B chromosomes

Jones, 1995; Bougard and Jones, 1997; Camacho et al., 2000; Pokorná & Reifová, 2021

Chromosome types:

- A = autosomal chromosomes
    - Contain all the genes
- B = supernumerary or accessory

- Discovered 1907. Wilson; *Science* 26:870-871 in bug, *Metapodius*

- Term 'B' derived from maize in 1928 (Randall; Anat. Record 41:102)

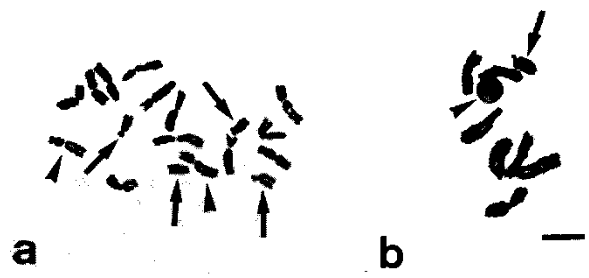
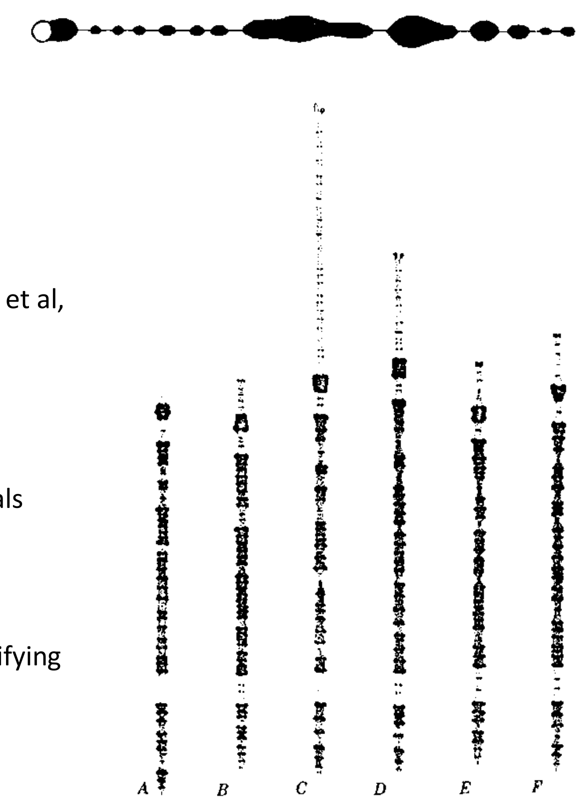


Figure 1. Niwa & Tsujimoto 1992, Plant Breeding109:78-81. Rye root-tip and diakinesis chromosomes. Arrows indicate B chromosomes (note pairing at diakinesis). Arrow heads are the satellite chromosomes. Bar = 10 µm.

B chromosomes

- Are not duplicates of any A chromosome
- Exist only in some individuals of a population
    - Found in 1372 spp. of seed plants, of which 12 are conifers.
    - Also in ferns & fungi
    - = 10-15% of flowering plants
    - All are outbreeders
    - Found in 500 animal spp. (Insects, fish, birds)
    - Found in 1.94% of mammalian spp. (Vujosevic et al, 2018)
- Are dispensable
- Do not pair or recombine with A chromosomes
- Some pair with each other during meiosis
- About ½ are highly heterochromatic, esp. in animals
- Their number is very variable
    - 0 to 34 (in maize)
    - Accounts for up to 155% of the DNA
- Have genes that deteriorate in the absence of purifying selection
    - Also have genes for their maintenance

Figure 2. Top: A B-chromosome from maize. Bottom: B chromosomes from rye plants from different countries.



