



# Genus *Gossypium*: history, economy, genetic origin, computational genomics and Ecuador as a reservoir of long staple cotton genetic resources

Ronald Oswaldo Villamar-Torres<sup>1</sup>, Byron Oviedo-Bayas<sup>2</sup>, Seyed Mehdi Jazayeri<sup>3</sup>, Christopher Robin- Viot<sup>4</sup>

## Abstract

Domestication of *Gossypium* species occurred at least 8,000 years ago in four different regions of the world: Asia, Africa, and Central and South America. China, India, and the United States of America were the three countries with the highest cotton production, with 6,532, 6,423, and 3,553 of thousand metric tons respectively in 2017. About 18% of the world's cotton consumption by 2000 was required for herbivore control. This decreased a lot thanks to the use of biotechnological tools, which allowed obtaining insect and herbicide tolerance. There are cotton genomic databases with different genome annotation versions, which are frequently updated, allowing more precise research on gene expression, genomic selection, proteomics and prediction of the functions of specific proteins. Evidence shows that *Gossypium barbadense* was domesticated in the Gulf of Guayaquil region of Ecuador and that its wild forms still coexist with wild forms derived from traditional cultivars, and with cultivars of its allotetraploid sister *G. hirsutum*. To conserve and exploit these genetic resources, it is essential to differentiate them, elucidate their history (domestication), as well as their genetic relationships (gene flow), and understand their interspecific relationships between species.

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**KeyWords:** Cotton; economy; origin; biotechnology; *Gossypium hirsutum*; *Gossypium barbadense*.

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<sup>1</sup> Universidad Técnica Estatal de Quevedo. Av. Quito. Km 11/2 vía a Santo Domingo. Quevedo, Los Ríos, Ecuador, rvillamart@uteq.edu.ec

<sup>2</sup> Universidad Técnica Estatal de Quevedo. Av. Quito. Km 11/2 vía a Santo Domingo. Quevedo, Los Ríos, Ecuador, boviedo@uteq.edu.ec

<sup>3</sup> Facultad de Ciencias, Universidad Nacional de Colombia, Bogotá, Colombia, smjazayeri@unal.edu.co

<sup>4</sup> CIRAD, UMR AGAP, F-34398 Montpellier, France, christopher.viot@cirad.fr

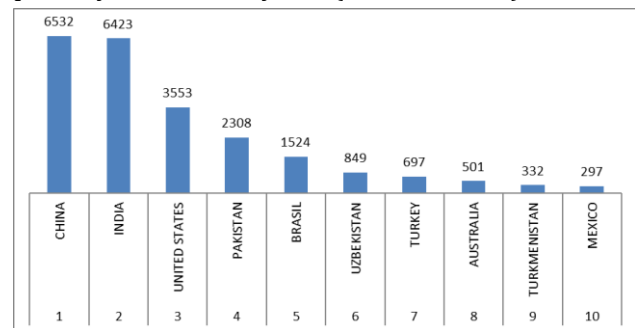


## Introduction

The textile industry for clothing has been for long periods in the history of human civilizations an essential component of the activity and economy, in direct relation to the technical progress and economic growth of many countries. The domestication of the *Gossypium* species occurred at least 8,000 years ago in four different regions of the world: Asia, Africa, and Central and South America (d'Eeckenbrugge and Lacape, 2014). Today cotton has become a leading textile fiber worldwide and is now the most important natural fiber for clothing and the basis of one of the largest industrial and commercial activities. The importance of cotton grew especially in the late 18th century with the mechanization of ginning and the increasing trade between the tropical regions where it was grown and the industrialized countries where it was processed and traded. At this time, it became the main player in the countries where cotton was produced and industrialized (Cuvi, 2011; Raymond, 2010; Roca, 2017) and today it still accounts for about half of the world's consumption of textile fibers (Claudio, 2007; Dugan, 2009). Cotton production spread to what was known as Mesopotamia, Egypt and Nubia. During the so-called late medieval period, cotton and several of its finished products were first introduced into Italy and Spain by Arab merchants, and subsequently, the cultivation of the fiber spread throughout the old continent (Wendel et al., 1992).

