# **Repetitive DNA**

The number of genes within a haploid complement is reasonably constant, or accounts for very little of the genome.

- Hence, fluctuations in DNA content must come mostly from repetitive DNA sequences, collectively known as repetitive DNA.
  - About 75% of the non-coding DNA is repetitive, in some cases = heterochromatin
  - Ranges from 3% in bladderwort to 25% in Arabidopsis to 95% in onion
  - Rest of non-coding DNA is single copy
    - Repetitive DNA can increase or decrease, but the genes will remain fairly constant.

Genes and non-genes can be repetitive or single copy- i.e., all possible combinations are found

	Repetitive	Non-repetitive
Genes	$\checkmark$	$\checkmark$
Non genes	$\checkmark$	$\checkmark$

# Arrangements

### Flavell, 1980

# Tandem

Identical repeating units

### **Telomeres**

### NOR

NOR is tandem array of the

- 18S-5.8S-25S ribosomal genes
- 5S ribosomal genes are also a tandem array

### Microsatellites

Zietkiewicz et al, 1993

Also called simple sequence repeats or SSRs or short tandem repeats (STRs)

• Are ubiquitous in eukaryotic genomes

The DNA sequences flanking SSRs are conserved, allowing the selection of PCR primers that will amplify the intervening SSRs



Original gel image of 24 soybean genotypes with 5 fluoresecent-labeled SSR loci. Akkaya et al., 1992

Variation in PCR product length is a function of the number of SSR units

- The mutation rate in copy number of dinucleotide repeats in maize has been calculated to be almost eight for every 10,000 meioses (Vigouroux et al., 2002)
  - = 1 change in one of every 625 soybean seeds produced in the field

### Minisatellites

### Schmidt et al., 2000

Short DNA repeats, which are characterized by longer repeating units (10-50 bp).

- They have been detected in many plant species
- They share a GC-rich core motif
- They make up a considerable faction of the repetitive DNA sequences of plant genome



- Originally identified when DNA folds on itself and single strands pair with themselves to form a "hair pin." Thought it was DNA folding that was of regulatory significance.
- Now know it is folding of the RNA that is important. Short inverted DNAs (micro RNA genes which give rise to miRNA) have been found which give rise to double-stranded RNAs which play a role in gene silencing.

### Interspersed



Short pieces (50-2000 bp) interspersed with single copy DNA

• Or, unrelated short repeats interspersed with each other in different permutations

### **Mitochondrial DNA**

Lough et al, 2008 (Birchler lab)



. Arrowheads indicated mitochondrial DNA that has been integrated into the genome.

## Chloroplast DNA

Roark et al, 2010 (Birchler lab)



### Movement of organellar DNA to the nucleus

### Huang et al, 2003; 2004 Sheppard et al, 2008

- 6 to 22 kb fragments
- 1 event per 16,000 pollen grains

KanR+ transgene in chloroplast, with nuclear promoter

- Thus, only expressed if moved from chloroplast to nucleus
- 1 per 11,231 plants via male gametes



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**GUS** transgene

Somatic transfer 1 per 18,000 leaf cells 0

### **Pararetroviruses**

### Staginnus & Richert-Pöggeler, 2006

Family Caulimovides

- Ubiquitous in plant kingdom •
- Usually in pericentric chromatin •
- Can become active after being dormant • for 100's or 1000's of years

Conservation over evolutionary time implies a useful function



### Stagginus et al, 2007; Liu et al, 2012 Rama Vamsi Somala



#### **Transient integration**

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Banana Streak Virus

### Geering et al, 2014 -

Florendoviruses have the same behavior



### Kyndt et al, 2015





Endogenous florendoviruses are major components of plant genomes and hallmarks of virus evolution

Andrew D. W. Geering, Florian Maumus, Dario Copetti, Nathalie Choisne, Derrick J. Zwicki, Matthias Zytnicki, Alistair R. McTaggart, Simone Scalabrin, Silvia Vezzulli, Rod A. Wing, Hadi Quesneville & Pierre-Yves Teycheney

