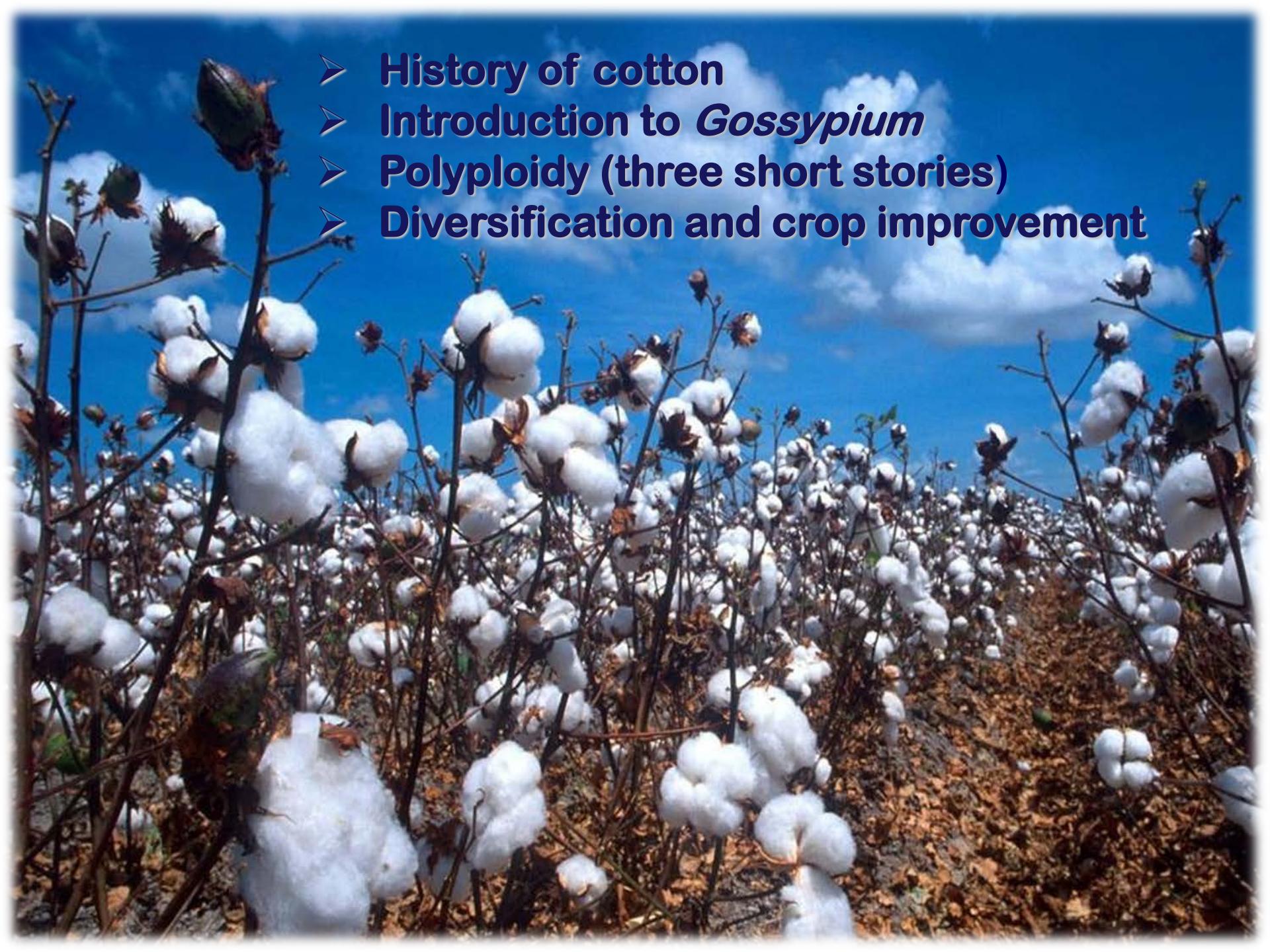


- 
- A photograph of a cotton field under a clear blue sky with scattered white clouds. The foreground is filled with cotton plants, their brown stems and branches bearing numerous large, fluffy white cotton bolls. Some bolls are fully open, while others are still green and closed. The ground is covered with fallen brown leaves.
- History of cotton
  - Introduction to *Gossypium*
  - Polyploidy (three short stories)
  - Diversification and crop improvement



J. Stewart









C<sub>1</sub>

5 mm

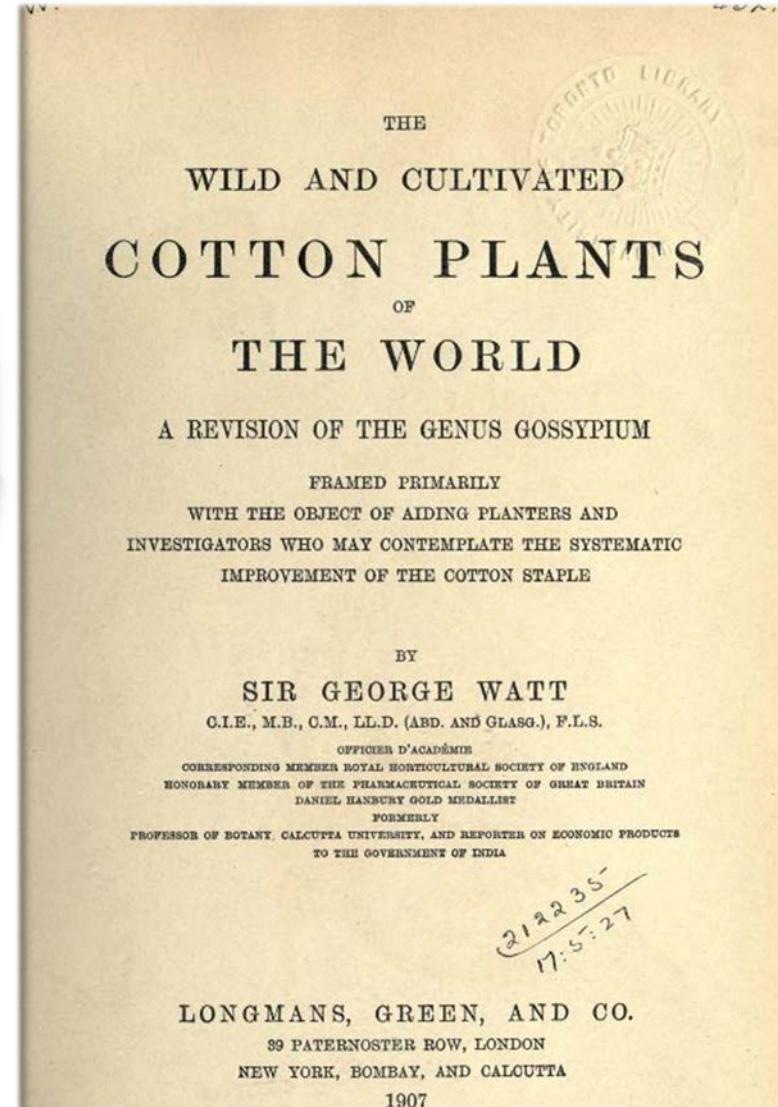




Agostino Todaro  
1818-1892



Sir George Watt  
1851-1930



“It would not be far from correct to describe cotton as the central feature of the world’s modern commerce” (Ch. 1)

INTRASPECIFIC DIFFERENTIATION IN  
*GOSSYPIUM HIRSUTUM*

J. B. HUTCHINSON  
Empire Cotton Growing Corporation Cotton Research Station,  
Namulonge, Uganda



Stanley G. Stephens  
1911-1986

Joseph B. Hutchinson  
1902-1986

Vol. 100, No. 912

The American Naturalist

May-June, 1966

THE POTENTIALITY FOR LONG RANGE OCEANIC  
DISPERSAL OF COTTON SEEDS\*

S. G. STEPHENS

J. B. HUTCHINSON, R. A. SILOW  
and S. G. STEPHENS

Wendel and Goodman, 2011, Nat.  
Acad. Sci. Biograph. Memoirs

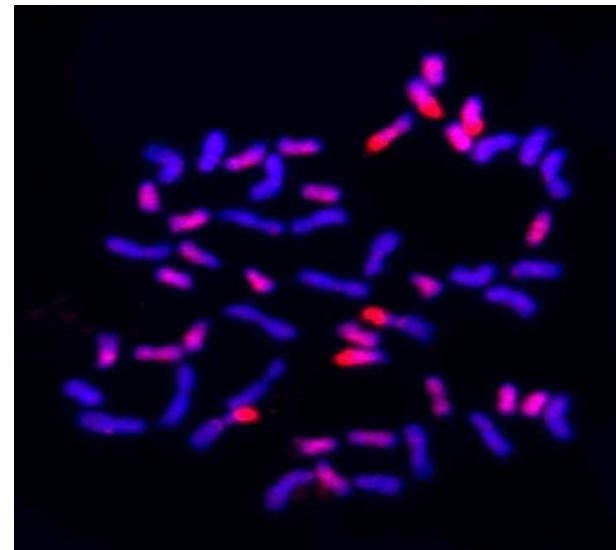
Gavriil S. Zaitsev  
1887-1929



- Denham (1924)
- Longley (1930)
- Webber (1935)
- Skovsted (1933, 1937)



**James Otis Beasley  
1909-1943**

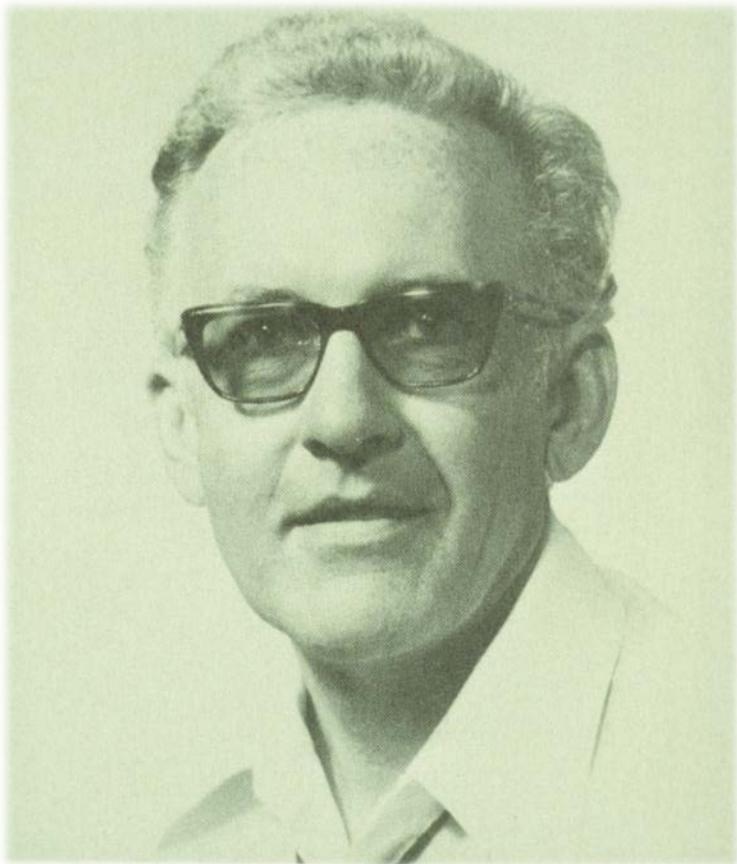


**The American Naturalist, Vol. 74, (1940)**

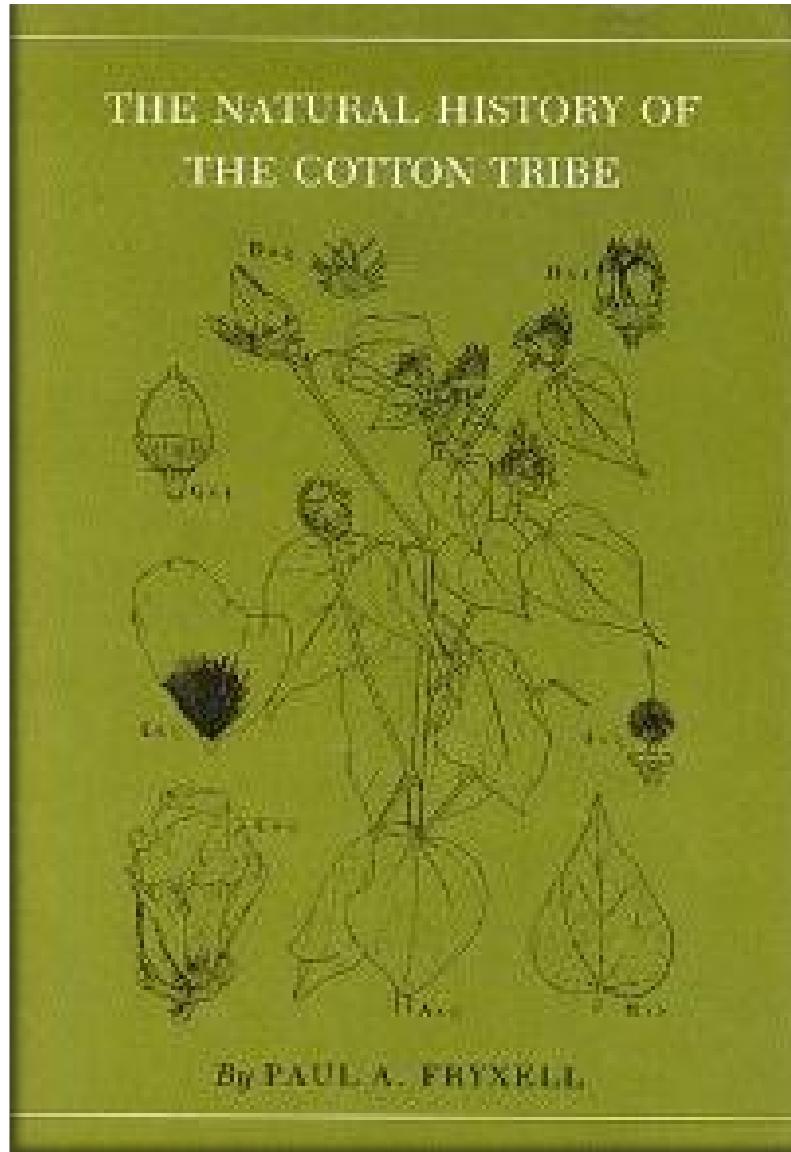
### THE ORIGIN OF AMERICAN TETRAPLOID GOSSYPIUM SPECIES<sup>1</sup>

13-chromosome with Asiatic 13-chromosome species. In the present work tetraploids of this type were produced by doubling the chromosome number in hybrids of *G. therberi* Tod. × *G. arboreum* var. *neglectum* Hutchinson and Ghose.

ploid type. These facts leave no doubt that the American 26-chromosome cottons are allotetraploids, with one parent species similar to existing American 13-chromosome species and the other similar to Asiatic 13-chromosome species. The synthesized tetraploid can be classified as a composite of chromosome species, but