- **Rhoades and Dempsey, 1973** [J. Hered. 64:12-18]
    - B chromosomes have the ability to eliminate knobs from A chromosomes

Rosato et al., 1998

As altitude increases, B number increases

- Suggests function

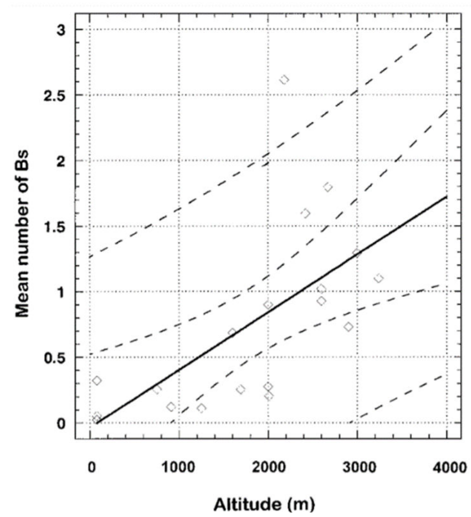


Figure 3. Rosato et al., 1998

Mitotic stability

- In about ⅓ of cases, B chromosomes are mitotically stable
  - esp. in grasses, but rare in *Allium*
- Can be lost in roots and other organs of some spp.

Mitotic drive

- In *Crepis capillaris*, Bs accumulate in reproductive organs

Meiotic drive

E.g., *Lilium callosum*: 1B × 0B ⇒ 80% 1B
rec ⇒ 50% 0B, 50% 1B

Figure 4. bdlilies.com

Non-disjunction

- 60% of spp. exhibit B drive, most due to non-disjunction during the second pollen mitosis, as observed in maize
- The sperm cell with the 2 B's is produced 50-100% of the time, and will preferentially fertilize the egg 60- 70% of the time

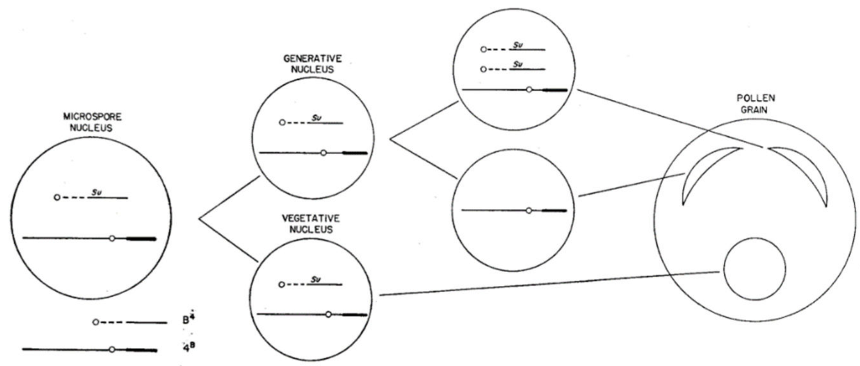
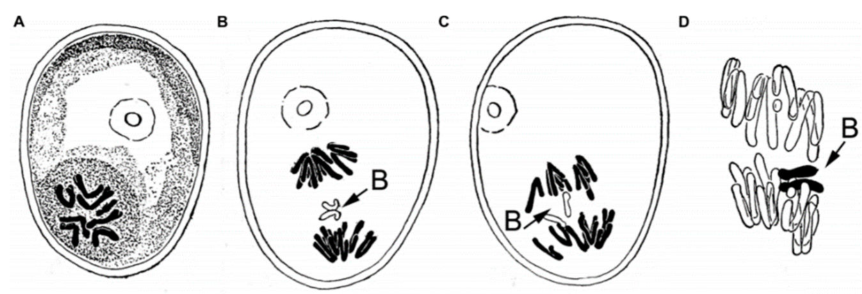


Figure 5. Non-disjunction of B chromosomes during microgametogenesis of maize.
Roman, 1947

- In rye, non-disjunction occurs at 1st mitosis (happens 85% of time for & and %)
- The phenomenon was first observed in rye by Hasegawa, 1934

*Figure 6. From **Hasegawa 1934**, redrawn by **Houben 2017**. A- pollen mitosis; B- non-disjoined, lagging B chromosomes; C - disjoined B's; D - B's showing non-disjunction*



Kamayo, 1957*:* B chromosomes in *Lillium callosum*

- In this species, it is the micropylar megaspore that gives rise to the gametophyte
- Bs tended to lie on the micropylar end of the Met I spindle, and again of the Met II spindle, and hence get included preferentially in the egg.