Affiliations | Contributions | Corresponding author

Nature Communications 5, Article number: 5269 | doi:10.1038/ncomms6269 Received 10 July 2014 | Accepted 15 September 2014 | Published 10 November 2014

### Stavnstrup et al, 2020



### Wang et al, 2020





CSH CENERAL HOME | ABOUT | ARCHIVE | SUBMIT | SUBSC Institution: Ge 2 million gene transfers between plants

Widespread and frequent horizontal transfers of transposable elements in plants

Moaine El Baidouri<sup>1</sup>,<sup>2</sup>, Marie-Christine Carpentier<sup>1</sup>, Richard Cooke<sup>1</sup>, Dongying Gao<sup>2</sup>, Eric Lasserre<sup>1</sup>, Christel Llauro<sup>1</sup>, Marie Mirouze<sup>3</sup>, Nathalie Picault<sup>1</sup>, Scott A. Jackson<sup>2</sup> and Olivier Panaud<sup>1,4</sup>

#### No. of LGT per 1000 genes 4 Bd 0.01 Ponide 0.05 0 Hv 10 Ta 0 Os Oryzoidea 4 Lp 9 Et 0 Ot O Zj 11 Zm Andropogonea 3 Sb 4 Do 10 Ec Panicoide 20 As No. of species 0 100 34 Pv 8 Ph $\bigcirc$ 1000 19 Ca 5000 7 Si 50 40 30 20 10 0 Myr



Bock 2009





Found HGT in 13 spp of grasses

Hibdige et al, 2021

# **Transposable Elements**

### Kazazian, 2004

DNA sequences that have the ability to integrate into the genome at a new site within their cell of origin.

# **DNA transposons**

These elements are excised from one genomic site and integrated into another by a "cut and paste" mechanism.

• Eg, = Ac/Ds in corn, Ping & mPing in rice

### **Retrotransposons**

# Wessler et al., 1995; Brandes et al., 1997; Kumar & Bennetzen, 1999; Moore, 2000; Bennetzen, 2000; Kazazian, 2004; Orozco-Arias et al, 2019

Are a major component in plant genomes

- Move to new chromosomal locations, via an RNA intermediate that is converted to extrachromosomal DNA by encoded reverse-transcriptase.
  - RNAseH enzyme digests the RNA in RNA:DNA
  - The dsDNA is reinserted into the genome

The replicative mode of transposition increases the copy numbers of elements and increases plant genome size.

- Often insert into preexisting elements
- The most responsible for rapid DNA changes

Main types: LTR-retrotransposons and non-LTR retrotransposons

### **LTRs** = contain **Long Terminal Repeats** at both ends

- Similar to retroviruses in structure
- Identify families based on sequence of LTRs
- Well known in plants -> major component of plant genomes



Genes contained: gag- for intracellular packaging of the RNA; encode for viral particle coat; RH = ribonuclease H; RT = reverse transcriptase; int = integrase (to provide enzymatic activities for making cDNA from RNA and inserting it into the genome); PR = protease; EN = endonuclease

### D'Hont et al, 2012

Wang and Dooner, 2006



### Differences in retrotransposon patterns in different inbreds of maize



### Non-LTRs (lack LTRs)

Full length non-LTR retrotransposons are 4 to 6 kb in length and usually have two open reading frame (ORFs).

- These elements encode activities necessary for their retrotransposition.
- They are called autonomous even though they probably also require host proteins to complete retrotransposition.

In contrast to reverse transcription of LTR retrotransposons and retroviruses, this process takes place on nuclear genomic DNA through target primed reverse transcription, or TPRT.

