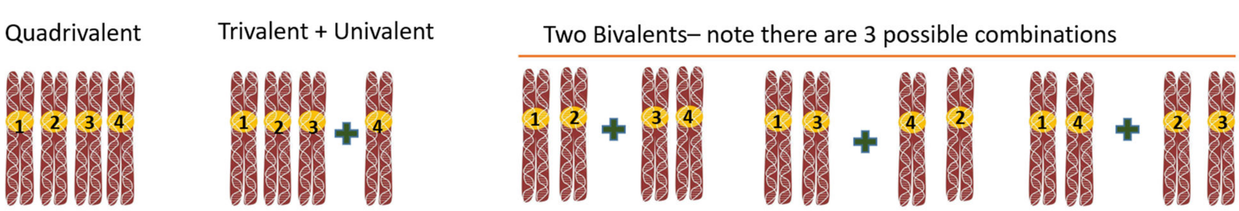
Designed analytic breeding for potato, extracting 2x potatoes from 4x, selecting at 2x level, and converting to 4x via analytic breeding



- Maximizes heterozygosity. It is not the heterozygosity that is important. Instead, it maximizes the odds of having at least 1 dominant allele at each locus → capitalizes on additive genetic variance

Fertility in autotetraploids

Darlington 1932



3 possible pairing configurations

Lowell Fitz Randolph
1894 - 1980

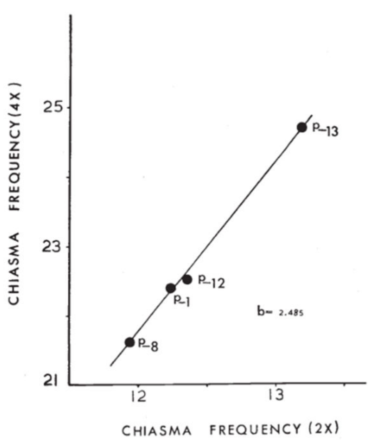
Randolph, 1941

Gilles & Randolph, 1951

Plant no.	Frequency of cells with ten to five quadrivalents 10	9	8	7	6	5	Total no. of cells examined
48-326 — 15	8	22	7	2	2	–	41
— 21	7	24	9	1	–	–	41
— 22	3	15	16	3	3	–	40
— 1	3	18	13	2	5	–	41
— 27	3	18	17	2	1	–	41
— 13	6	18	11	4	2	–	41
— 24	6	18	11	4	2	–	41
— 26	4	16	13	5	3	–	41
— 52	3	19	12	4	3	–	41
— 53	5	16	14	4	2	–	41
— 75	4	15	15	4	3	–	41
Total	52	199	138	35	26	–	450
per cent	11.5	44.2	30.7	7.8	5.8		

Plant no.	Frequency of cells with ten to five quadrivalents 10	9	8	7	6	5	Total no. of cells examined
48-327 — 5	–	6	16	11	6	2	41
— 14	–	5	18	12	5	1	41
— 22	–	5	14	15	6	1	41
— 37	–	6	12	13	10	2	43
— 39	–	5	13	16	6	2	42
— 50	–	4	18	13	6	1	42
— 17	–	4	21	11	5	–	41
— 24	–	5	19	13	3	1	41
— 26	–	3	15	15	7	1	41
— 44	–	6	18	13	4	–	41
— 72	–	7	17	12	5	–	41
per cent	–	12.0	40.0	31.6	13.8	2.4	
Total	–	56	181	144	63	11	455

Hazarika and Rees, 1967



Stebbins, 1971

1906 - 2000

Umesh Chandra Lavania

Lavania, 1991

	2x		4x C_2			
	% rod II	% ⊙ II	II	III	IV	I
Lolium perenne	82↑	18	46↑	--	53↓	--
Amaranthus hypochonriacus (C_1)	71	29	43	1	55	--
A. caudatus	66	34	33	1	64	1
Hyoscyamus muticus	65	30	28	4	67	1
A. edulis	60	40	30	--	68	2
H. niger	58	41	10	2	76	2
H. algus	59	38	7	6	84	3

Species	Generation	% IV	% Seed Set
Hyoscyamus muticus	C_0	45↓	65
	C_1	--	--
	C_2	30	78↑
H. niger	C_0	27↓	75
	C_1	24	80
	C_2	22	92↑
H. albus	C_0	24↓	43
	C_1	17	54
	C_2	12	83↑