*Table 1. **Kamayo, 1957**: B chromosomes in Lillium callosum*

Stage:	% Bs @ micropylar pole
Metaphase I	75.4
Anaphase I	84.1
Met II / Ana II	80.0
Postmeiotic mitoses	73.1
% Eggs with B's	83.8

Wu et al, 2019

Showing the 1st pollen mitosis. Note that 85% of the time, the B chromosomes will end up in the generative cell, which will divide to form the sperm.

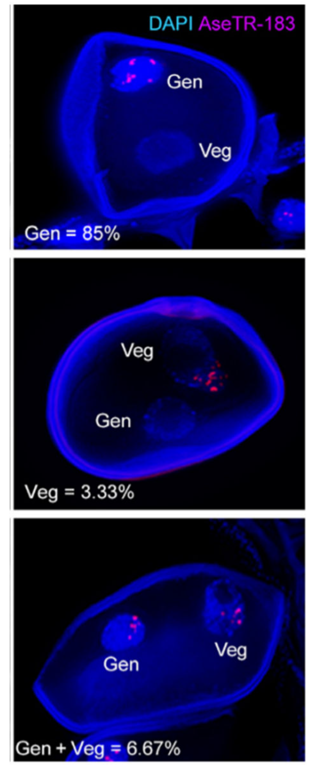


Figure 7. Wu et al, 2019 (Houben lab)

Carlson and Roseman, 1992

Using translocations with chromosome 9 of maize, have identified 4 regions of the B chromosome necessary for non disjunction to occur:

- heterochromatic block = nonessential
- region 2 = responsible for preferential fertilization
- region 3 = sticking receptor
- region 4 = regulates rate

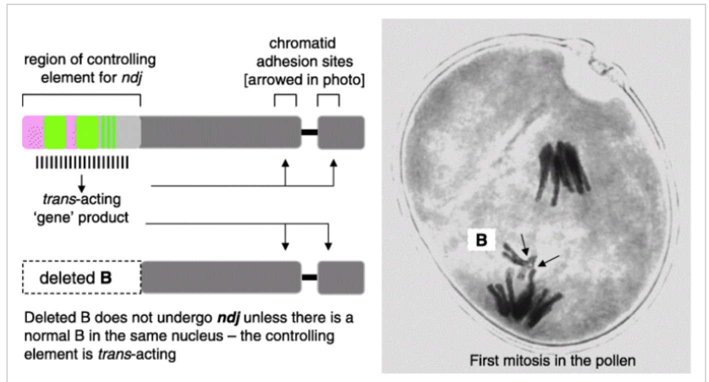
Regions 2, 3, and 4 also prevent meiotic loss during megasporogenesis. The unpaired B chromosomes go to the functional pole and get included in the egg (not due to nondisjunction).

Blavet et al, 2021

- B-repeat responsible for non-disjunction in cis
- Derived from knob sequence → delayed replication may cause sister chromatids to not separate in time for mitosis
- Preferential fertilization related to sequences linked to centromere
- Trans factor for non disjunction located at distal end, which contains 34 genes

Jones and Puertas, 1993; Jones and Pasakinskiene, 2004

- In rye, a gene for non disjunction is located in the distal end of the long arm
- Causes sequences around the centromere to stick together during pollen mitosis
- If the end of the chromosome is missing, then centromeric sequences do not stick together
- However, it does not explain why there are different frequencies of B chromosomes in different populations



Banei-Moghaddam et al., 2012

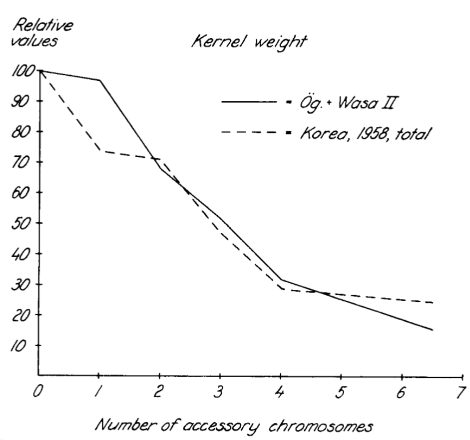
- Non-coding RNA coded by the distal end involved in stickiness and asymmetrical spindle