Spring, 2025 PBGG 88

PBGG 8890, Plant Cytogenetics





LINES: long-interspersed nuclear elements

- Typified by LINE-1 (L-1 of mammals).
  - BNR1 family in beet = 2-5% of repetitive DNA • Are autonomous

### Wenke et al, 2011

•

VII-B • Repetitive DNA



SINES = Short Interspersed Nuclear Elements

o non-autonomous versions of LINES

Very poorly characterized

- Rice 10,178 copies per genome
- Potato ~6500 copies = 0.15% of genome
- *B. oleracea* 4290 copies
- Maize 1991 copies

### Number of retrotransposons in a plant genome

### Joseph et al, 1990 DOI:10.1007/BF02099941

Del 1 varies from 130 to >13,000 copies per haploid genome in Lilium spp

- No relationship between phylogeny and copy number of del1, showing that increases in number are sporadic and occur at random
- Accounts for 2.2 to 9.7% of the genome

### Leeton and Smyth,1993 DOI: 10.1007/BF00282789

Lilium speciosum has 250,000 copies of the 4.5 kb del2 LINE retrotransposon

• = 4% of its genome

### Manninen & Schulman, 1993 DOI: 10.1007/BF00027369

• In barley, the BARE1 retrotransposon is present in 50,000 copies

### Moore et al, 1991 DOI: 10.1016/0888-7543(91)90334-B

• Bis-1 in wheat = 5% of genome

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### **Relative abundance in genomes** Bennetzen & Park, 2018

To put the relative abundance of the TE types in perspective



### Vitte et al, 2014

Transposon abundance and diversity varies across the plant phylogeny





### **Retrogenes**

### Wang et al., 2006; Elroubi and Bureau, 2010

Genes captured by retrotransposons

Characterized by a lack of introns and by the presence of flanking direct repeats associated with transposition

Of 898 such gene fragments identified in rice (Wang et al., 2006)

- 55% seem to be expressed with ~35% of them being chimeric in nature
- Non-expressed ones are the pseudogenes
- Based on the synonymous substitution rate, some appeared more recently than others, suggesting that these genes are created at a slow but steady rate

Other examples

• Bs1 gene in maize, a gene expressed early in ear development (Elroubi and Bureau, 2010)

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### Xiao et al, 2018 (van der Knaap lab) Elongated fruit in tomato

A Rider retrotransposon-mediated duplication of a 24.7-kb segment that includes the SUN gene from chromosome 10

- Moved the copy into the DELF1 gene on chromosome 7
- This movement allows the DELF1 promoter to drive SUN, leading to altered auxin levels or distribution in the fruit, thus leading to the elongated phenotype



Mutation probably happened in Spain after the arrival of tomato there [Rodríguez et al, 2011, Plant Physiol 156: 275-285]

### Zabala and Vodkin, 2005; 2007

The wp mutation in soybean turns purple flowers into pale pink

- Increases protein content
- Due to a retrotransposon insertion in the second intron of flavanone-3-hydroxylase gene



1987 Illinois – Wp mutation



Contains parts of 4 other gene fragments, including one for cysteine synthesis



- This example from soybean illustrates the point, as it affects the phenotype
- Think of it as a gene in the process of being created
- Other elements perform similar functions in plants
  - Mu-like elements (MULES): maize, arabidopsis, rice (Hanada et al., 2009)

## **Transposable elements & mutations**

### Kazazian, 2004

### **Allele creation**

### Eg, Giroux et al, 1996

2 amino acids were added to an enzyme in maize, leading to higher grain weight

• Large subunit of starch synthetic enzyme adenosine diphosphoglucose pyro-phosphorylase

### Eg, Montgomery et al, 2024

Herbicide tolerance in kochia (Bassia scoparia), tumbleweed

- 3,466 bp Ty1/Copia retro insertion into beginning of exon 2 of BsAUX/IAA16 gene
  - Disrupts splicing
    - 1st 16 bases of exon get replaced with last 19 bases of insert
    - Replaces 4 aa and adds 1
    - Changes gly to threonine in active site  $\rightarrow$  resistance



Photo: Wu et al, 2020. Pest Management Science, https://doi.org/10.1002/ps.6080

### Gene knockouts

### Eg, Vollmann & Ruckenbauer, 1997

Shriveled pea phenotype used by Mendel is due to insertion in starch branching enzyme