China, India, and the United States of America are the top three countries with the highest cotton production. Measuring cotton production in thousands of metric tons, China produced 6,532 thousand metric tons and India produced 6,423 thousand metric tons of cotton in 2017, while the United States reached a production of 3,553 thousand metric tons respectively (Figure 1). Cotton production in Africa, although it does not reach remarkable importance on a global scale, is the only reliable cash crop for numerous smallholder farmers in different regions of this continent, thus representing an essential basis for industrial (ginning, oil, textile) and artisanal (textile) activity.

Several countries in West and Central Africa are considered among the poorest nations on the planet. According to the United Nations Human Development Index, Burkina Faso and Mali rank, respectively, third and fourth among the poorest countries in the world (United Nations Development Program, 2017). In the 1990s, cotton provided a considerable boost to their economies; during this time, cotton production and exports enabled farmers in the region to improve their standard of living. In Burkina Faso, for example, cotton production increased by 175% between 1993 and 1998, leading to an increase in the net household income of smallholders in particular. As a result, poverty declined significantly from 50% to 42% in cotton-producing areas, compared to the rest of the non-cotton-producing areas, where poverty increased by 2% (Goreux, 2003).



**Figure 1. Cotton production represented in thousand metric tons for the year 2017.**

Source: Sheth, 2017

In the Americas, until about 2000 in Mexico, cotton production had declined by ~74% from 1990, when bale production reached 1 million (Gil and Mascorro, 2001). Although the United States of America (USA) is by far the world's leading exporter, followed only by China and India (Escobal and Salcedo, 2004). In 2012/13, its production had a 14.3% reduction compared to 2011 (Lopez et al., 2015). In South America, countries such as Peru experienced increased activity in their textile production during the last decades. The expansion of its commercialization was due to the appearance of a long and extra-long fiber variety such as Tangüis (Escobal and Salcedo, 2004). However, for Colombia, the lack of genotypes adapted to the manufacturing process represented



marketing problems in the face of the quality of the external industry, mostly English fabrics (Raymond, 2010). Something similar happened in Spain due to external products and (state) policies and investments until before the beginning of the 20th century other European textile industries had a progressive need for raw materials, encouraging cotton countries to increase their production (Roca, 2017).

Due to its excellent characteristics, cotton continues to be preferred by the textile industry and customers around the world. Fabrics made from this fiber absorb moisture, provide a good fit and are very durable. Today, consumers continue to buy large quantities of cotton products, demonstrating their preference for the lightness and comfort of this material. The genus *Gossypium* belongs to the family Malvaceae (Coppens d'Eeckenbrugge and Lacape, 2014; Wendel et al., 1992), Bastidas, (2019). *Gossypium* is native to tropical and subtropical regions of the Old and New World (Coppens d'Eeckenbrugge and Lacape, 2014; Wendel et al., 1992). The genus name derives from the Arabic word *goz*, which refers to a soft substance. There are about 50 species of *Gossypium*, but cotton production is limited to a small number of species, the four domesticated *Gossypium* species: *G. arboreum* L. and *G. herbaceum* L. (diploid species), *G. hirsutum* and *G. barbadense* (tetraploid species) are present in America, Africa and India (d'Eeckenbrugge and Lacape, 2014).

Currently, the tetraploid species *G. hirsutum* L. and *G. barbadense* L. have replaced the diploid species *G. arboreum* L. and *G. herbaceum* L., which were most commonly used in South Asia (Renny-Byfield et al., 2016). Now, most planted cotton tracts are developed with modern genotypes, particularly of the allotetraploid species *G. hirsutum* Upland cotton, which is grown in nearly 40 nations. While *G. Barbadense*, with a long, strong, and fine fiber, much desired by the textile industry, does not account for a large amount of world production, due to its low yields (8% of world production), it is not a major contributor to world cotton production).

