

COMMENT

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Unraveling the puzzle of the origin and evolution of cotton A-genome



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Abstract

Gossypium hirsutum, the most widely planted cotton species, its evolution has long been an unsolved puzzle because of its hybrid origin from D-genome and A-genome species. To better understand the genetic component of cotton, Huang et al. recently sequenced and assembled the first A_1 -genome *G. herbaceum*, and updated the A_2 -genome *G. arboreum* and $(AD)_1$ -genome *G. hirsutum*. On the basis of the three reference genomes, they resolved existing controversial concepts and provided novel evolutionary insights surrounding the A-genome.

Keywords: Cotton genomes, *Gossypium herbaceum*, Origins, Evolution, Structural variations

Main text

Cotton is one of the most important economic crops in the world, and more than 90% of the cotton fiber is derived from the $(AD)_1$ -genome Upland cotton (*G. hirsutum*) (Ma et al. 2018). The $(AD)_1$ -genome is formed by the natural hybridization between D- and A-genome (Li et al. 2015). *G. herbaceum* (A_1 -genome) and *G. arboreum* (A_2 -genome) are the only two extant diploid A genomes. Abundant studies supported that the D_5 -genome *G. raimondii* could be regarded as the D-subgenome donor of $(AD)_1$ -genome (Wendel 1989). However, as commented in *Science* (Zahn 2012), the A-subgenome donor in tetraploid genome has been an unsolved mystery and attracts a great research interest. Previously, either A_1 - or A_2 -genome has been reported to be the actual A-genome donor of tetraploid cotton.

First A_1 genome sequence and high-quality genome updates of A_2 and $(AD)_1$

Since the release of the first D_5 -genome in 2012 (Wang et al. 2012), the genome of the second D_5 (Paterson et al. 2012; Udall et al. 2019), and that of A_2 (Du et al. 2018; Li et al. 2014), $(AD)_1$ (Hu et al. 2019; Li et al. 2015; Wang et al. 2019; Yang et al. 2019; Zhang et al.

2015) as well as $(AD)_2$ (a much less cultivated *G. barbadense*) (Hu et al. 2019; Liu et al. 2015; Wang et al. 2019; Yuan et al. 2015), were sequenced and assembled with great updating efforts resulted in much improvements for these genomes. Recently, Huang et al. sequenced and assembled A_1 variety *africanum* for the first time and re-assembled high-quality A_2 cultivar Shixiya1 and $(AD)_1$ genetic standard Texas Marker-1 (TM-1) genomes on the basis of PacBio long reads, paired-end sequencing and high-throughput chromosome conformation capture (Hi-C) technologies. The resulting A_1 assembly captured 1 556 megabases (Mb) of genome sequences and 95.69% of total genome sequences spanning 1 489 Mb were categorized and ordered into 13 pseudo-chromosomes. They substantially improved the existing A_2 and $(AD)_1$ genome assemblies, mainly from aspects of genome completeness and accuracy (Huang et al. 2020). These updated A_2 - and $(AD)_1$ -genomes will certainly replenish earlier assemblies as chromosome-scale references. With high-quality assembly of the three cotton species, a more complete landscape of genome architecture, gene annotations and transposable element (TE) insertions were provided, which is critical to evolutionary and comparative genomics as well as genetic variation analysis.

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Origin of allotetraploid cotton and two diploid A-genomes

On the basis of multiple evidences, such as molecular tree, whole-genome phylogenetic relationships and population analysis, the authors propose that all existing A-genomes may have originated from a common ancestor, referred to here as A_0 (Huang et al. 2020). The ancient and extinct A_0 lineage is likely the ancestral form of one of the original species parents of $(AD)_1$ rather than the extant A_1 and A_2 lineages. Relatively, A_0 was more phylogenetically related to the present A_1 than A_2 . Hybridization of this A_0 genome with a D_5 species eventually produced the current allotetraploid cotton at ~1.6 million years ago (MYA), which preceded the speciation of current A_1 and A_2 at ~0.7 MYA. This genome-based analysis will likely close down the A_1 versus A_2 argument, especially if archaeological data is dugged up someday to pinpoint out the existence of the currently-extinct A_0 genome. Since the publication of these new findings, our knowledge of cotton genome evolution will have to be revised and updated.

Developing novel methods to detect genome expansion and evolution

The authors suggest that cotton genome evolution is characterized by bursts of transposable element (TE) activity. The two A-genomes and the A-subgenome of $(AD)_1$ experienced expansion in genome size that was highly correlated with TE bursts. As much as 72.57% of the A_1 -genome and 73.62% of the A_2 -genome were composed of LTR-type TEs. By using fragmented coding sequences of LTR-type TEs, they developed a novel method, named Gaussian probability density function (GPDF) analysis, to overcome a major pitfall related to traditional method that relied on the presence of both ends of full-length LTRs, such that more recently inserted LTRs are likely over-represented. They suggested that several long-terminal-repeat bursts which occurred from 5.7 MYA to less than 0.61 MYA contributed compellingly to A-genome size expansion, speciation and evolution.

Characterization of structural variations related to cotton fiber development

The authors characterized structural variations (SVs) in cotton genomes using comparative genomic analysis, which provided dozens of putative candidate genes to investigate phenotypic differences among the three cotton species. Abundant species-specific SVs in genic regions changed the expression of many important genes, some of which were found to alter expression intensities of genes involved in fatty acid biosynthesis, leading probably to spinnable fiber improvement in $(AD)_1$ compared with A_1 or A_2 , as confirmed by several transgenic cotton lines that overexpressed *KCS6* gene.

In conclusion, Huang and colleagues assembled three high-quality cotton reference genomes, and performed systematic and comprehensive genome analysis, especially for cotton A-genomes, which represents a major step toward understanding the evolution of the cotton A genome. They not only have provided the scientific community with valuable genomic and genetic resources to facilitate genetic evolution, comparative genomic analysis, but also will accelerate the process of cotton genetic improvement with advanced methodology and new varieties.

Acknowledgements

We thank editorial board for inviting us to write comments on this interesting work and thank them for their suggestions in the manuscript revision.

Author's contributions

Ma ZY wrote the manuscript. The author(s) read and approved the final manuscript.

Funding

No Funding.

Availability of data and materials

No other data related to this study is available at this time.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The author declares no competing interests.

Received: 28 April 2020 Accepted: 11 May 2020

Published online: 02 June 2020

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