Kobayashi et al, 2004; Review by Lisch, 2013

Skin color of Cabernet vs Chardonnay grapes is due to inactivation of CHS



### **Chromosomal reconfigurations**

#### Zhang & Peterson, 1999

Cause the double strand breaks needed for inversions and translocations

### **Change expression patterns**

### Palaisa et al, 2003 (Rafalsksi lab)

Maize endosperm was originally white, due to the lack of phytoene synthase expression

• A 382 base pair Is2 insertion into the y1 locus for phytoene synthase permits its expression in the endosperm, leading to the accumulation of carotenoids that give yellow maize kernels their color





### Zhang et al, 2019

Butelli et al., 2012; Review by Lisch, 2013



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### Summary of major changes

Review by Lisch, 2013



### **Transposons affect gene expression in the vicinity** Makarevitch et al, 2015

The presence of a transposon near certain maize genes correlated with differential gene expression when a line was compared to another line that lacked the insertion





Anderson et al, 2019

2,380 genes in the B73 genome are within variable TEs

### Summary of repetitive DNA types

Modified from Biscotti et al, 2015



# **Movement of DNA in the plant genome**

### Belyanev et al., 2000

Wheat graphic from www.mpizkoeln.mpg.de/pr/garten/schau/Triticumaestivum/wh eat.html

The point is that sequences from the spelt (B genome) have moved to the einkorn (A genome) since tetraploidization took place some 370 KYA.



### Note:

- The same repeat can be found on different chromosomes. This means that repeated sequences must have a way to move between chromosomes.
- Many repeats are not conserved across genera within a family– means they evolve very rapidly

# Movement by transposon capture

### Malacarne et al, 2012

Helitrons moved NBS-R genes to nonsyntenic positions in the ancestral genomes of grape

• Flanked by tetranucleotide repeats that form a stem loop (hairpin)- hallmarks of a helitron

### Movement during double strand break repair

### Freeling et al, 2008

25-30% of arabidopsis genes have transposed to new locations within the genus.

- Low transposition: transcription factors (5%)
- High transposition: disease resistance genes, MADS-box, B3 transcription factors

### Wicker et al., 2010; 2011

Notice that chromosome 1 of the triticeae has fewer syntenic genes than non-syntenic ones

• Most genes in that chromosome got moved there from elsewhere



chromosomes 1A, 1B, 1D and 1H



1-2 2-3 3-4 4-5

-1



9-10 0-11 1-12 2-13 3-14 4-15 5-16 6-17 7-18 8-19 9-20 X axis is size (kb) of DNA fragments. Y axis represents the number of fragments in each size class

>20

8-9

7-8

6-7

5-6

Most of the non-syntenic genes are not expressed

- Are pseudogenes that got moved there •
- Some moved by transposon capture •
- Most moved by double strand break repair

Guo et al, 2023



### Carbonell-Bejerano et al, 2017

Mutation from Tempranillo to Tempranillo Blanco





Repetitive DNA & chromosomal reconfigurations

### Gaut et al., 2007



Intrachromosomal crossing over between inverted repeats can invert a whole segment

Crossing over between direct repeats on different chromosomes can result in a translocation

Recombination between duplicated genes can also result in novel alleles

# Amplification and deamplification of repetitive DNA Unequal crossing over

### Flavell, 1985; Jelesko et al., 1999

Repetitive DNA, due to its copy number, is prone to rapid change.