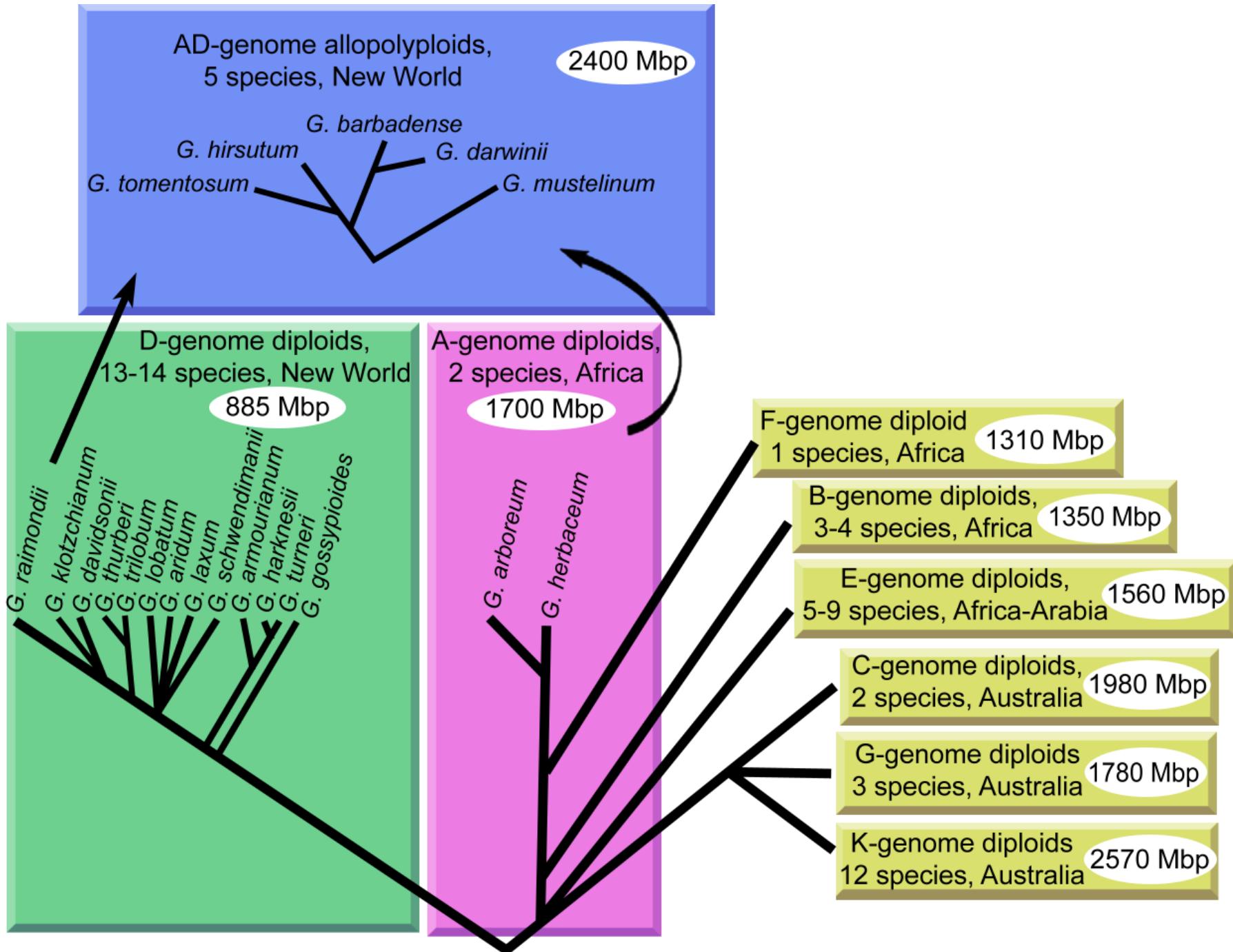
**Paul Fryxell**



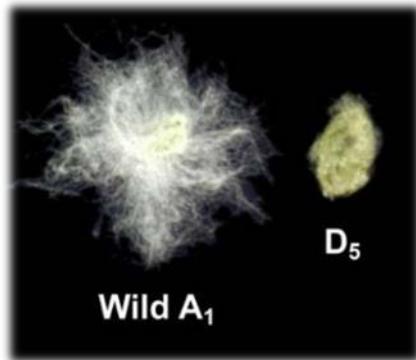


**“We were dwarfs on the shoulders of giants, so that we can see more than they, and things at a great distance, not by virtue of any sharpness of sight on our part, or any physical distinction, but because we are carried high and raised up by their giant size”**



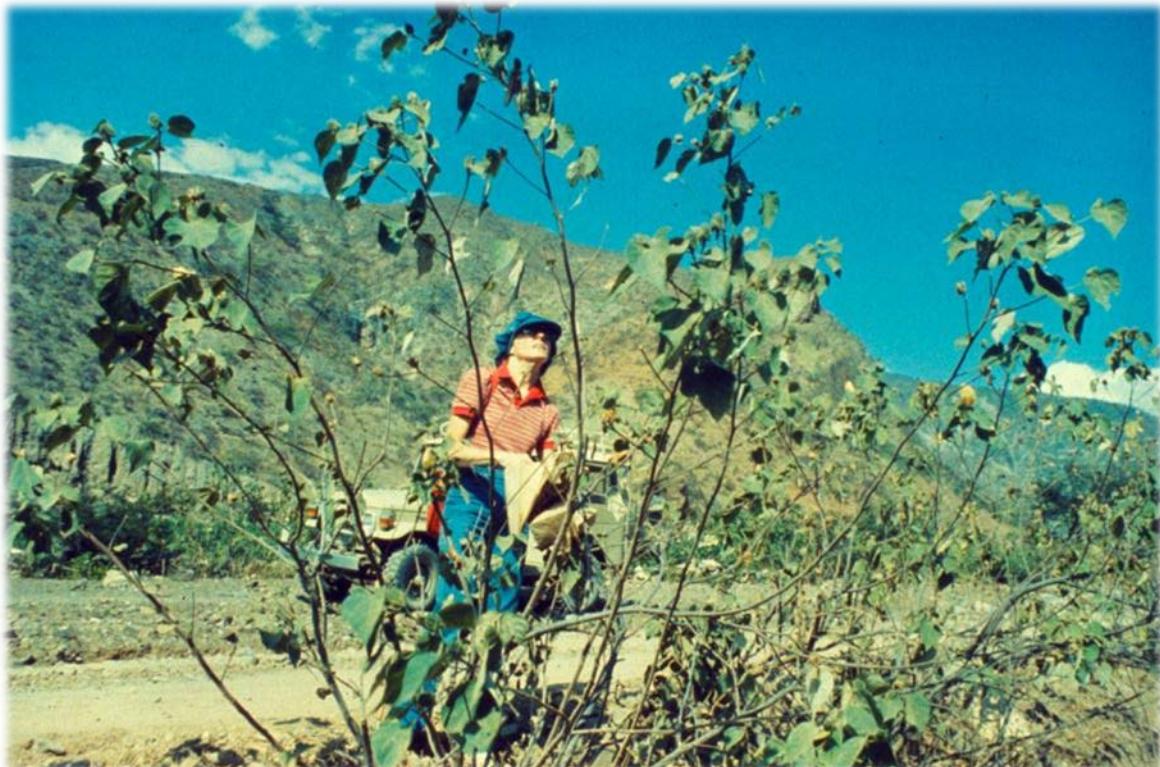


# *Gossypium raimondii*



- Not even described until 1932 (by Oskar Ulbrich)
- Work by Harland, Gerstel, Phillips, Stephens, showed that this is among the best models of the D-genome ancestor of the allopolyploids
- Phillips (1966) states that the species was "represented by a relatively few individuals, and that these are confined to a narrow geographical range"
- Intentional eradication as a "dangerous plant" (along with many other Malvaceae) by the Peruvian government

# *Gossypium raimondii*

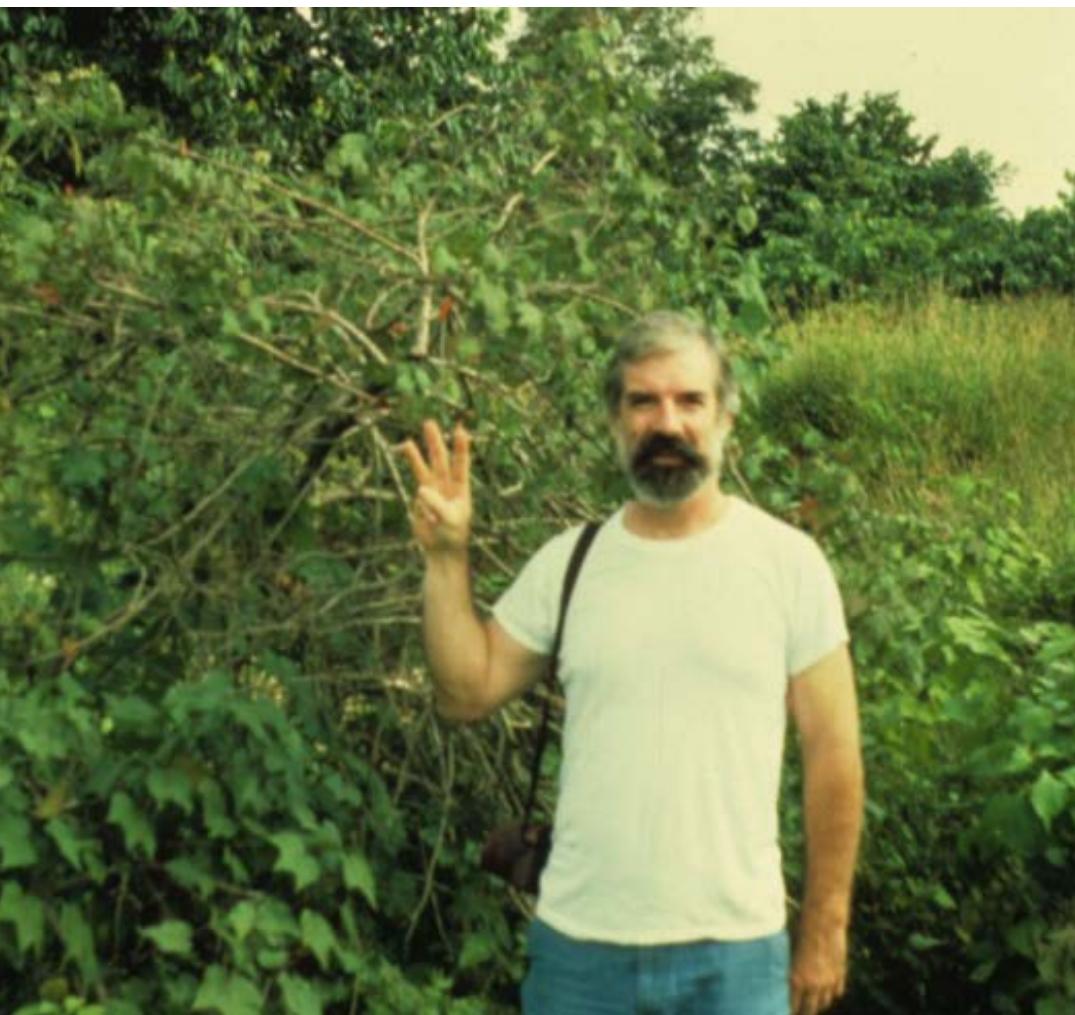


***Gossypium raimondii***

## Collections in Northern Peru

Plant Genetic Resources News!, 1985

B.B. Simpson 1/, J.M. Vreeland 2/ and R. Ferreyra 3/



**James “Mac” McD. Stewart**



**Ed Percival**

**Sumario. Krapovickas, A. & G. Seijo. 2008. *Gossypium Ekmanianum* (Malvaceae), algodónsilvestre de la República Dominicana. Bonplandia 17: 55-63.**



- First proposed as a species in 1928 by Wittmack
  - Endemic to the Dominican Republic; “perfectly wild” characteristics
- Reclassified as *G. latifolium* var. *ekmanianum* by Roberty in 1942
- Reclassified as *G. hirsutum* var. *ekmanianum* by Roberty in 1950
- Reclassified as *G. tricuspidatum* var. *ekmanianum* by Mauer in 1954
- Treated as a form of *G. hirsutum* by Fryxell and modern workers

DOMINICAN REPUBLIC (A.S. 1211 to A.S. 1225)

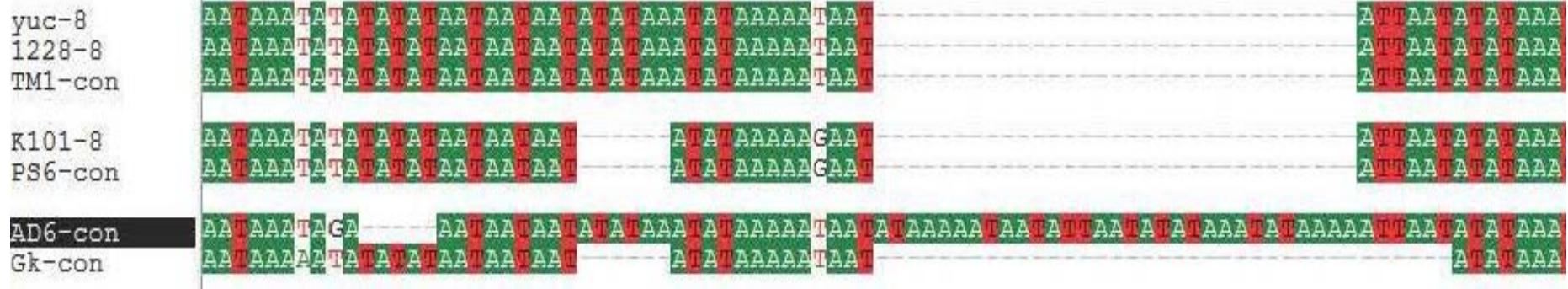
# Cotton Collecting on Caribbean Islands and South Florida

J. Schwendiman, 1/ A.E. Percival 2/ and J.L. Belot 3/

In the Dominican Republic collecting was carried out in only a very limited area, namely the areas bordering the old and new highways (Carretera Sanchez) between Azua and Barahona. A collecting mission was undertaken in this country in 1980 and, in an electrophoretic survey of this material carried out by Bourdon (1984), samples from this area showed a surprising degree of enzymatic variability.