Cotton production and uses

The cotton plant is a perennial shrub considered

an annual crop. The word cotton comes from Arabic, which became cotton in Spanish and cotton in English. The Arabic word for cotton meant a finely woven fabric. The product is cotton fiber, which is the basis of one of the trades carried out by modern industry worldwide and its cultivation is one of the oldest. The fibers are obtained from seeds that clearly show the fiber at maturity.

The length and thickness of the fiber depend on several factors, including its genetic and geographical origin, as well as climatic conditions. In addition, because it is a labor-intensive crop, it generates employment in the countryside and is therefore of great importance to millions of rural families in less developed countries (Villamar et al., 2018). The temperatures and environment in which cotton grows optimally are highly considered by farmers, as it is a plant very susceptible to low temperatures, and very well adapted to warm temperatures.

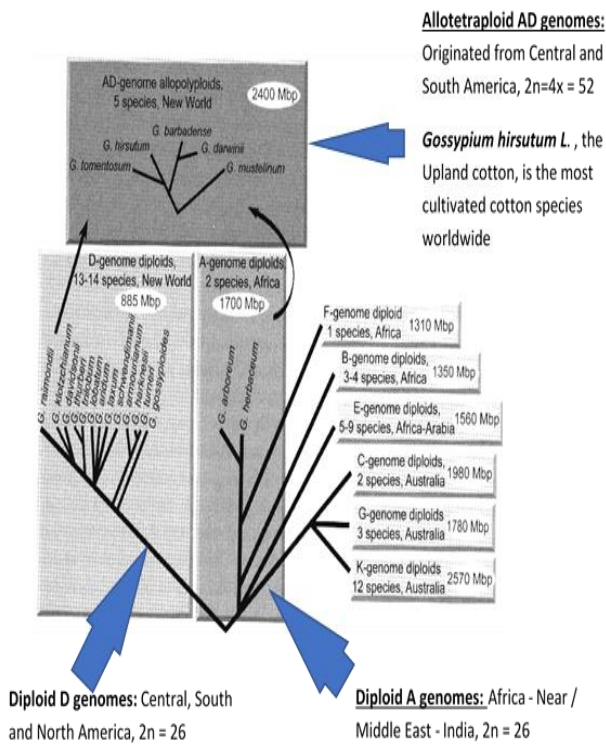
Cotton grows in warm climates, mainly between latitudes 37° N and 32° S. Its optimum development occurs in a range between 0 and 500 meters above sea level. There are other places where it exceeds 500 meters of optimum altitude, however, the higher the altitude, the yield will be affected (Wolf and Otero, 2016). Therefore, its cultivation is possible in tropical and subtropical areas of the world (Vincent and Fajardo, 2007), but its production is not located only in the tropics. In recent centuries, adaptation processes and the generation of new varieties have made possible the expansion of this crop. Today it is planted in both hemispheres, although the northern hemisphere is home to almost 90% of world cotton production (Sinclair, 2014). In the Americas, since Mexico is considered the center of origin of 11 species of *Gossypium*, cotton has a high cultural, economic and biological relevance in this continent and in the world in general (Pérez-Rodríguez et al., 2015).

Origin and Domestication of *Gossypium* species

More than two decades ago, Brubaker and Wendel (1994) stated that "the origin of domestication in Mesoamerican populations of *G. hirsutum* is obscured by several factors, including the absence of a clearly identified wild



progenitor, a complex population genetic structure, and many centuries of human-mediated dispersal and gene flow". Subsequently, some evidence individually demonstrated that cotton species had been domesticated in four distinct regions of the world: *G. hirsutum* L. in Mesoamerica, *G. barbadense* L. in South America, *G. herbaceum* L. in Arabia and Syria, and *G. arboreum* L. in the Indus Valley of India and Pakistan (d'Eeckenbrugge and Lacape, 2014). The formation of tetraploid species occurs from the hybridization of Old World (Africa and the Middle East) diploid species with A genomes ( $2n = 26$ ) and New World (North, Central and South America) species with D-type diploid genomes ( $2n = 26$ ). (Figure 2).