- This is known as DNA plasticity
- Repetitive DNA is either present in excess copy number or non-coding
  - Changes in it are survivable by a species.



https://eichlerlab.gs.washington.edu/research.html

Works for tandem DNA repeats

- Results from unequal alignment
- Leads to chromosomes with more or fewer repeat sequences
- Frequency of unequal crossing over in arabidopsis is 3 per million meiosis [Jelesko et al., 1999. PNAS 96:10302-10307]

### **Allele creation**

E.g., a1 locus of maize Yandeau-Nelson et al, 2006

The *a1* locus of maize consists of tandem repeats that can undergo unequal crossing over to generate new alleles



https://www.nature.com/scitable/topicpage/genetic-mutation-441

# Herbicide tolerance

Patterson et al, 2019



Kochia contains saponins, alkaloids, oxalates and nitrates that can be toxic to livestock, so it must be controlled in their diet. | File photo

Kochia is one of the Prairies' more damaging weeds. https://www.producer.com/2015/06/weed-of-the-week-kochia/

Unequal crossovers facilitated by transposon homology leads to increased copy number of EPSPS and thus glyphosate tolerance in kochia.



Note: unequal crossing over does not explain change in copy number in haploids

# **Replication slippage/ stutter**

Strand et al, 1993

aka Slipped strand mispairing

- Works for tandem DNA repeats
- DNA polymerases slip during DNA replication.

Using yeast mutants unable to repair mismatched DNA, suggested that replication slippage is more important than unequal crossover.

- During DNA replication, 1 strand temporarily disassociates from the other
- Re-anneals in misaligned configuration
- If mismatch is in primer strand (shown)
- Increased tract length if mismatch is in template strand
- Otherwise, decreased tract length



#### Flavell, 1985

Intrastrand recombination leads to deletions, unless the circles replicate



SIMPLIFIED SCHEME http://pathmicro.med.sc.edu/mhunt/dna18.jpg

In some organisms, circle will undergo rolling circle replication, followed by integration of the replicated DNA, resulting in amplification

Alternatively, the circle or the DNA replicated could become integrated in elsewhere in the genome.



Cohen et al, 2008



Cohen et al., 2008; Navrátilová et al., 2008

Found 2 - 20 Kb DNA rings of 5S rDNA or of the Bdm29 repetitive element in arabidopsis



Same repeats are often found on separate chromosomes, suggesting there is a way for repetitive families to move from one chromosome to another.

Probably responsible for moving NOR and R gene clusters to new locations

Eg, Taketa et al, 2015 NOR in Hordeum



Note the 2 extra NOR sites in H. guatemalense relative to H. jubatum.

# **Concerted evolution**

Once DNA has become repetitive, expectations are for different repeats to accumulate mutations at random, leading to divergence of repeated sequences over time

Repeats in tandem arrays are more similar than predicted if they were evolving independently.

This is achieved by

# **Unequal crossing over**

Repeats with accumulated mutations get deleted.

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Remaining repeat will get amplified with copies of itself

NOTE: Any divergent repeat that survives a deletion event and then amplifies itself provides a method by which variants can be spread throughout a genome and then maintained homogenous.

Whether a given sequence will become amplified or deleted is an entirely random process.

# **Gene conversion**

Also refers to interchromosomal strand replacement

- Migration of a DNA strand from donor DNA to acceptor DNA
- Replacement of acceptor sequence by donor sequence, process not clear
- Proofreading mechanism recognizes a mismatch, and repairs DNA using donor sequence as a template
  - The repeat preferred during conversion could then get amplified
  - Helps concerted evolution of sequences in different chromosomes or different parts of a chromosome



Gene Conversion.

http://obiweb.bcgsc.ca/medgen/medgen520/Block6\_files/im age011.gif

# **Tandem duplications**



Gu et al, 2016

#### Schiml et al., 2016

Found that multiple single strand DNA breaks in the same vicinity resulted in tandem duplications



# **Genome expansion and contraction**

### Shirasu et al., 2000

#### Hawkins et al., 2009

- Found only the LTR regions in barley
- Means there must be a way to lose retrotransposon DNA
- Suggest intra-strand recombination between LTRs

If DNA increases are not matched by deletions of old sequences, DNA content increases

Upper limit on DNA content may exist due to limits that DNA content imposes on rates of development, duration of life cycle, and cell size



A: Structure on an LTR retrotransposon. B: Barley DNA showing LTRs, but not the middle sequences. C: the retrotransposons that must have been there. D: A proposed mechanism for the loss of the internal sequences