2245	JAMAICA	466	4	4	4	4	4	4	4	6	4	6	4	1	4	4	4	4
2246	JAMAICA	467	4	4	4	4	4	8	4	2	4	N	4	2	4	4	4	4
2247	JAMAICA	468	4	4	4	4	4	8	4	2	4	N	4	2	4	4	4	4
2249	GRAND CAYMAN	469	4	4	4	4	4	8	N	2	4	6	5	2	4	4	4	4
2250	GRAND CAYMAN	470	4	4	4	4	4	2	4	6	4	6	4	2	4	4	4	4
2252	GRAND CAYMAN	471	4	4	4	4	5	2	4	2	4	6	4	2	4	4	4	4
2253	GRAND CAYMAN	472	4	4	4	4	4	2	4	2	4	6	4	2	4	4	4	4
2254	GRAND CAYMAN	473	4	4	4	4	5	2	4	2	6	6	5	2	4	4	4	4
2255	GRAND CAYMAN	474	4	4	4	4	4	2	4	2	4	4	1	4	4	4	4	4
2265	DOMINICAN REP	475	2	4	4	4	4	4	5	6	4	6	4	2	4	4	4	4
2266	DOMINICAN REP	476	4	4	4	4	4	4	4	6	4	6	4	1	4	4	4	4
2267	DOMINICAN REP	477	4	4	4	4	4	4	4	6	4	N	4	2	4	4	4	4,6
2268	DOMINICAN REP	478	4	4	4	4	4	4	4	6	4	6	4	2	4	4	4	4,6
2270	DOMINICAN REP	479	4	4	4	4	4	4	4	6	4	6	4	2	4	4	4	4,6
2271	DOMINICAN REP	480	4	4	4	4	4	4	4	6	4	6	4	1,2	4	4	4	4
2272	DOMINICAN REP	481	4	4	4	4	4	4	4	6	4	6	4	1	4	4	4	4,6
2274	DOMINICAN REP	482	4	4	4	4	4	8	4	6	4	N	4	1	4	4	4	4
2276	DOMINICAN REP	483	4,2/4	4	4	4	4	4	5	6	4	6	4	1	4	4	4	4
2277	DOMINICAN REP	484	4	4	4	4	4	4	4	6	4	6	4	1	4	4	4	4
2278	DOMINICAN REP	485	4	6	4	4	4	8	4	2	4	N	5	2	4	4	4	4
2280	PUERTO RICO	486	4	4	4	4	4	8	4	2	4	N	4	2	4	4	4	4
2283	PUERTO RICO	487	4	4	4	4	4	8	N	6	4	6,N	5	2	4	4	4	4
2284	PUERTO RICO	488	4	4	4	4	4	8	4	6	4	6,N	5	2	4	4	4	4
2285	PUERTO RICO	489	4	4	4	4	4	8	4	2	4	N	4	2	4	4	4	4

# *G. ekmanianum*: a sixth polyploid species?



**Paul A. Fryxell, 09:42 PM 8/20/98 , Wake Island cotton**

---

Date: Thu, 20 Aug 1998 21:42:41 -0500 (CDT)

To: jfw@iastate.edu

From: pfryxell@mail.utexas.edu (Paul A. Fryxell)

Subject: Wake Island cotton

Dear Jonathan:

A seed sample of the Wake Island cotton is on its way to you. It is not a large sample, but I am sending half to you and half to Ed Percival to put in the germplasm collection -- and presumably be multiplied. The seed comes courtesy of Derral Herbst of the Bishop Museum in Honolulu. I have seen a poor herbarium specimen of this many years ago, and could only learn enough to be intrigued. Derral calls it *G. hirsutum* and it may be kin to the *G. hirsutums* from Tahiti, but my recollection from seeing the herbarium sheet (collected by the late Ray Fosberg) was that it might show some kinship with *G. tomentosum*. Having living material should put that question to rest. Cheers. --Paul

Paul A. Fryxell

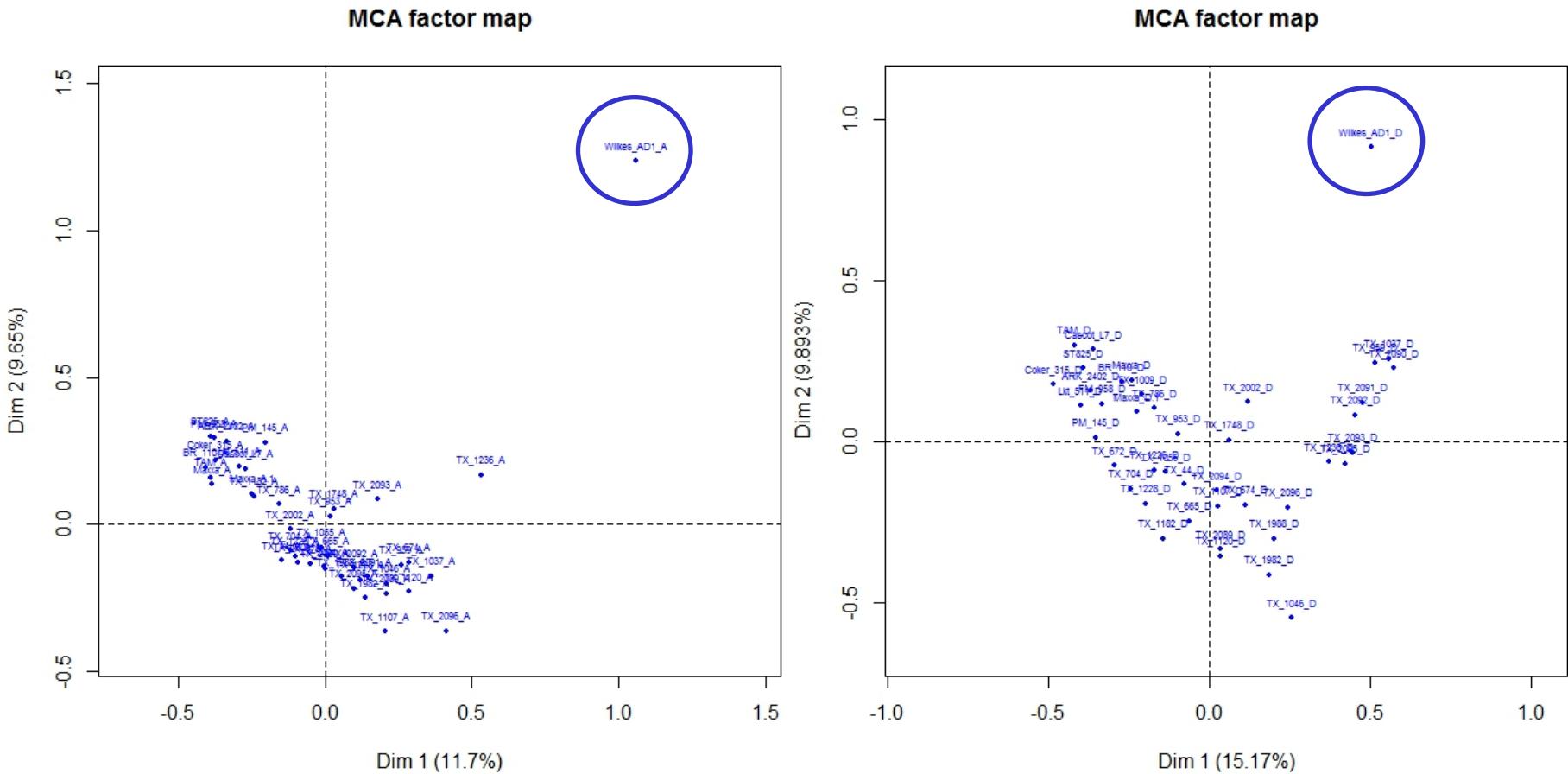
Dept. Botany

University of Texas

# Wake Island Cotton: a seventh polyploid species?

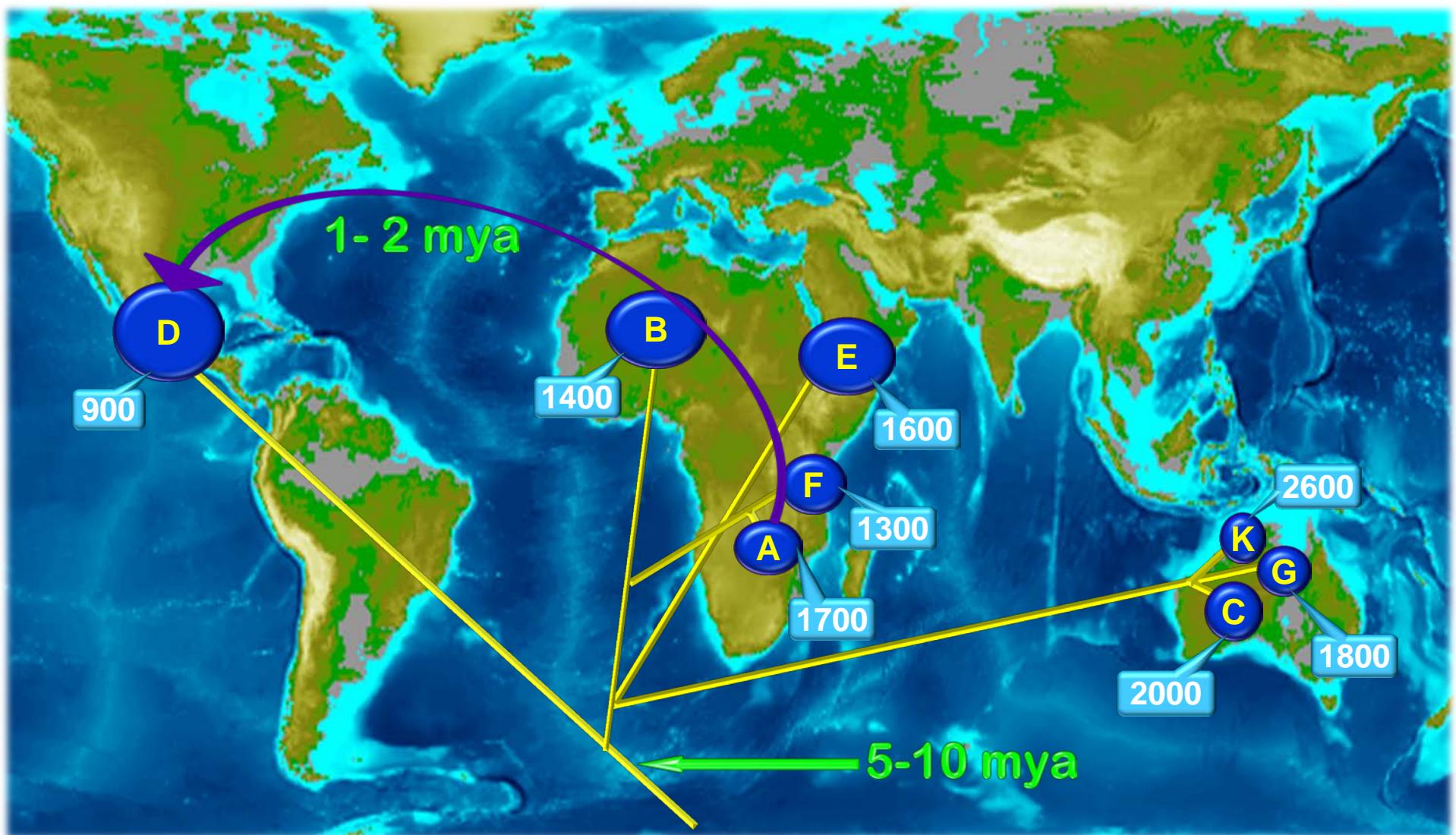


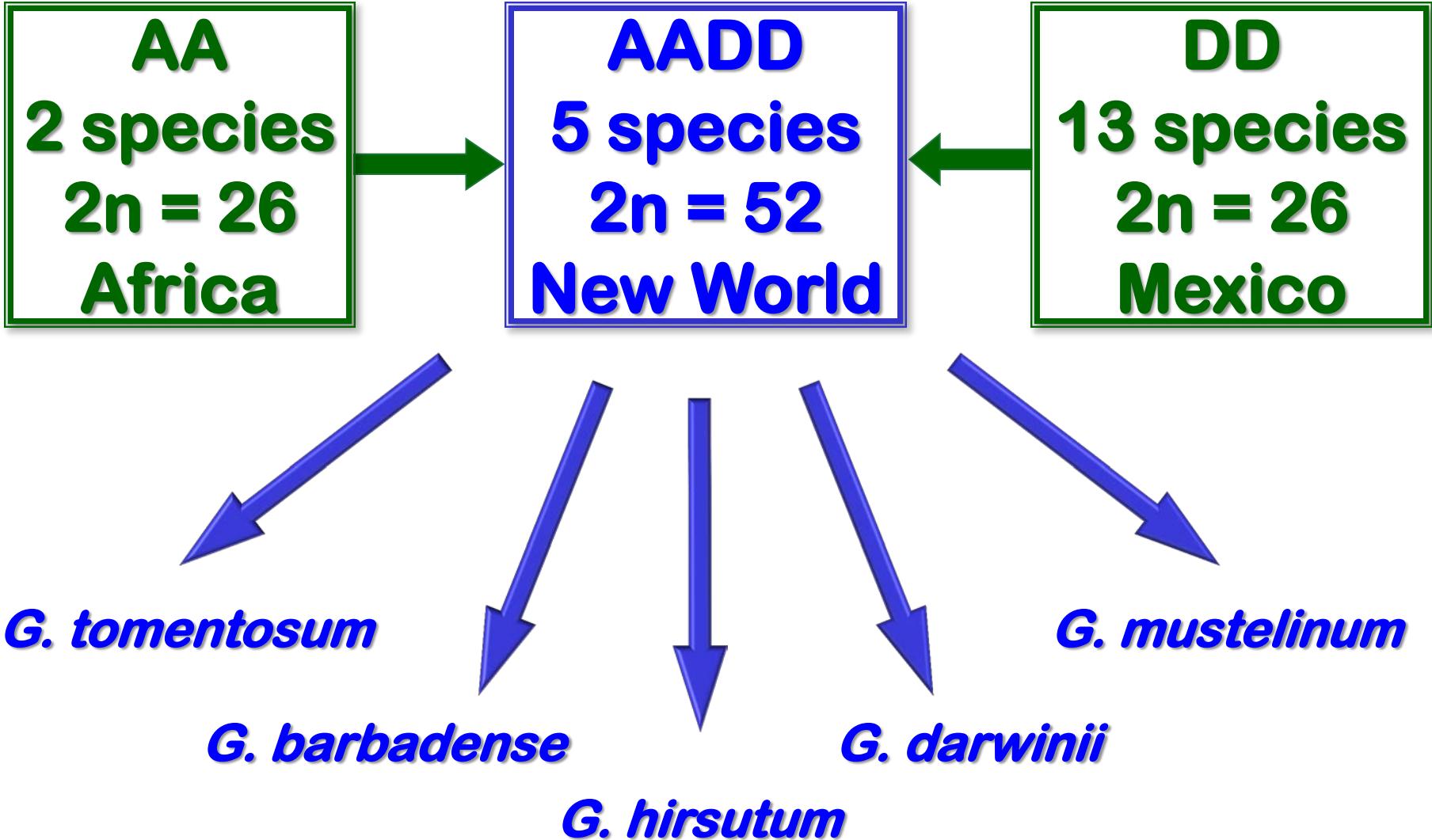
- Sequenced ~100 genes in a diverse panel of all allopolyploids
- Separately analyzed both the At and the Dt homoeologs



*Gossypium stephensii* or *G. fryxellii*?