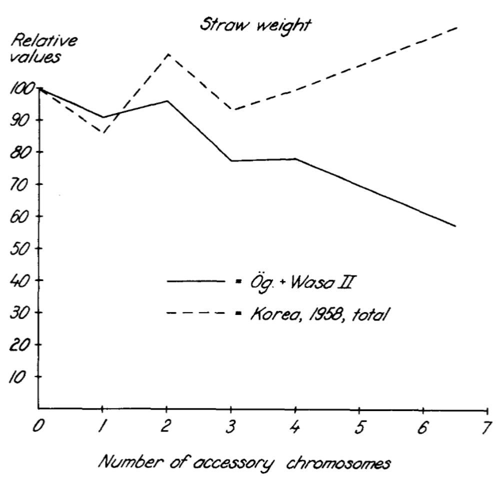
Chen et al., 2024

- Candidate gene: *DCR28* =coding a microtubule-associated protein
  - 15 copies in rye B chromosome
  - Highly expressed at 1st pollen mitosis

Balancing forces

Müntzing, 1963

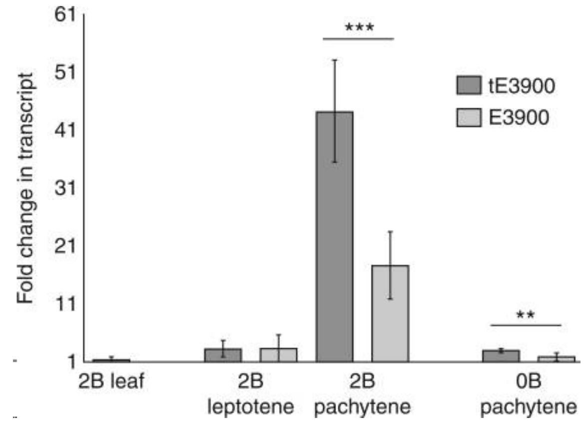




As B number increases, plant growth decreases in Swedish varieties & increases in Korean ones, but, fertility decreases

Pereira et al, 2016

- B subtelomeric domain highly enriched in E3900-related sequences
    - B-specific repetitive sequences
- Full length E3900 is 3.9-kb long
- A truncated version is 2.7 kb
    - Contains heat-responsive cis-acting regulatory elements
- The short version is upregulated at pachytene under heat stress.
- Pachytene cells with non-truncated B's also exhibit fewer chromosomal abnormalities



Percentage abnormal cells, mean ± s.d. (*n*)		
0B	**2B**	**2B-del**
94 ± 9 (108)	29 ± 19 (90)	55 ± 17 (30)
t-test (*P*)	0·01	0·04