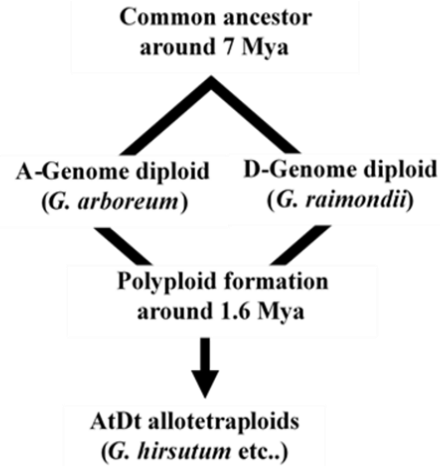


**Figure 2. Evolution of recent *Gossypium* genomes: diploid A ("Old World cottons") to K, diploid D ("New World cottons"), and allotetraploid AD genomes (see text).**

Source: Percy et al., 2009.

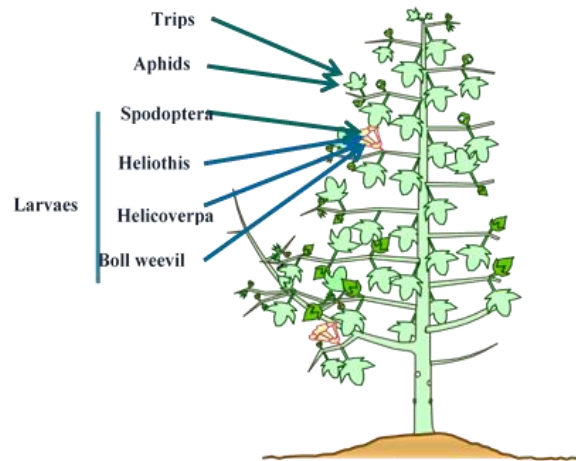
Origin of Upland cotton *Gossypium hirsutum*  
 The allotetraploid cultivated species *G. hirsutum* is the result of hybridization between an A-genome diploid (*G. arboreum*) and a D-genome

diploid (*G. raimondii*), followed by a doubling of chromosome number  $2n = 4x = 52$  chromosomes (Figure 3). Meiotic behavior is similar to that of a diploid, that is, no tetravalent or other combinations between non-homologous chromosomes = "amphidiploid" behavior. All cotton grown with an AD genome have a native cytoplasm of the A genome.



**Figure 3. Origin of allotetraploid genome species AD.**

Cotton breeding and genome



**Figure 4. Schematic cotton plant (Upland type, *Gossypium hirsutum*) with different stages of the reproductive organs: buds, flowers, bolls, and the main insect pests attacking it.**

Cotton is one of the most vulnerable crops to stress (biotic and abiotic). Therefore, stress-resistant cotton breeding is critical in breeding programs (Viot, 2016). For example, rainfed cotton *Gossypium hirsutum* is heavily attacked by pests (Figure 4), including boll parasites,



responsible for very significant yield and quality losses, and soil diseases and pests such as nematodes. Boll parasites are arthropods present in foliage, flower buds, or bolls. Consequently, cotton cultivation is a major consumer of pesticides, posing health risks to cotton growers and their families and local populations, environmental pollution, and financial costs (Villamar et al., 2018).

The African cotton bollworm (*Helicoverpa armigera*), also known as the old world caterpillar, is a lepidopteran species of the family Noctuidae whose larvae feed on a wide range of plants, including cultivated rainfed cotton plants *Gossypium hirsutum* (Figure 5). They are polyphagous and cosmopolitan pests. It represents the main pest of cotton. The species is widespread in Africa, Central, and Southern Europe, Asia, Australia, and Oceania.



Figure 5. Intact cotton boll (A) is frequently attacked by *Helicoverpa armigera* (cotton bollworm); larva (B). Photo credit authorized.

#### Cotton Biotechnology: Insect and Herbicide-Resistant Cotton

Through the development of insect and herbicide-resistant plants, genetic engineering is presented as a powerful tool to help farmers and offer them ways to increase the yield and quality of cotton, reducing production costs and limiting the use of synthetic pesticides that represent a danger to the environment (John, 1997).