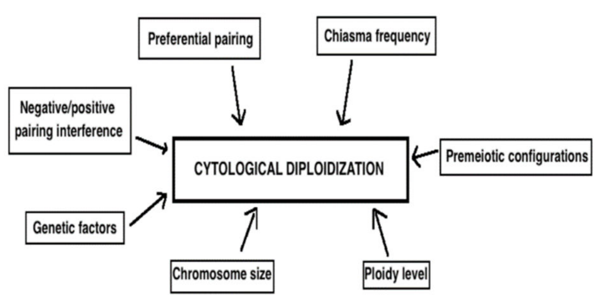
Rivero-Guerra, 2008

Auto4x individuals of *Santolina pectinata*: “Chromosome number doubling produces statistically significant decreases in the lengths of the short arm, long arm, and whole chromosome”

Santolina pectinata

Cytological diploidization

Dorone, 2013



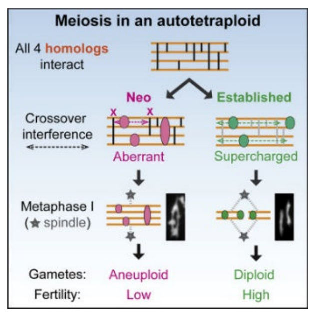
Arabidopsis arenosa as a model

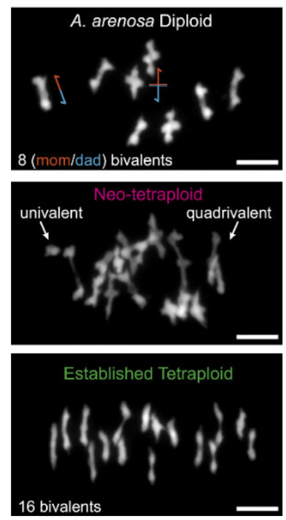
https://extremeplants.org/species/arabidopsis-arenosa/

Hollister et al., 2012; Yant et al., 2013 (Bomblies lab)

Evolution of CO interference

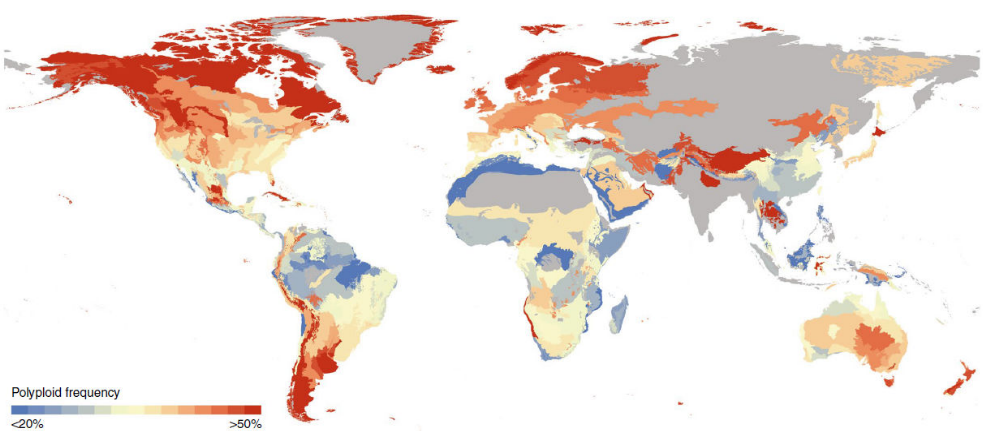
Morgan et al, 2021

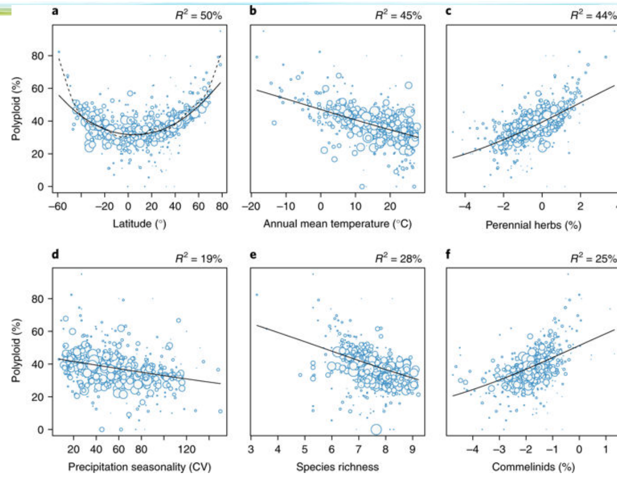




Prevalence

Rice et al., 2019




a
R^2 = 50%
Polyploid (%)
Latitude (°)
b
R^2 = 45%
Annual mean temperature (°C)
c
R^2 = 44%
Perennial herbs (%)
d
R^2 = 19%
Polyploid (%)
Precipitation seasonality (CV)
e
R^2 = 28%
Species richness
f
R^2 = 25%
Commelinids (%)