# Phylogenetic history of *Gossypium*









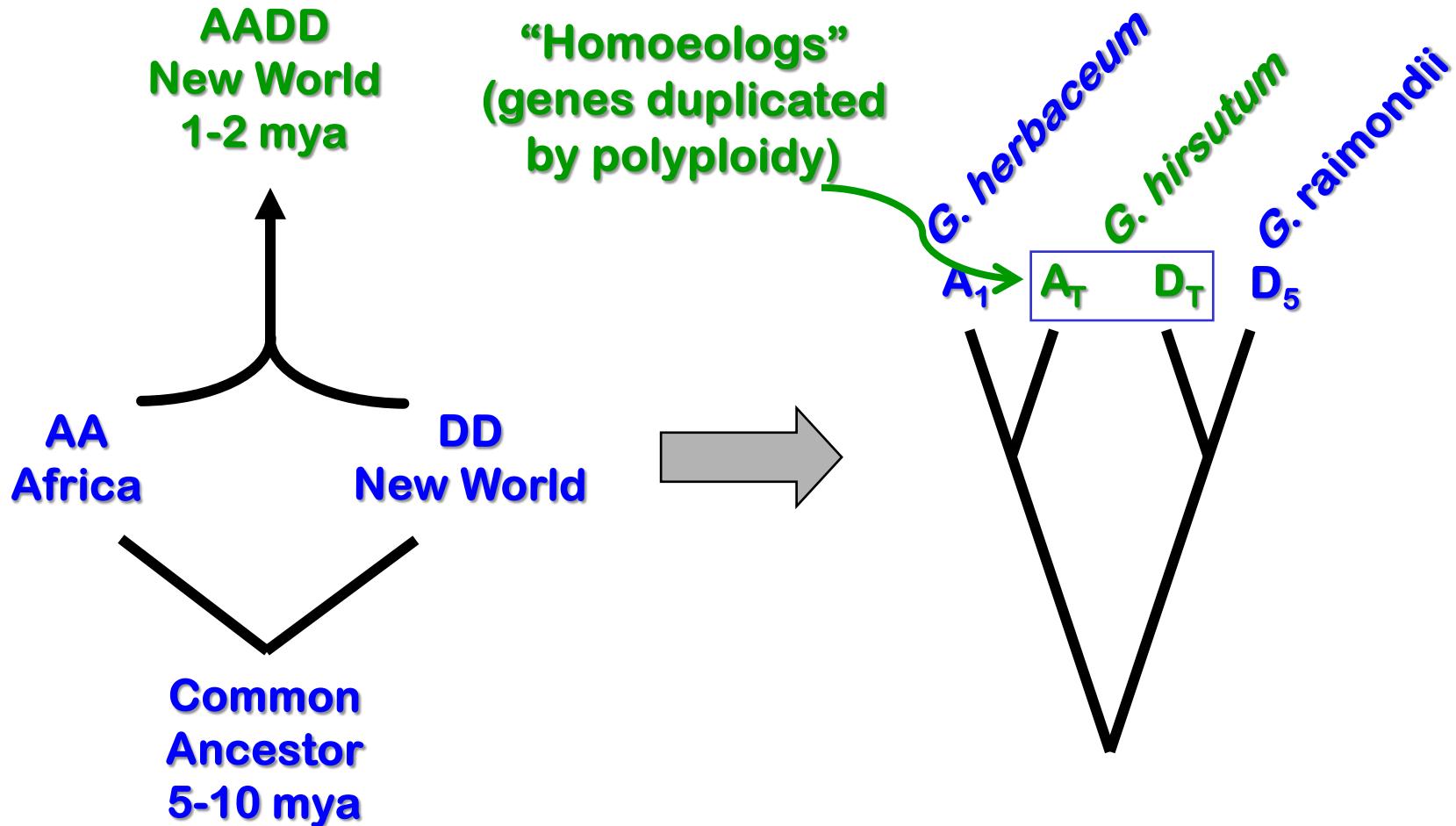




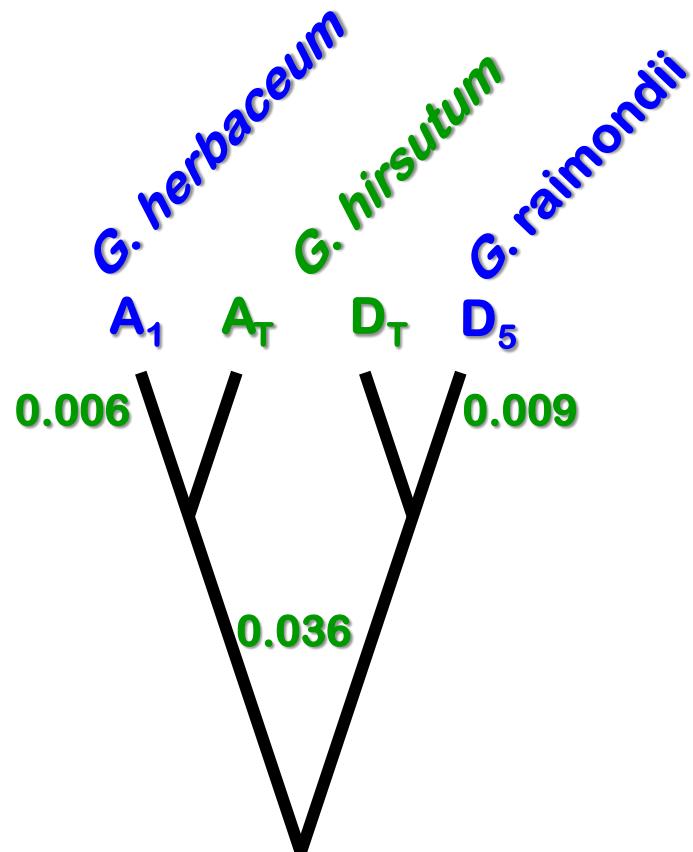


© Y. Arthus-Bertrand

# A framework for studying polyploidy in *Gossypium*



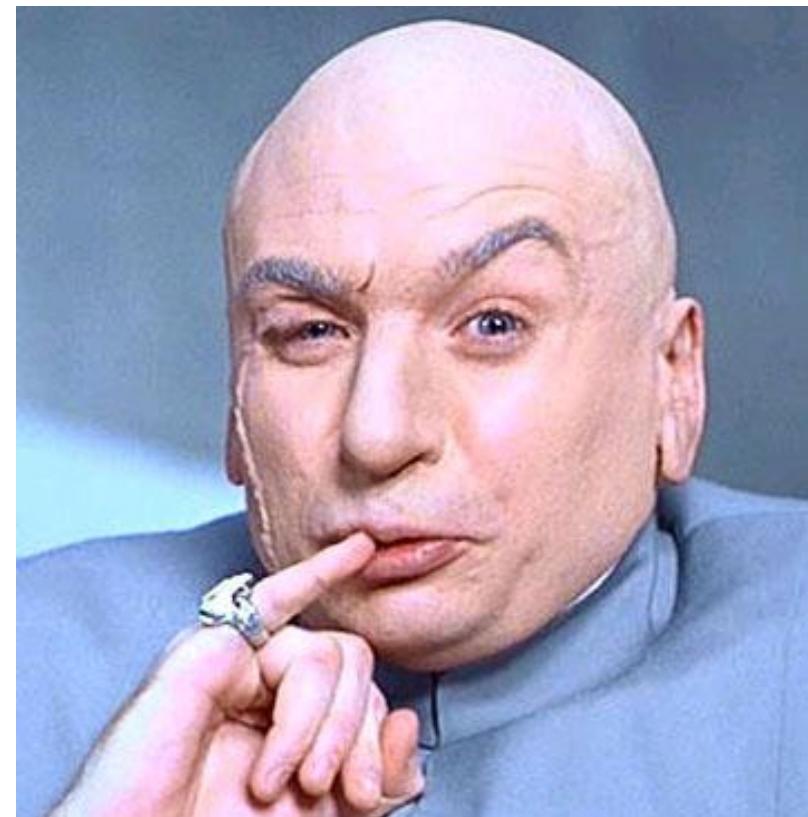
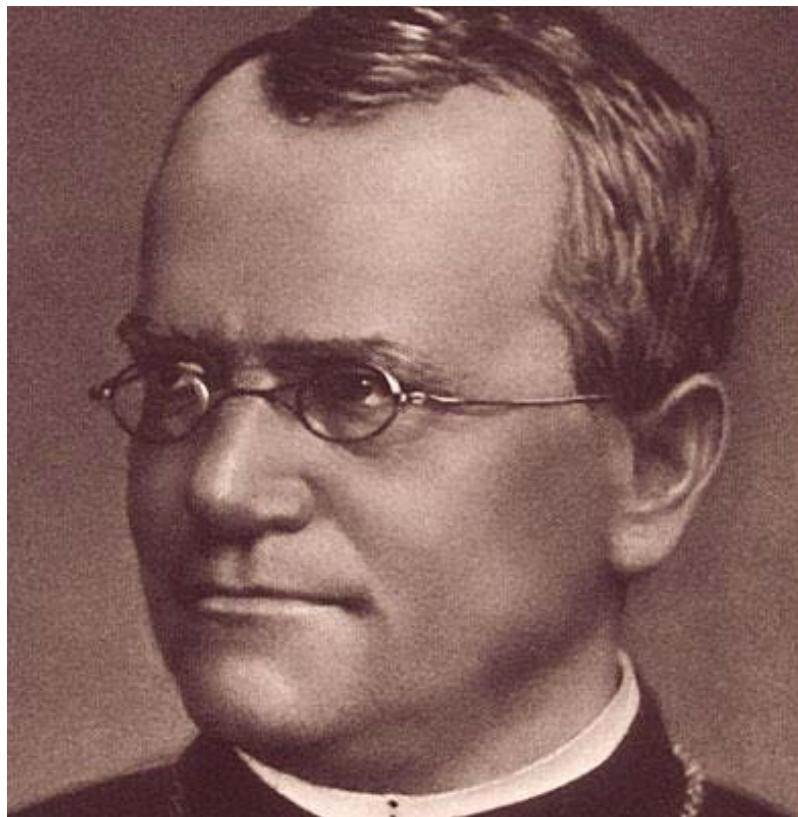
# Evolutionary of diploid and polyploid cotton (~10,000 genes)



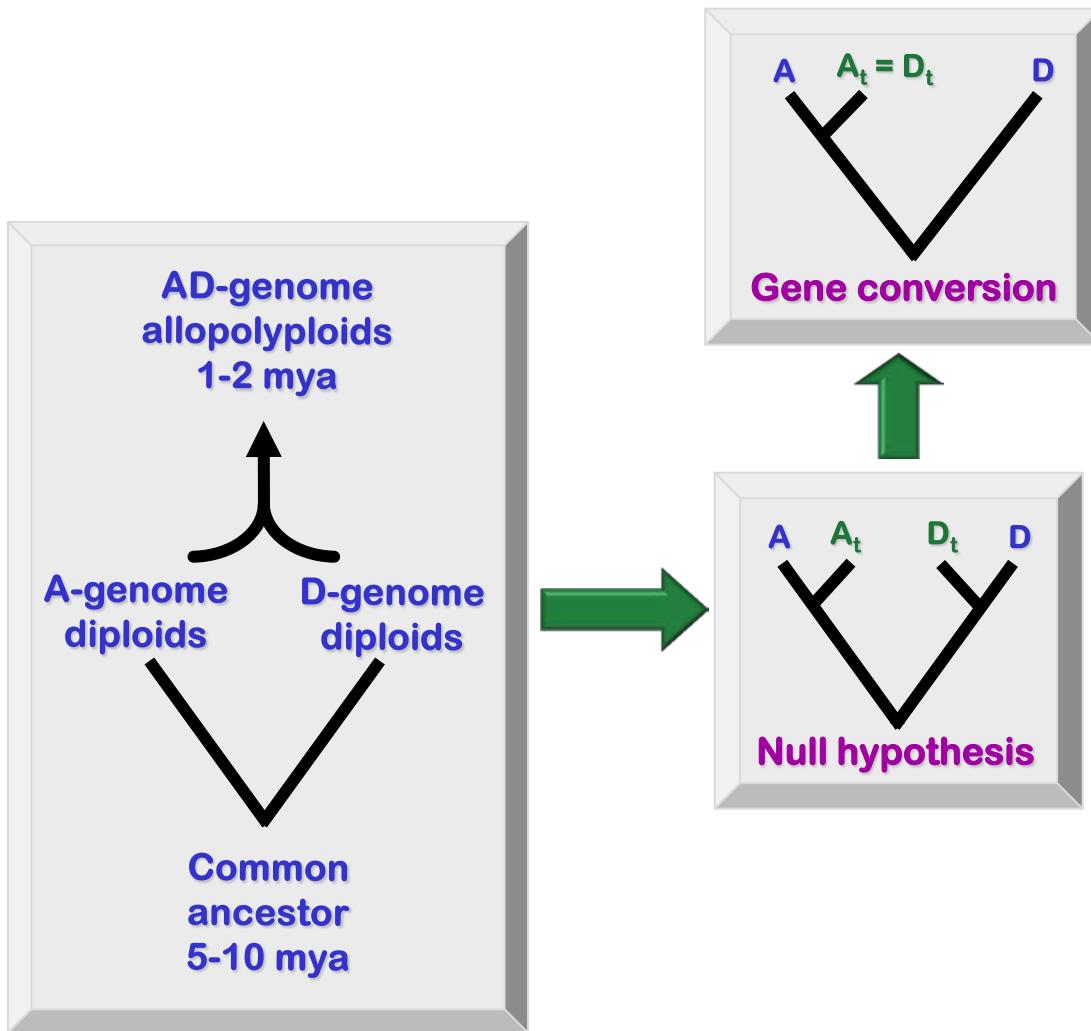
- A-genome parent ~50% better model than D-genome parent