Despite the efforts made by cotton growers to control pests, these problems have increased every day, causing difficulties to control them since chemicals have produced resistance in these herbivores, and being synthetic, they are harmful to the environment and very expensive (Pretty and Pervez Bharucha, 2015). Today, there is a need for other means that can support and solve these problems in cotton production.

Since 1996, genetic engineering and biotechnology have been incorporated into cotton breeding programs (Boopathi et al., 2015). Since then, the production of transgenic plants with commercial use to protect crops against pests has multiplied in several regions of the world (National Research Council (USA) Committee on Genetically Modified Plants for Protection from Pests, 2000). Researchers have used a gene encoding an insecticidal protein, from *Bacillus thuringiensis* (Bt), which has been inserted into the genome of *Gossypium hirsutum* cotton to produce an insect-resistant transgenic cotton plant. Bt is a specific and very potent insect toxin, thus introducing resistance to insect attack in plants (de Oliveira et al., 2016; Perlak et al., 1990).

In recent years, researchers have developed cotton plants resistant to bollworms and other pests of importance in cotton cultivation, such as bollworms and spider mites (Pretty and Pervez Bharucha, 2015). According to several environmental protection regulators in the US, exposure to transgenic Bt cotton is safe for humans, insects and other types of animals. Although genetic engineering has contributed significantly, making it a technology with great potential, it has not been correctly effective in all cases. In some cotton plants the Bt gene is not expressed correctly and the plant loses its protective genetic characteristics (Li et al., 2011). In addition, there are certain groups of insects whose behavior is not affected by the Bt toxin (Xu et al., 2008).

Genomes of *Gossypium* species and computational genomics databases available for cotton breeding

The first version of the cotton genome was published in 2007, thanks to the joint efforts of cotton researchers involving several institutions around the world (Chen et al., 2007). As an initial strategy, the consortium decided to sequence the genome of *Gossypium raimondii*, a species native to South America and one of the progenitors of cultivated tetraploid cottons (*G. hirsutum* and *G. barbadense*). Due to the size of its genome, it is much smaller than the tetraploid progeny because of less repetitive DNA samples (mainly retrotransposons). Each chromosome is present

only once and has approximately one-third the number of bases of tetraploid cotton (AD). These characteristics facilitate their use for designing gene expression and genomic selection research (Wang et al., 2012).

*G. arboretum* (old world) (Li et al., 2014) was sequenced as the second ancestral species of *G. hirsutum*, donor of the A genome. This strategy was initially conceived to (1) assemble both genomes to subsequently facilitate sequencing of the tetraploid cultivated *G. hirsutum* and *G. barbadense* cottons, (2) to rely jointly on the euchromatic DNA sequences of the A and D genomes, and (3) to avoid making an independent assembly of the sequences, without being able to compare them with their diploid counterparts.

Finally, Li et al. (2015) sequenced the genome of the tetraploid cotton *G. hirsutum*, using the available genomes of the ancestral species *G. raimondii* and *G. arboreum*, to investigate the evolution of the subgenome and the function of genes leading to relevant results. The genome of *G. hirsutum* (AtDt) shares 67.2% of the repeated sequences with the two diploid

genomes *Gossypium arboreum* (AA) and *Gossypium raimondii* (DD). In addition, transposable elements (TEs) originating from Dt have higher activity than those from At. The genome of *G. barbadense* was also characterized.

Two versions of the *G. barbadense* genome were published in 2015 by (Yuan et al., 2015) and Li et al., (2015). Among the most relevant differences from its sister species *G. hirsutum* in total, 1,778.6 Mb of TEs were observed in the *G. barbadense* genome (69.1% of the tetraploid cotton genome), including 1.098 0 Mb of At TEs sequences (73.5% of the subgenome) and 541.6 Mb of Dt TEs sequences (63.5% of the subgenome), while accounting for 1,339 Mb (64.8%) and 1,445 Mb (66%), respectively, of the *G. hirsutum* subgenomes. Cotton genomic databases exist with different genome annotation versions, which are frequently updated (Table 1). Based on these findings, cotton breeders have more easily and accurately conducted research on gene expression, genomic selection, proteomics, and prediction of the functions of specific proteins.