How B's influence the A's

Huang et al, 2020

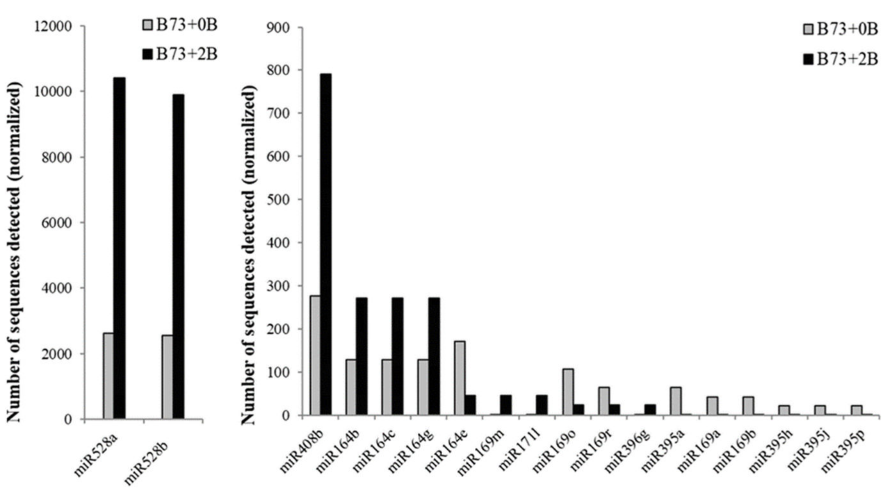


Figure 8. Differential expression of 18 known miRNAs

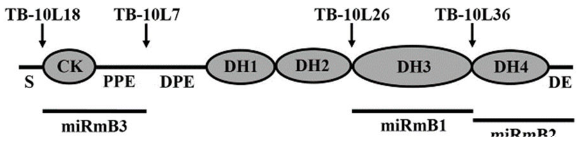


Figure 9. Map positions of B-derived miRNA genes.

Genetic control

Romera, Jiménez, and Puertas, 1991

- Looked at different rye cultivars from Korea
  - 'Paldang'-- 20% of its plants naturally have B chromosomes
  - 'Puyo' -- 60% of its plants naturally have B chromosomes
- Synthesized a population of Paldang with 60% B chromosomes, and one of Puyo with 20% B chromosomes
  - These were grown in 2 locations in Spain for 2 seasons:

Population:	Year	Madrid		La Coruña	
		% B's	#B/plant	% B's	# B/plant
Paldang 20	1987	17	0.33		
	1988	21	0.42	22	0.44
	1989	20	0.40	30	0.63
Paldang 60	1987	55↓	1.21		
	1988	42	0.89	54↓	1.19
	1989	38	0.82	47	1.02
Puyo 20	1987	22↑	0.44		
	1988	47	0.98	19↑	0.39
	1989	57	1.30	34	0.66
Puyo 60	1987	57	1.36		
	1988	71	1.78	52	1.15
	1989	74	1.74	50	1.04

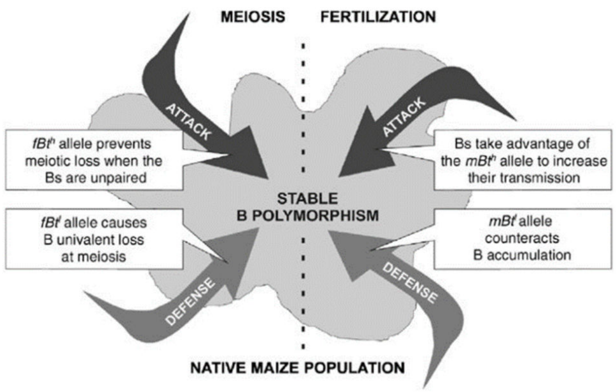
The trend is for the populations to return to their original frequency of B chromosomes, suggesting that genetic factors probably determine the equilibrium frequency of B chromosomes.

- selfish
- adaptive value

Interplay between these two forces determines the number of B's found in a given plant.

- Some Bs appear to survive as they benefit the host; others do so due to drive.
- This is balanced against detrimental effects their accumulation provides to the host.
- There must be some sort of genetic control

González-Sánchez et al., 2003



The mBt autosomal gene in corn controls B preferential fertilization in maize.
- Eggs with the mBt^h are preferentially fertilized by B-containing sperm
- B's in eggs controlled by the fBt gene in the A chromosomes
- The fBtl allele is dominant –> loss of B's at meiosis.

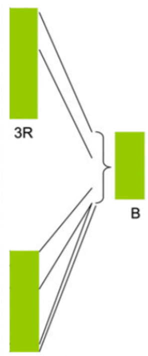
Origin & composition

Origin is unknown. In plants may be derived from fragment of centromere and surrounding heterochromatin