# Story 1

## Gregor Mendel Has an Evil Twin

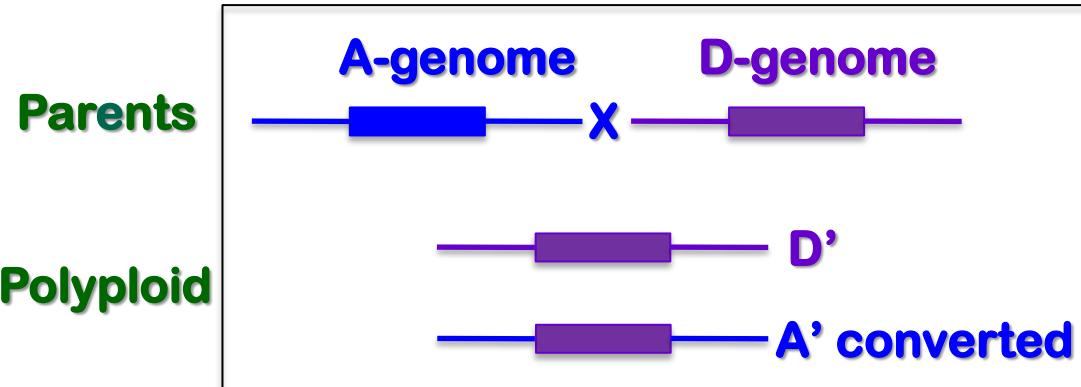


Non Mendel



Parents

Polyplloid



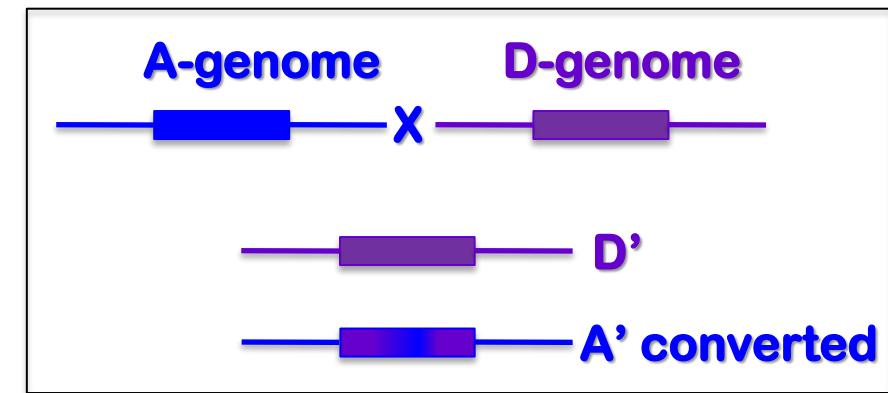
Diversity eliminating process

*G. hirsutum* *G. barbadense*

1818

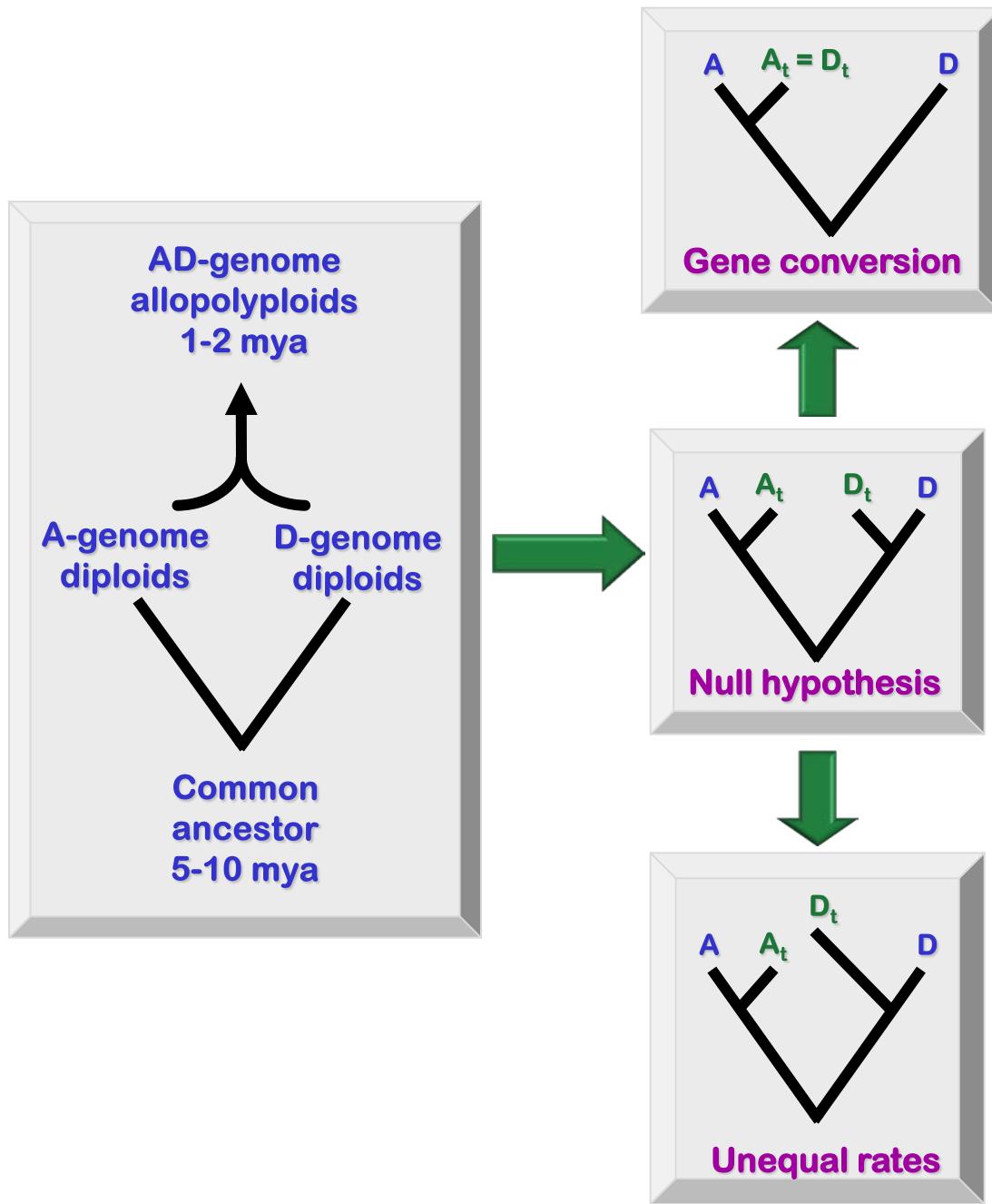
1315

927



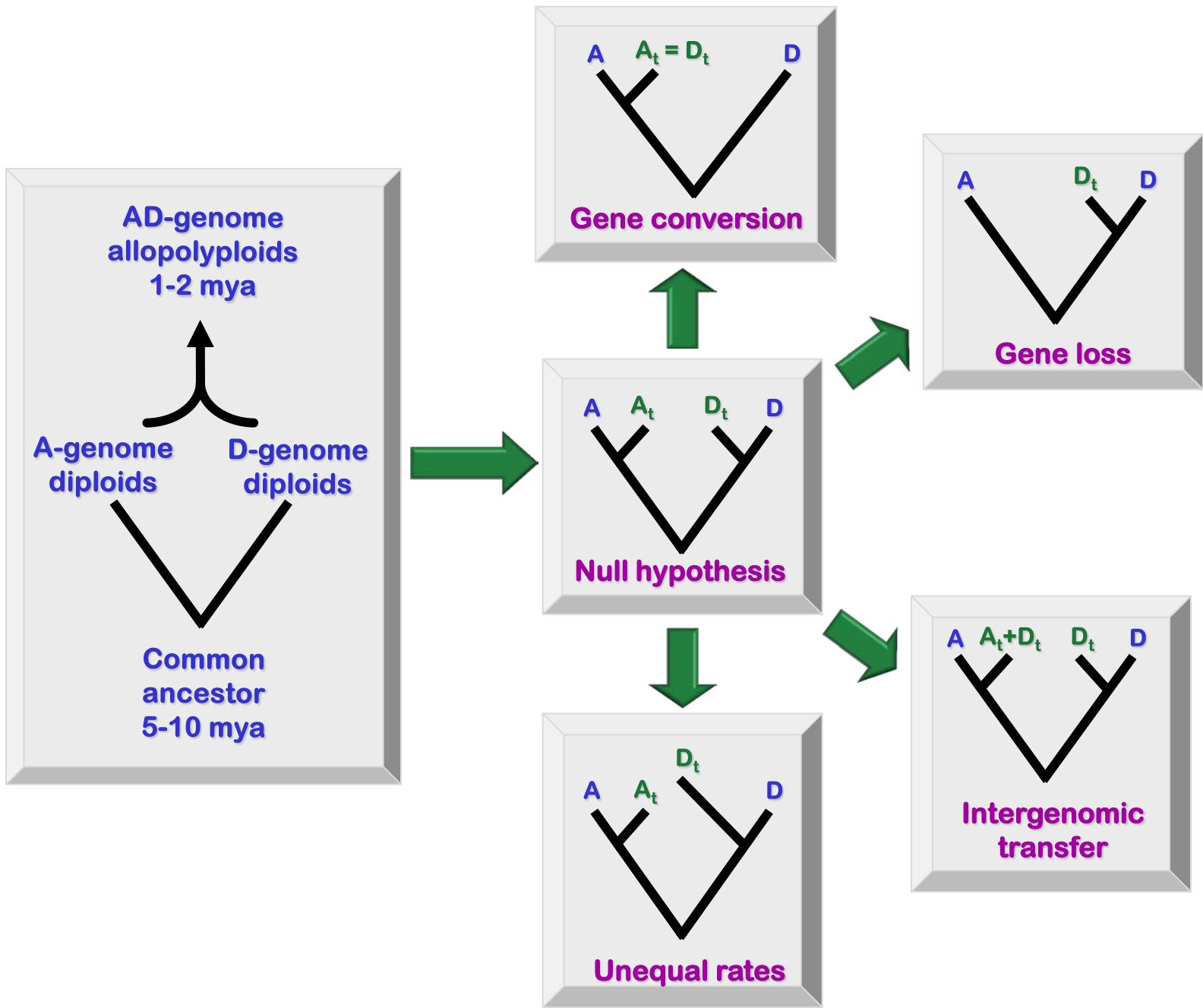
Diversity creating process

- Detected for 3852 genes (~5%)
- Ongoing process



## Nucleotide diversity for 375 homoeolog pairs in 48 accessions of *Gossypium hirsutum*

	A <sub>T</sub>	D <sub>T</sub>	A <sub>T</sub> :D <sub>T</sub>
5' UTR	0.0064	0.0031	2.065
Exon	0.0032	0.0017	1.882
Intron	0.0066	0.0029	2.276
3' UTR	0.0084	0.0037	2.270

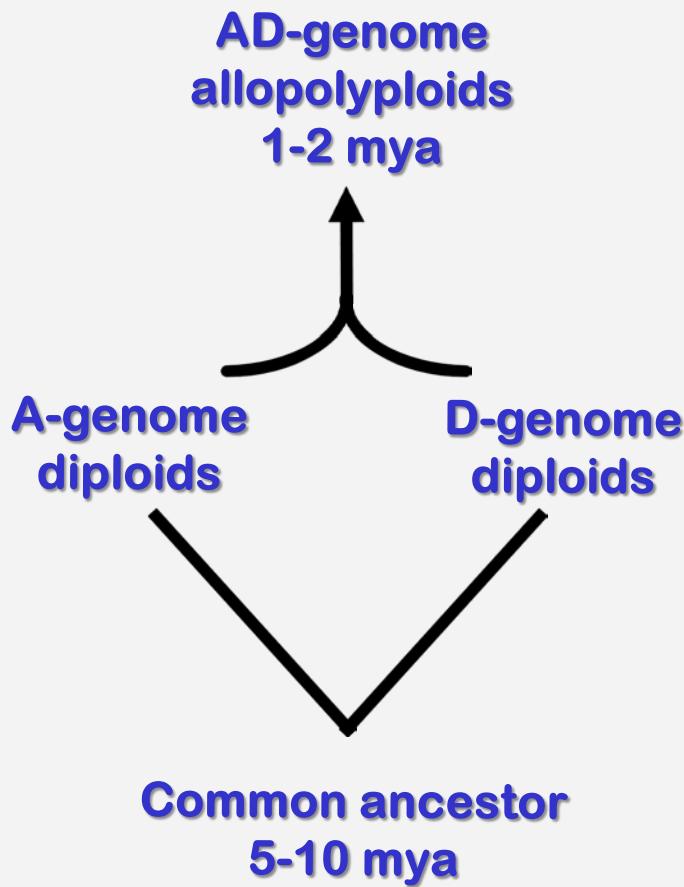


# Story 2

Why  $1+1 \neq 2$ ;  $\frac{1+1}{2} \neq 1$

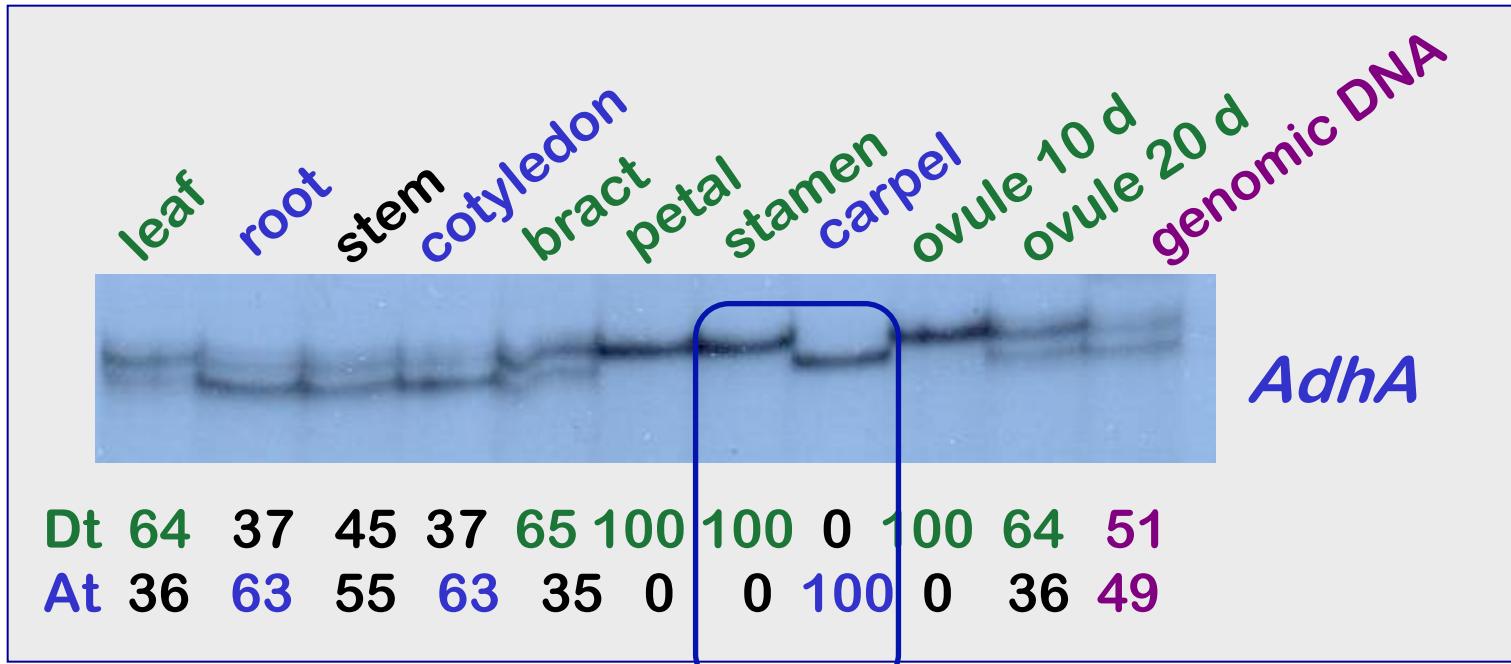


Fuzzy Math



Gene expression?

# Biased expression of duplicated genes

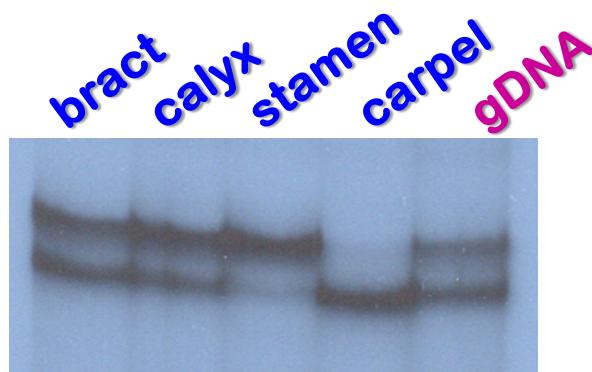
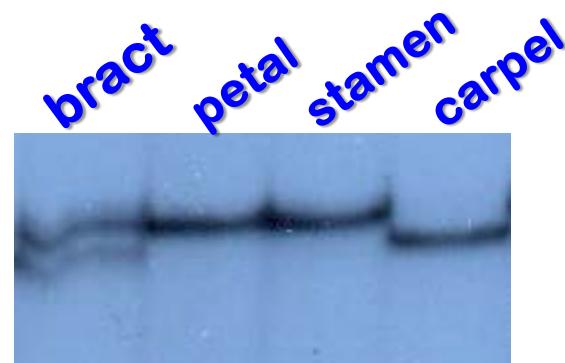


Reciprocal silencing of alternative homoeologs

*G. hirsutum*  
Natural allopolyploid (1-2 mya)