# **Case study**

Wang et al, 2021 (Ma lab)

The *Rps11* locus in soybean contains the variability from all the mechanisms covered

There are 4 haplotypes



### **Source of genetic variation** Eg, Rasmussen & Phillips, 1997

"Plant breeding progress and genetic diversity from de novo variation and elevated epistasis"

The point is there is more genetic diversity in modern barley than was present in the ancestral lines. Hence the question, where did this come from?



https://www.flickr.com/photos/53400673@N08/12921979305



Don Rasmusson 1931 - 2024

Ron Phillips 1940 - 2023 Transposable elements are a major source of genetic variation that ranges from gross chromosomal alterations up to very fine tuning of the expression of cellular genes.

This, together with the observation that transposons are activated by stress and environmental changes, led to the hypothesis that TE are involved in host adaptation to environmental changes.

Through modification of gene regulation, TE have been proposed as major factors in macroevolution

# **Genomic shock**

# The significance of responses of the genome to challenge McClintock, 1984

"In the future, attention undoubtedly will be centered on the genome, with greater appreciation of its significance as a highly sensitive organ of the cell that ... senses unusual and unexpected events, and responds to them, often by restructuring the genome."

When a plant becomes ill-adapted to its environment, (i.e, major stresses are imposed on the plant) the mechanisms that normally prevent too much change are disrupted.



This allows for a burst of change in the genome, permitting the creation of a new genotype better adapted to the new environment.

• The new individual(s) can then establish a new population.

# Activation of retrotransposons & transposons

### Flax genotrophs

### Durant, 1962

Flax genotype "Stormont Cirrus" = 'plastic genotroph'

- Grow under hot greenhouse conditions for 5 weeks
- Get phenotypic changes depending on fertilizer
- These changes are stable and cannot be reversed
  - NPK → Large form
  - NK → Small form

#### Cullis, 2005

- The genomic effects are reproducible
- Some genotypes "stable" and don't respond
- Crosses responsive × stable indicate "responsive" under genetic control

### Evans et al, 1966; Cullis, 1974

L genotrophs have 10% more DNA than plastic types

• Large increase in moderately repetitive DNA sequences

S genotrophs have 6% less DNA than plastic types

have 70% less rDNA than plastic and L types



Large and Small genotrophs of flax.





#### Chen et al, 2005; Henikoff, 2005

One particular DNA insertion LIS-1 (Linum Insertion Sequence); appeared in same position in 5 independent lines and also found in various flax and linseed varieties