- Evolve rapidly to prevent pairing with A chromosomes

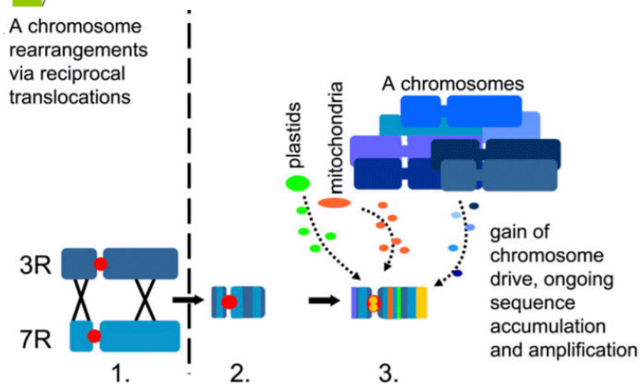
Martis et al 2012

The rye B chromosome

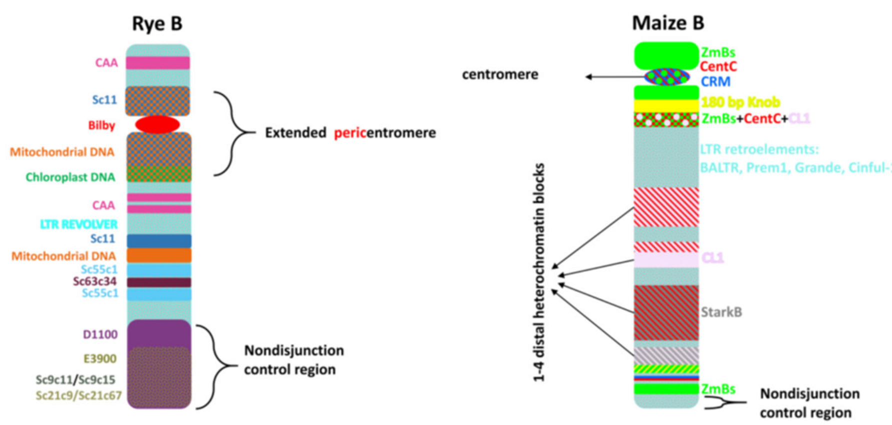


Rye B's derived from parts of chromosomes 3 & 7

- Therefore, the first step appears to be a reciprocal translocation that results in a 'proto-B' chromosome
- Followed by loss of genes and other homologous sequences to A chromosomes to prevent pairing
- And accumulation of other DNA sequences
- Accumulation also happens in A chromosomes, but many of them get discarded by recombination and segregation



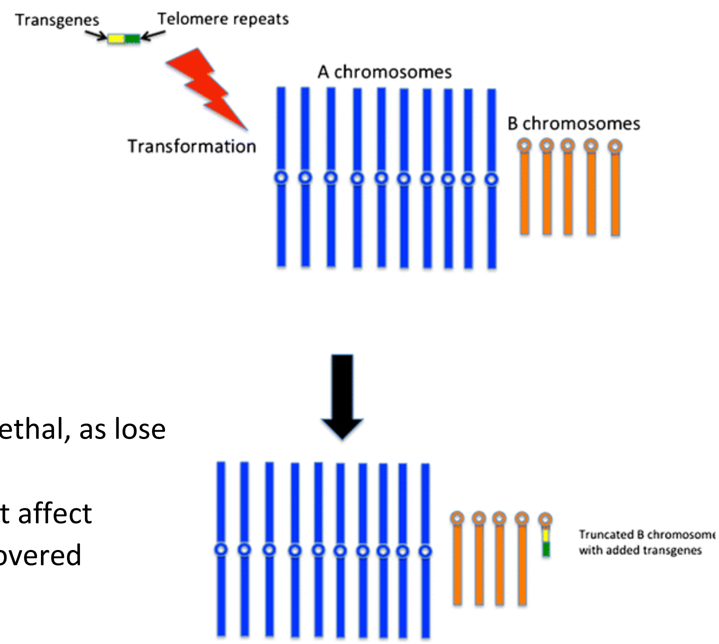
Marques et al, 2018



Use in breeding

Birchler, 2015

Limitation to artificial chromosomes has been the inability to clone centromeres and transfer them due to their epigenetic nature. So, need an alternative



• Transgenes normally integrate into chromosomes– requires recombination on both sides

• But, if flank the transgene with telomeric sequences on one side, it will still integrate, but the side with telomeric sequences will not integrate

- Therefore, end of chromosome is lost
- Integration into A chromosomes can be lethal, as lose necessary genes
- Integration into B chromosomes does not affect viability; therefore are preferentially recovered
- Result is a minichromosome