*AdhA*

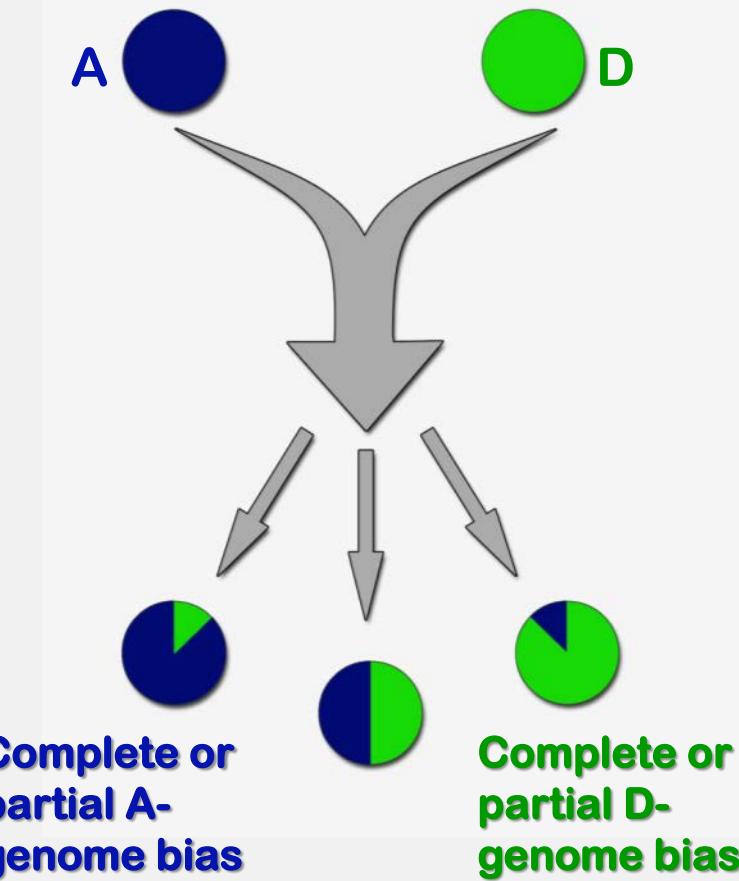
Synthetic allopolyploid  
2(A2D1)



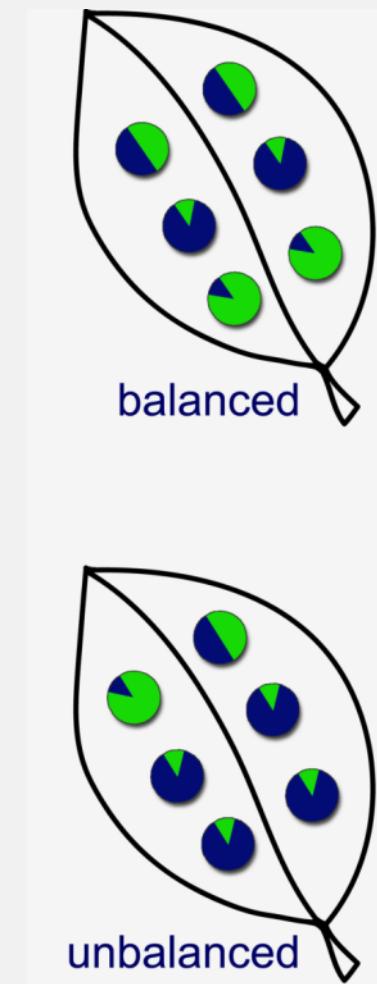
- Organ-specific silencing of homoeologs can be immediate
- Epigenetic phenomenon
- Instantaneous sub-functionalization
- Genomic in scope

# Biased homoeolog expression in polyploids

## Gene level



## Genomic scale



# Homoeologous ESTs

*Imagine a contig of ESTs ...*

Homoeologous SNPs

A

GACGGGATCGGACCTTGGTGACGAACGCCGGTGGAAACAAGTGATGGAAGCGATGCACGCTCCG  
GACGGGATCGGACCTTGGTGACGAACGCCGGTGGAAACAAGTGATGGAAGCGATGCACGCTCCG  
GACGGGATCGGACCTTGGTGACGAACGCCGGTGGAAACAAGTGATGGAAGCGATGCACGCTCCG  
GACGGGATCGGACCTTGGTGACGAACGCCGGTGGAAACAAGTGATGGAAGCGATGCACGCTCCG

GACGGGATCGGACCTTGGTGACGACCGCGGTGGAAACAAGTGATGGAAGCGATGCACGCGCCG  
GACGGGATCGGACCTTGGTGACGACCGCGGTGGAAACAAGTGATGGAAGCGATGCACGCGCCG  
GACGGGATCGGACCTTGGTGACGACCGCGGTGGAAACAAGTGATGGAAGCGATGCACGCGCCG

D



CTTGTTGACGAACGCCGGTGGAAACA



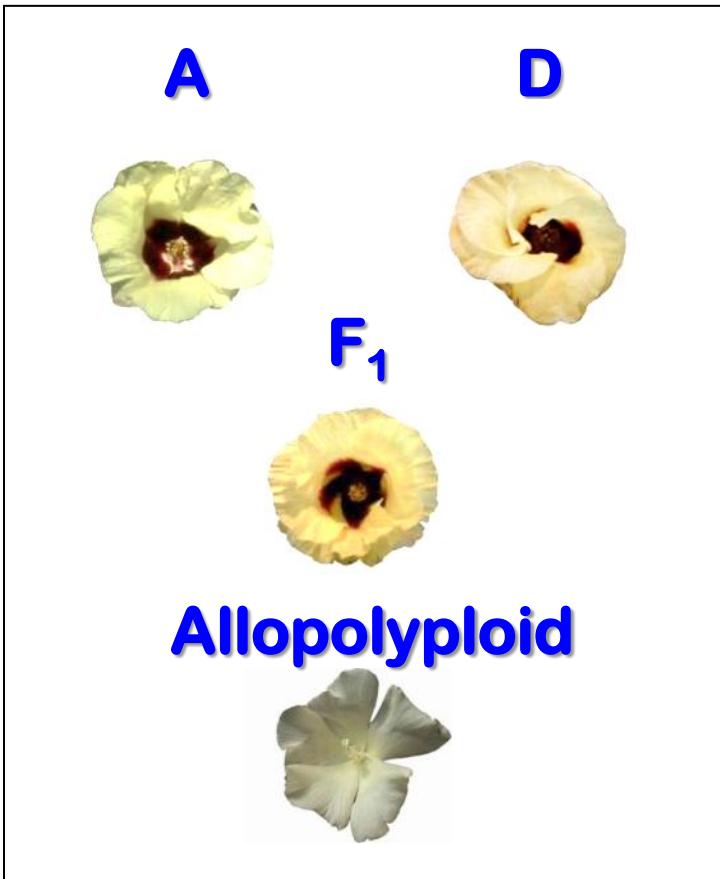
A genome probe

CTTGTTGACGAAACGCCGGTGGAAACA



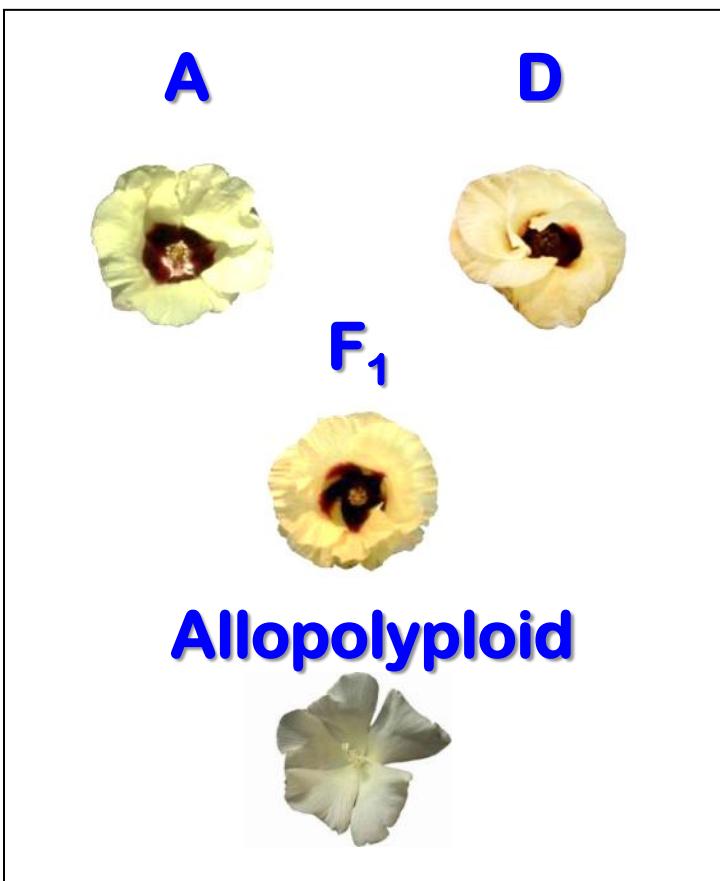
D genome probe

## Results (1383 genes)



Sample	Bias 'A'	Bias 'D'	A & D Equivalent
F <sub>1</sub>	121	301	961
<i>G. hirsutum</i>	423	546	414
Intersect	51	184	324

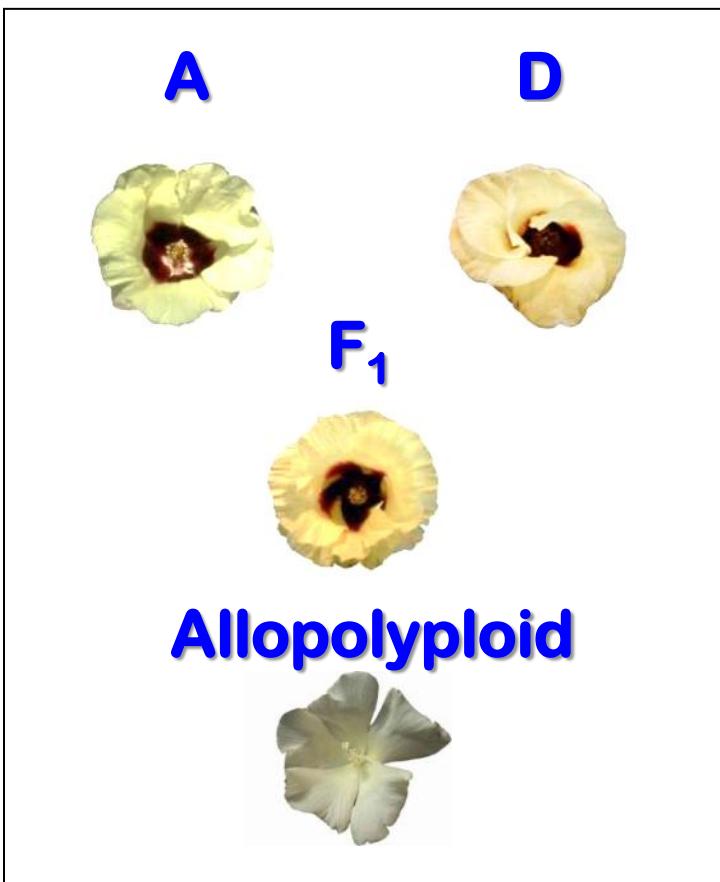
## Results (1383 genes)



Sample	Bias 'A'	Bias 'D'	A & D Equivalent
F <sub>1</sub>	121	301	961
<i>G. hirsutum</i>	423	546	414
Intersect	51	184	324

Overall D bias

## Results (1383 genes)

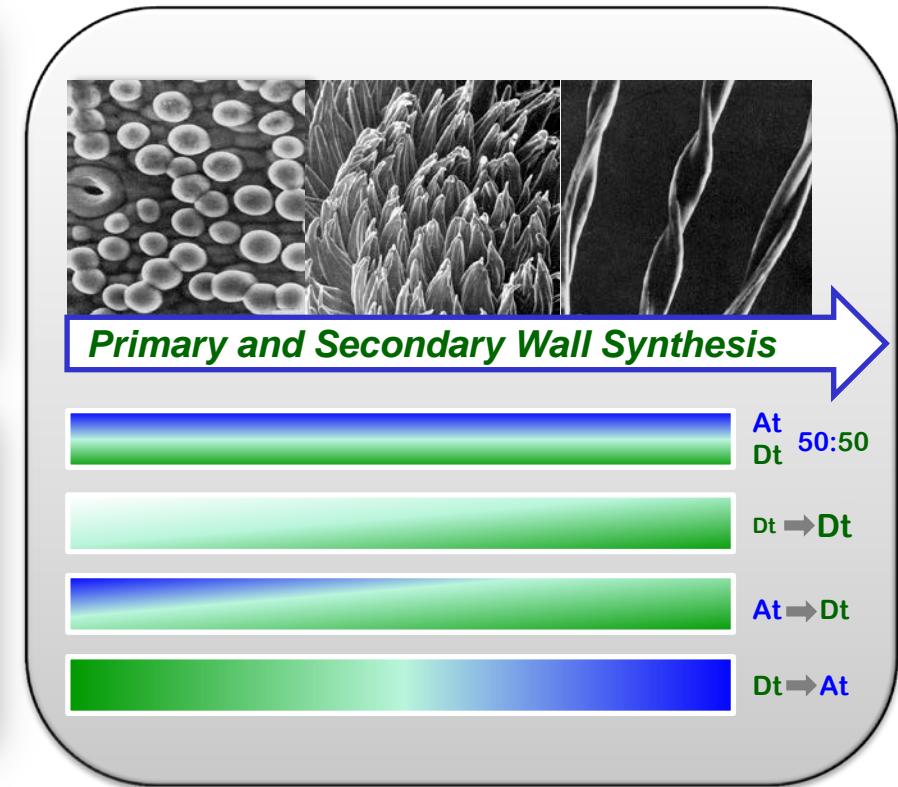
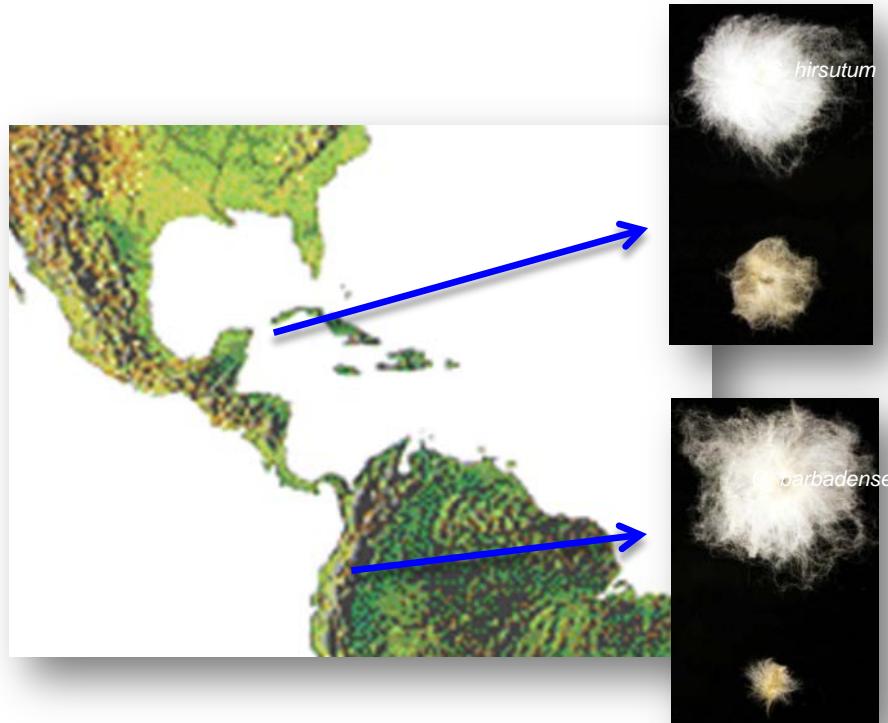


Sample	Bias 'A'	Bias 'D'	A & D Equivalent
F <sub>1</sub>	121	301	961
<i>G. hirsutum</i>	423	546	414
Intersect	51	184	324