Like changes in rDNA, appears in shoot apical meristem first

### **Effect of Tissue Culture**

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DePaepe et al., 1982
```

Although most changes take place over evolutionary time, they can be very rapid, as illustrated by doubled haploids in tobacco.

Note changes as large as 10% obtained in just one generation.

Most times, the change will not be as dramatic.





DNA content of doubled haploids of tobacco

#### Joachimiak and Ilnicki, 2003

2-year old callus cultures of *Allium fistulosum* showed increasing occurrence of cell polyploidization and chromatin elimination.

Chromatin elimination was associated with "heterochromatic spikes" protruding from surface of the nuclei, was observed to be released into micronuclei.



#### Grandbastien, 1998

Activation of retrotransposons by stress and environmental factors is common.

• The activity of retrotransposons is tightly controlled, and abiotic and biotic stresses are major factors in their transcriptional and transpositional activation.

The most well characterized plant retrotransposons are particularly affected by protoplast isolation or in vitro cell or tissue culture.

- Insertion of retrotransposons into coding sequences after protoplast or cell culture was demonstrated in *Nicotinana plumbaginifolia* and in rice, indicating that retrotransposition might make a significant contribution to somaclonal variation.
- The first direct evidence of activation of a plant retrotransposon by stress came from the discovery that expression of *Tnt1A* was highly induced in protoplasts isolated from tobacco leaf tissue.

Found that protoplast isolation, as well as cell and callus culture, induces major modifications of cell metabolism and gene expression.

- This is characterized by the activation of growth and stress-related genes, (or defense genes, which are activated after pathogen attack).
- Is the activation of several plant retrotransposons linked to the activation of cell division or the activation of stress responses, or both?
- Ex: The expression of *Tto1* (element in tobacco) is induced by viral attacks, wounding, salicylic acid and jasmonate.



Amplification of pong elements in rice C5924 before (L) and after (R) cell culture. Jiang et al., 2003

Same effect seen in tissue-cultured rye, but foldback transposon inserted in consistently the same genomic positions both in in vivo and in vitro cultivated rye (Alves et al., 2005)

### **Adverse environments**

### Ceccarelli et al, 1992



Effect of germination temperature on tall fescue

### Polyploidy as a trigger of instability

McClintock believed that genomic incompatibilities unmasked by interspecific hybridization are among the causes of genomic shock

Problems introduced by polyploidy: increased gene dosage and genome size, replication of multiple genomes, ensuring homologue pairing while preventing homoeologous pairing



Grass family includes young and old polyploids. Levy and Feldman, 2002

# DNA plasticity and species divergence

Kato et al, 2004 (Birchler lab)

As variant repeats get amplified at random, isolated populations would be expected to differ in their repeats

	1	2	3	4	5	6	7	8	9	10
A188		1 - 1 8 - 8				1	11			
A632			81							
B37						1				
B55		11.1		-			11			
B73	11	**** 1973	81			10				
BMS		1								
K10								1	*	
KYS	1:	25	88							

Used a FISH mixture of different repetitive probes to uniquely "paint" maize chromosomes

# Standing variation

### Anderson et al, 2016 (Stupar lab)

Notice the amount of standing variation in soybean, as compared to the changes from fast neutron mutagenesis.



### Shen et al, 2018



• 46.13 Mb > Williams 82

### Ohtsubo et al., 1991

355 bp repeat in rice

Genome	Copies/haploid
O. sativa cv. C5924	2000-3000
cv. Sasanishiki	700-900
cv. Koshihikari	3400-4300
cv. Nipponbare	4600-6000
O. glaberrina	540-680
Setaria italica foxtail millet	-0-

### Cumulative effects of DNA plasticity lead to large effects



e.g., maize (Rayburn et al., 1989)		
Inbred	pg DNA/4C nucleous	
Va35, pop. 1	10.31	
Va35, pop. 2	10.06	
Gaspe Flint	10.06	
KYS	11.46	
Zapolote Chico	14.35	



	-red pepper (Mukherjee & Cultivar pg DNA/4C n	Sharma, 1990) <u>ucleous</u>
ł,	69/33	18.38
-	K-2553	19.30
21	6C-173358	20.58
3	U8-45	21.34
	BDJ/NKG-297	22.98



Díez et al, 2013. Genome size in Mexican maizes relative to B73. Median +  $\frac{1}{4}$  and  $\frac{-3}{4}$ . Yellow = maize; purple = teosinte.

### Effect of DNA amplification on chromosome pairing

Reed and Burns, 1989; Reed et al., 1992





As changes accumulate between diverging populations, meiotic pairing becomes more difficult, increasing speciation

E.g.- pairing abnormalities in tobacco with increased DNA content

Doubled haploid lines of tobacco had more (up to 41%) DNA than the parents

Interpretive drawing of multivalent in photo A cell with 21 II and 1 VI in semiclosed configuration.

Increase in repeats on different chromosomes allows non-homologues to pair - Note multivalent and interpretive drawing

# Role of repetitive DNA in speciation

Repeated DNAs hybridized together	pg DNA	% <i>L. hirsutus</i> repeated DNA hybridized
hirsutus + hirsutus	20.3	100
hirsutus + tingitanus	17.9	50
hirsutus + odoratus	17.2	62
hirsutus + sphaericus	14.2	17
hirsutus + clymenum	13.8	14
hirsutus + articulatus	12.5	44
hirsutus + angulatus	9.2	21