**Table 1. Computational genomics databases available with sequence data and genome annotations of the four cultivated species of *Gossypium* cotton.**

Genome	Species	Reference	Observations, availability of genome sequence
A2	<i>G. arboreum</i>	(Li et al., 2014).	Cotton Genome Project (CGP), <a href="http://cgp.genomics.org.cn/">http://cgp.genomics.org.cn/</a> (browser, blast, login ChrRV x vcigopt1)
D5	<i>G. raimondii</i>	(Paterson et al., 2012).	Reference sequence NCBI PRJNA171262 browser etc.: <a href="https://phytozome.jgi.doe.gov/pz/portal.html">https://phytozome.jgi.doe.gov/pz/portal.html</a>
D5	<i>G. raimondii</i>	(Wang et al., 2012)	<a href="https://www.nature.com/articles/ng.2371">https://www.nature.com/articles/ng.2371</a>
AD1	<i>Gossypium hirsutum</i> <i>TM-1</i>	(Li et al., 2015).	NCBI BioProject, number <a href="https://www.ncbi.nlm.nih.gov/bioproject/PRJNA259930">PRJNA259930</a> <a href="http://cgp.genomics.org.cn">http://cgp.genomics.org.cn</a>
AD1	<i>Gossypium hirsutum</i> <i>acc. TM-1</i>	(Zhang et al., 2015)	laboratory website <a href="http://mascotton.njau.edu.cn">http://mascotton.njau.edu.cn</a> (no browser, raw fa file only) CottonGen database <a href="http://www.cottongen.org">http://www.cottongen.org</a> (working: sequence, mRNA, gene, cacao protein, etc.)

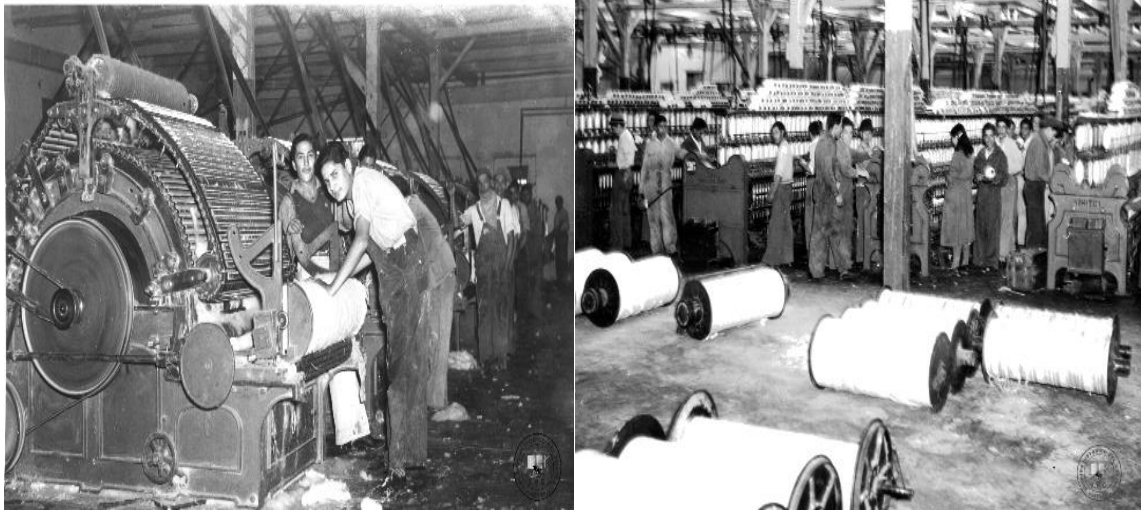


AD2	<i>Gossypium barbadense</i> acc. 3-79	(Liu <i>et al.</i> , 2015).	<a href="https://www.nature.com/articles/srep14139">https://www.nature.com/articles/srep14139</a>
AD2	<i>Gossypium barbadense</i> acc. 3-79	(Yuan <i>et al.</i> , 2015)	<a href="https://www.nature.com/articles/srep17662">https://www.nature.com/articles/srep17662</a>

**Cotton production in Ecuador**

In Ecuador, due to the world wars, economic recession, and the cocoa crisis, cotton imports were restricted during the last century. Domestic textile mills, from Ibarra to Cuenca and Guayaquil (Figure 6) supplanted imports to supply domestic demand and subsequently exported to neighboring countries (Cuvi, 2011), limiting the progress of companies engaged in this activity.