Increase in bias

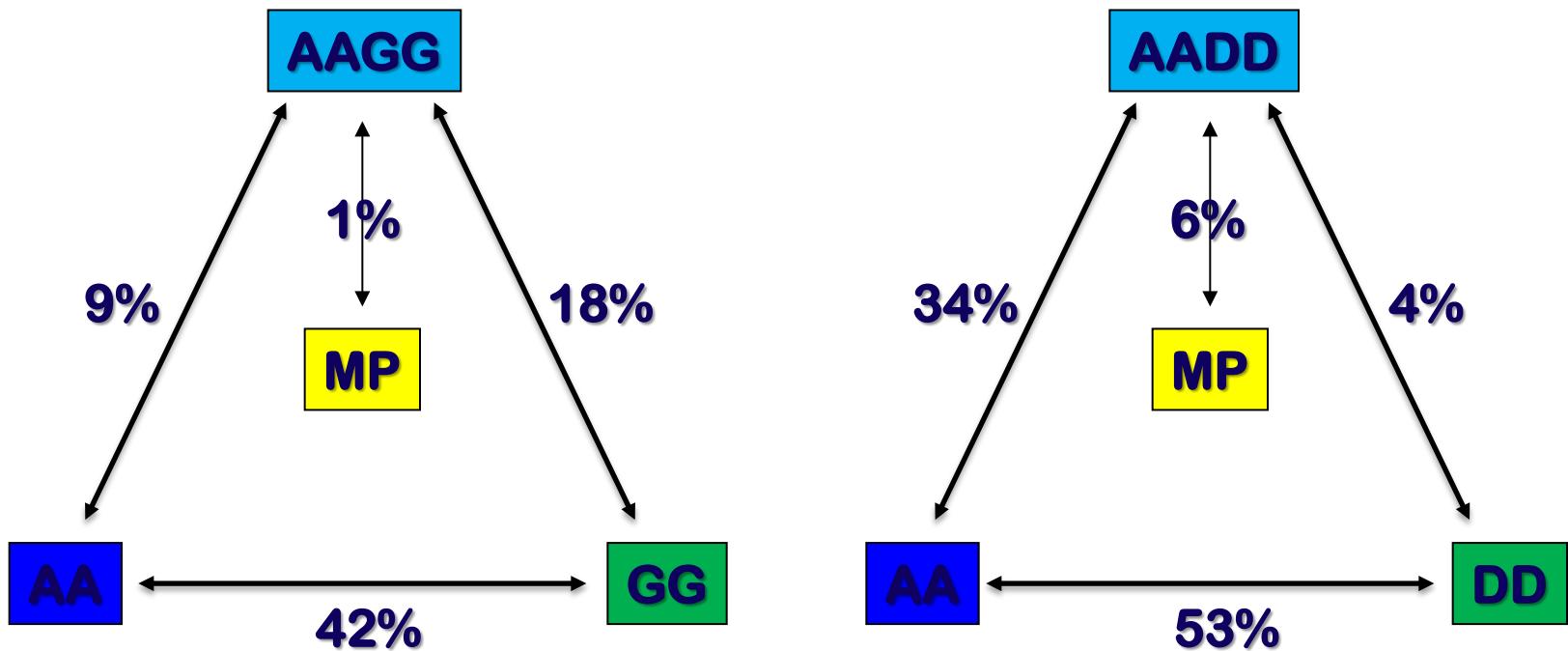
Temporal partitioning of expression evolution: 30% genes showing bias in polyploids already do so in the F1

# Duplicate expression in single-celled fibers



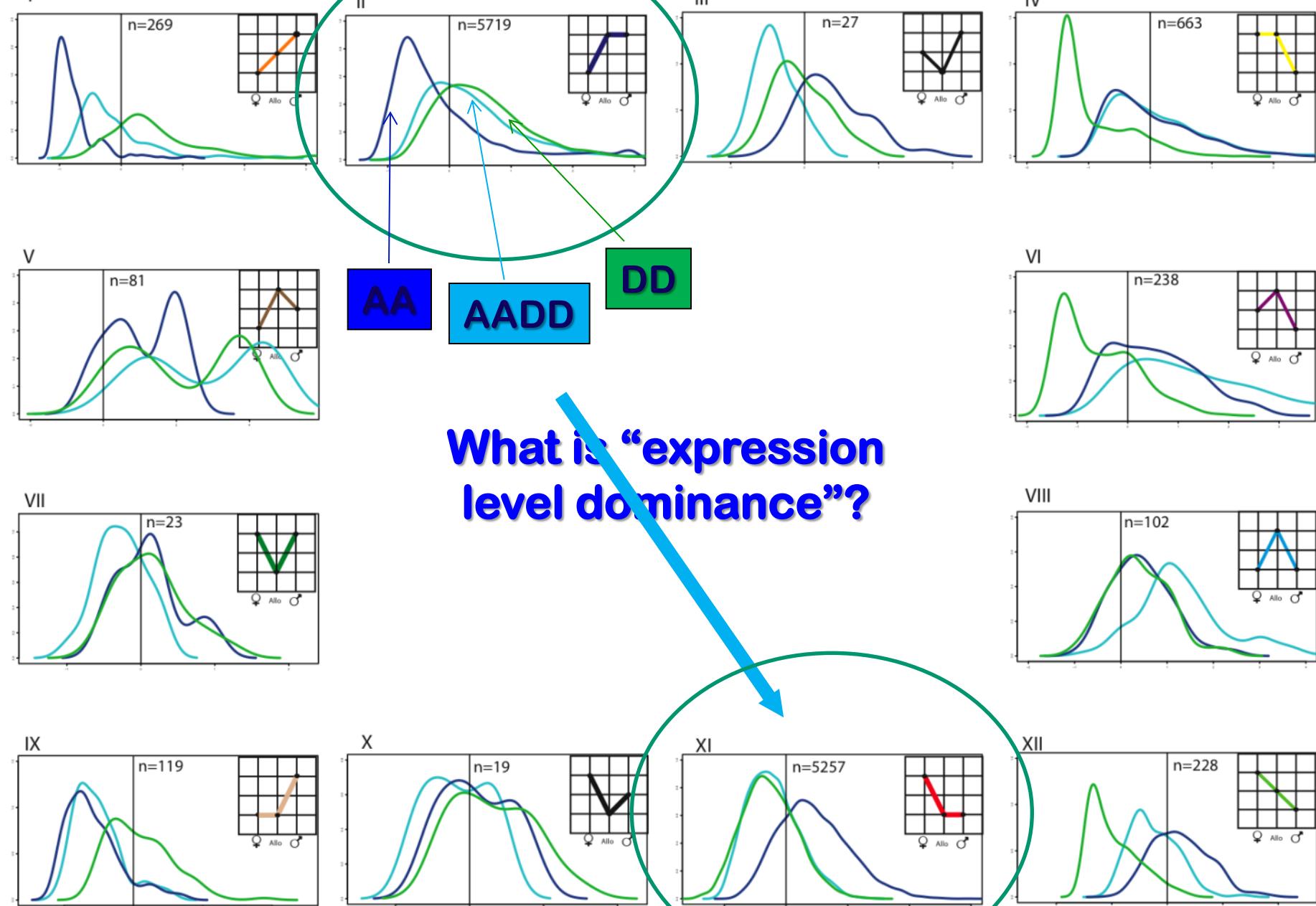
- 33% change duplicate gene expression, even in a single cell

# Expression level dominance

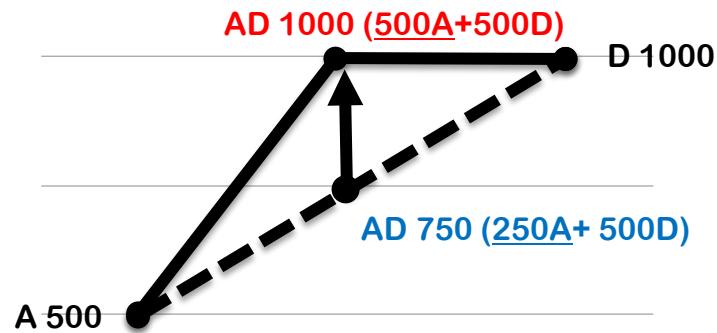


- Differential expression between diploids and polyploids is asymmetric
- Most genes expressed at mid-parent level: *expression level dominance* (level of gene expression resembles one parent)
- Differs in magnitude and direction among systems

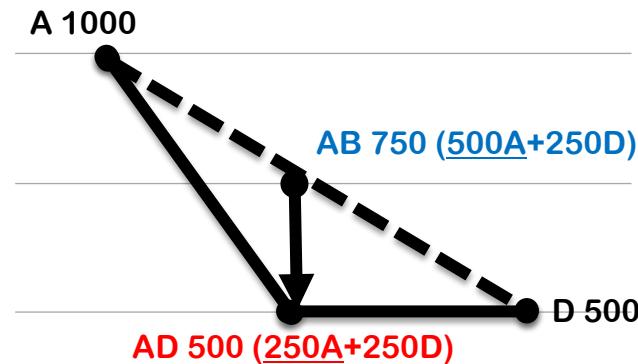
Figure 3.



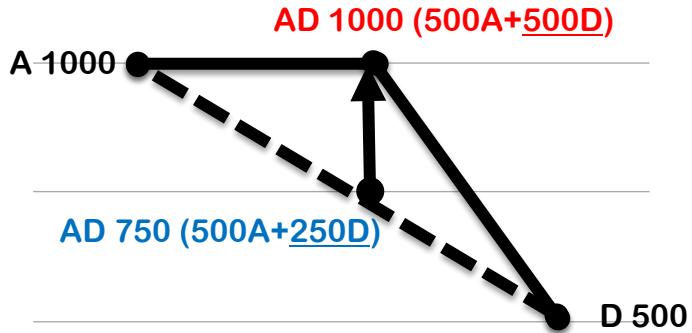
### A up-regulation



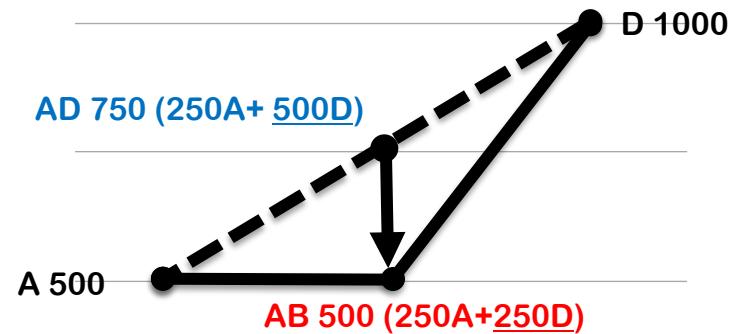
### A down-regulation



### D up-regulation

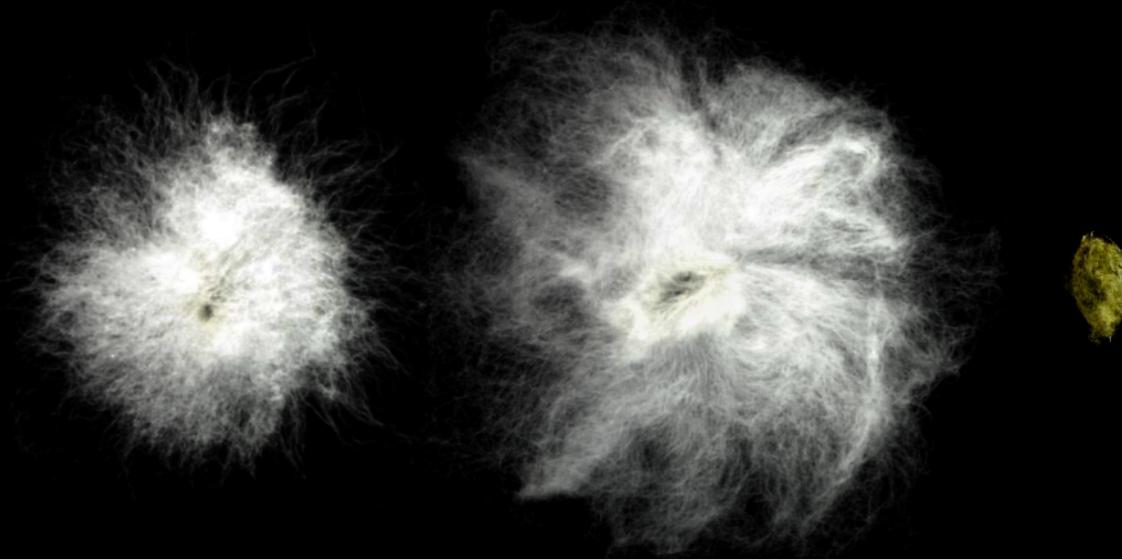


### D down-regulation



# Story 3

$1 + 1 \gg 2$



A

AD

D

# Genome duplication and crop improvement

Meta-analysis of 196 fiber QTLs

---



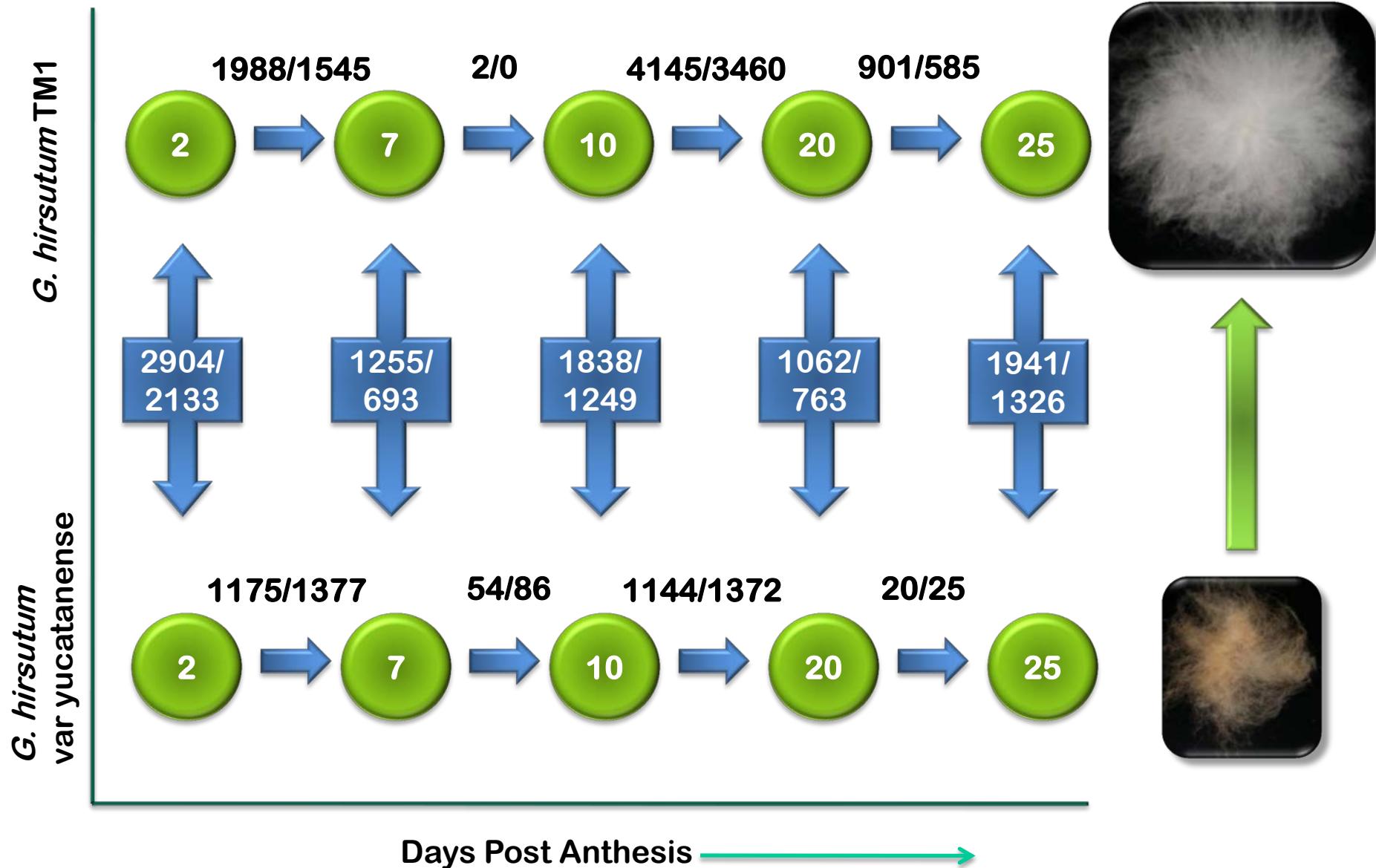
A-genome — 84



AD

D-genome — 112

# Gene expression during fiber development



# Wild versus domesticated *G. hirsutum*



TX2094



TX2090



TX2095



TX665



TX1228



MAXXA



TM1



Cascot L-7



Coker 315



CRB252

1cm  
—

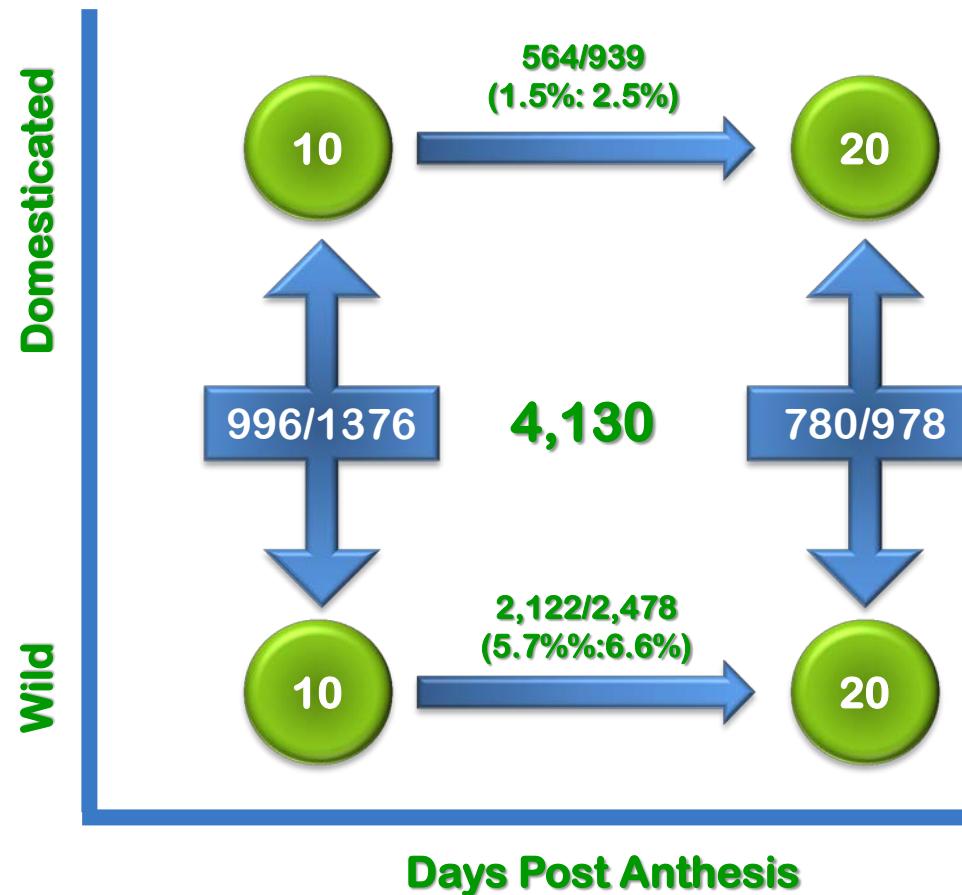
\*TX2094, TX2090, TX2095: race *yucatanense* (Yucatan, Mexico)

\*TX665: race *palmeri* (Yucatan, Mexico)

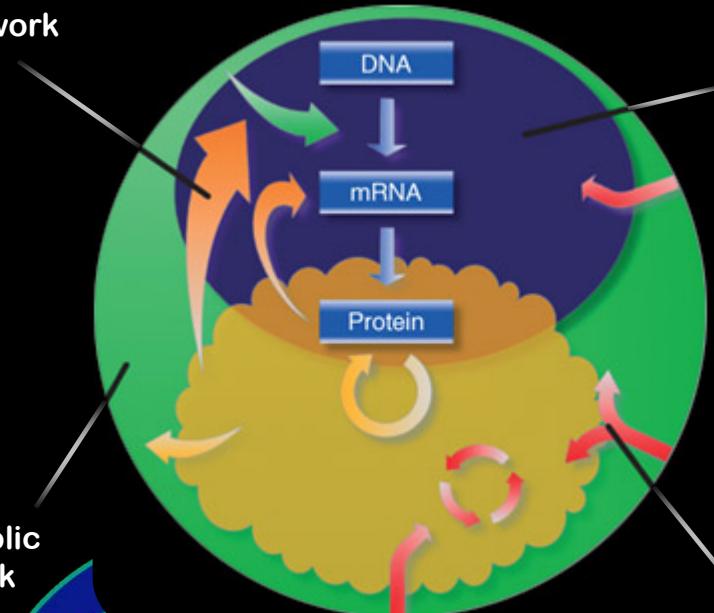
\*TX1228: not classified (Veracruz, Mexico)

# Gene expression during fiber development

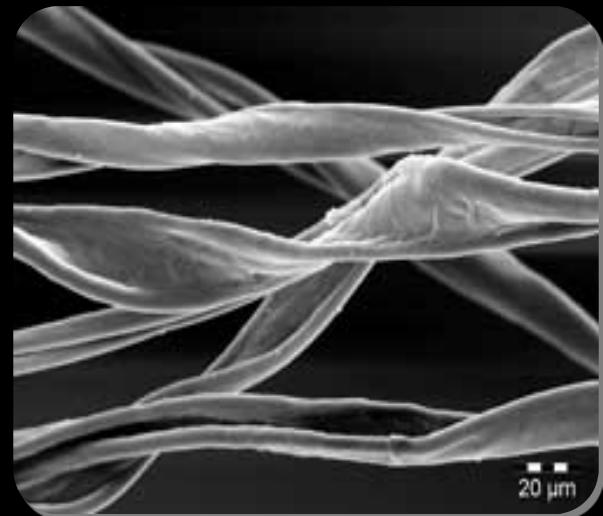
## Multiple accessions, RNA-seq data



Protein network

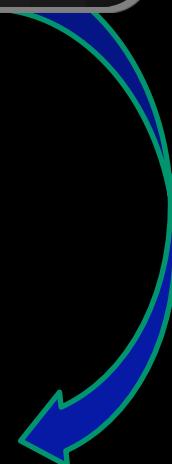
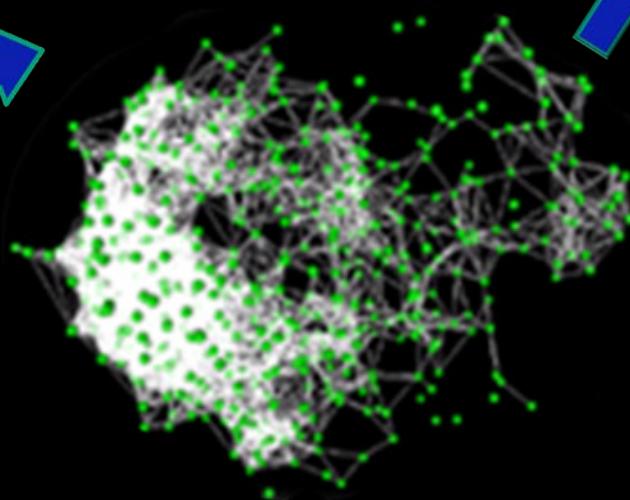
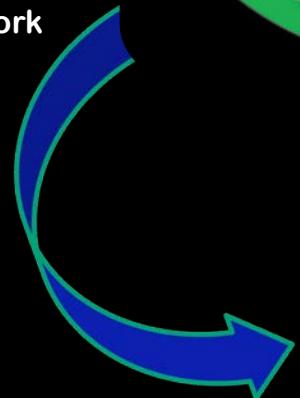


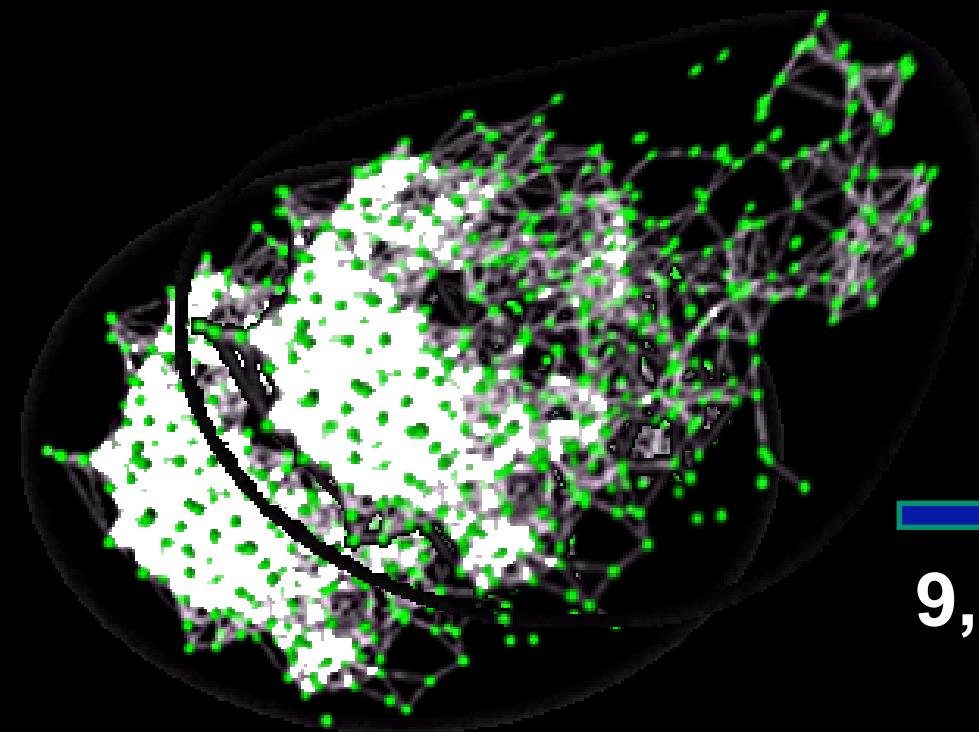
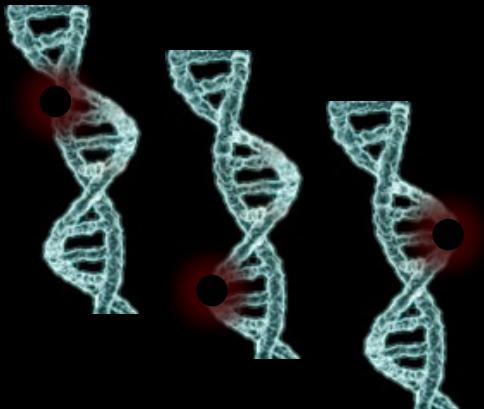
Transcriptional  
regulatory  
network



Metabolic  
network

Signaling  
network



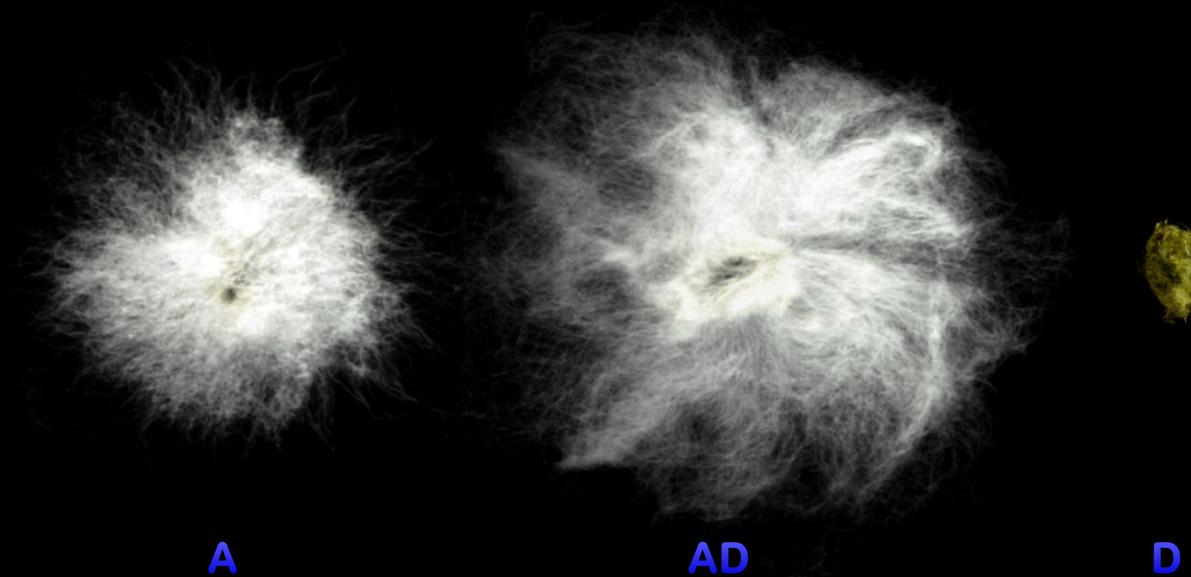


9,000 genes



# Story 3

$1 + 1 \gg 2$



- Approximately 15,000 genes expressed in fiber
- Domestication dramatically alters the transcriptome
- Enriched GO terms in each comparison; rich source of data for gene discovery, manipulation

We are the beneficiaries of generations of taxonomists,  
cytogeneticists, others

Much remains to be learned, studied, preserved

Power of phylogenetics, genomics to reveal organismal history,  
and hence genome evolution

Polyploids exhibit a variety of types of non-Mendelian evolution  
at the DNA level

➤ Gene conversion or “concerted evolution”; unequal rates  
of evolution (higher in polyploids); gene loss; Intergenomic  
transfer of sequences

Gene expression in polyploids is radically altered

➤ Bias and silencing of duplicate genes is ubiquitous;  
➤ Expression partitioning occurs even in a single cell  
➤ Expression level dominance is common  
➤ Novel up- and down-regulation (transgressive  
expression)

Selection affects networks of thousands of genes; single cell

Duplicate genes may be responsive to selection (domestication)

Polyploidy offers novel avenues for evolution, crop improvement



Many thanks to:

Keith Adams, Wendy Applequist, Ying Bao, Curt Brubaker, Bhupendra Chaudhary, Jeff Chen, Rich Cronn, Lex Flagel, Alan Gingle, Lei Gong, Corrinne Grover, Kara Grupp, Candace Haigler, Jennifer Hawkins, Ran Hovav, Guanjing Hu, Andy Paterson, Ryan Rapp, Armel Salmon, Mac Stewart, Emmanuel Szadkowski, Josh Udall, Thea Wilkins, Rod Wing, Mi-Jeong Yoo, many others

NSF, USDA,  
Cotton, Inc.