According to information collected by the Central Bank of Ecuador for the year 2007 cotton production was reduced by 50% compared to 2008, in that year it caused production and prices to experience a sharp decline for approximately a decade (Gómez and Reategui, 2013) causing serious problems for millions of people in countries whose main source of income was cotton (Cuvi, 2011).



**Figure 6. (Photo left) the industrial factory.**

The machinery of the cardas section, Hilo’s section. Taken from the Historical archives of Guayas. (Photo right): Spinning factories and cotton fabrics. Taken from the Ecuadorian History Magazine.

**Ecuador as a genetic reservoir for cotton**

Several authors (Deynze *et al.*, 2011; Escobal and Salcedo, 2004; McGregor, 1976) have cited South America as the origin of *Gossypium barbadense*, specifically, between southern Ecuador and northern Peru. Evidence shows that it was domesticated in the Gulf of Guayaquil region (Figure 7), where its wild forms still coexist with wild forms derived from traditional cultivars, and with cultivars of its sister *G. hirsutum*. These wild forms, which have maintained their adaptations to extreme climatic conditions (aridity,

temperatures), are little known and are in danger of extinction. In addition, there is an imminent risk of genetic contamination due to the use of transgenic cotton varieties present in neighboring countries, where their cultivation has grown exponentially.





**Figure 7. The domestication of *Gossypium barbadense* most probably took place on the coasts of the Gulf of Guayaquil.**

To conserve and exploit these genetic resources, it is essential to differentiate them, to elucidate their history (domestication), as well as their genetic relationships (gene flow). It is also necessary to understand interspecific relationships. For example, hybrids between *G. hirsutum* and *G. barbadense* are viable and fertile; however, many geneticists observed a global return for one or the other type in the following generations, with introgression of chromosomal segments (Viot et al., 2016).

Cotton varieties cultivated in Ecuador

Research programs on cotton cultivation in Ecuador began in 1962 at the INIAP (Instituto Nacional de Investigaciones Agropecuarias) Experimental Station in Portoviejo, Manabí, where the Coker 124B variety of *G. hirsutum* was introduced from the United States. Currently, cotton of the lowland group (*G. barbadense*) is grown only in Loja, for the fiber used in typical handicrafts. In the more northern regions of Manabí and Guayas, cotton cultivation is based on modern varieties (Upland, *G. hirsutum*); the main ones are Coker 5110 (bred by INIAP) and others from Delta Pino and Stoneville. INIAP has a collection of 168 accessions of the genus *Gossypium*, conserved in the germplasm repository of the Department of Plant Genetic Resources located at the Experimental Research Station "Pichilingue" in Quevedo, Ecuador, obtained from the Germplasm Bank of the United States Department of Agriculture. Among the

most important constraints currently identified by farmers is resistance to pest attacks, drought and tolerance to low temperatures.

### Conclusions

As detailed in this manuscript, cotton cultivation has been of worldwide importance since its origins. The use of tools such as biotechnology has made it possible to define several aspects and to improve certain varieties especially resistance to pest attack, which is one of the main problems to be solved by cotton breeders to date. The diversity of genomes available, both diploid and tetraploid species, allows knowing more about the asymmetric contribution of several genes that lead to metabolic processes of interest, which can be used for genetic improvement.

In Ecuador, cotton cultivation has been declining in production and interest among farmers for several decades, so several actions have been carried out through national and international organizations dedicated to research to recover the importance it had decades ago. A correct exploration of the genetic resources of the tetraploid sister species of *Gossypium hirsutum*, *Gossypium barbadense* cotton, whose fiber is considered fine and very desirable in the international textile market, could be a good start to initiate a cotton genetic improvement plan in Ecuador, considered a natural reservoir of genetic resources of this species.

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