

Research Article

Natural Variation in Wild *Gossypium* Species as a Tool to Broaden the Genetic Base of Cultivated Cotton

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Abstract

Cotton is the world's most important natural textile fiber and a significantly growing source of food stuff, oil and feeds. Among the 53 *Gossypium* species, only 4 are cultivated, with *G. hirsutum* and *G. barbadense* comprising over 90% of the total cotton cultivation area worldwide. The extensive use of only a few closely related genotypes of cotton, coupled with the widespread adoption of transgenic cultivars, has greatly reduced the genetic base of the crop. This genetic uniformity makes cotton highly vulnerable to emerging biotic and abiotic challenges. Future breeding targets have to seriously consider infusing novel genetic variation into the gene pool of cultivated cotton that can buffer the crop against agro-environmental challenges brought about by shifts in climate. The wild *Gossypium* species hold a tremendous amount of untapped genetic diversity that can be exploited to broaden the genetic base of cotton. This review highlights the important agronomic traits that have been reported in wild *Gossypium* species and discusses the various pre-breeding strategies that have been utilized to incorporate genomes of wild *Gossypium* in cultivated cotton. Genetic and molecular studies towards understanding *Verticillium* wilt resistance and salt tolerance in wild cotton relatives are presented in brief.

Keywords: Cotton; *Gossypium*; Salt tolerance; *Verticillium* wilt; Wild species

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Introduction

Modern plant breeding has profoundly impacted agricultural production through the development and deployment of varieties with increased yield and improved agronomic performance. However, intensive selection that accompanies contemporary breeding strategies has also introduced a very high degree of genetic uniformity in the field, making crops vulnerable to emerging biotic and abiotic challenges [1]. Crop failures due to the heavy dependence on only a few crop varieties have been documented throughout the history of agriculture. In 1845 for example, a strain of *Phytophthora infestans* ((Mont.) de Bary) that was accidentally introduced from North America to Ireland decimated the genetically uniform potato varieties cultivated by farmers, leading to the Irish potato famine [2]. In the 1950s, the Panama disease caused by *Fusarium oxysporum* wiped out the banana variety Gros Michel that was widely cultivated in Central America [3]. The widespread planting of a single corn hybrid variety in the southern US resulted in economic losses of more than a billion dollars in the 1970s due to an outbreak of a new race of the fungal pathogen, *Bipolaris maydis* [4,5]. In the 1980s, monocultures of a single type of grapevine root forced California grape growers to replant approximately two million acres of vines following an outbreak of a new race of the grape phylloxera, *Daktulosphaira vitifoliae* [6].

As in the case of most cultivated crops, the overriding emphasis on only a few agronomic traits (i.e., yield and fiber quality) during domestication has severely narrowed the genetic base of cotton. Generations of industry-scale cultivation of a relatively small number of genetically related varieties has further reduced the available genetic variation in this crop. In the US, 98% of cotton that is currently being grown is *G. hirsutum* [7] and 85% are genetically modified for improved herbicide and pest resistance [8]. The genetic uniformity in cultivated varieties put the cotton industry at a high risk of collapse in the likely event of a disease or pest outbreak or upsurge.

Compounding the threats of disease and pest epidemics are abiotic challenges such as drought, heat and cold, as well as salinization of agricultural lands from years of intensified cultivation. While breeding objectives for cotton remain focused on improving baseline production and product quality, the emerging challenges in agriculture require that new cotton cultivars are developed with adaptation to extremes of temperature, reduced precipitation and saline soils, as well as resistance to new biotypes of pathogens and pests [9]. To this end, cotton breeders need to expand the cultivated germplasm base for the crop and consciously bring in genetic variation from diverse genetic resources that can provide tolerance to a multitude of environmental stresses as well as durable forms of resistance to pests and diseases.

Wild or exotic germplasm constitutes an important resource that can provide novel genetic diversity in cultivated crops that has been lost during domestication. Utilization of naturally occurring genetic variation from wild relatives of crops has been generally perceived as a better option (as opposed to artificial variation) in plant breeding because of the certain selective pressures that has already acted on the fitness of the organism [10]. Wild progenitors of domesticates

are commonly found in marginal habitats that are unsuitable for agriculture and that are subject to severe biotic and abiotic stresses. Without human intervention, these wild relatives evolved adaptive mechanisms that allow them to survive harsh environments [10,11]. One such example is *Solanum lycopersicoides*, a tomato-like nightshade species that thrives in the western slopes of the main Andean cordillera in the Chile-Peru frontier. At 3800 m above sea level, *S. lycopersicoides* survives frosts and light freezes in well-exposed sites where the cold air from glaciers and snowfields drains. Field cultures of this wild species also exhibit resistance to viral diseases and Lepidopteran pests [12,13]. Yet another example is *Hordeum spontaneum*, a wild relative of barley. *H. spontaneum* shares a niche with halophytic vegetation in the Dead Sea coast which receives only a minimum average precipitation of 55 mm per year [14]. The autoecology of *S. lycopersicoides* and *H. spontaneum* suggests the presence of considerable genetic variation that lends phenotypic plasticity in both species, allowing them to withstand marginal environments.

The genus *Gossypium* to which cotton belongs has more than 50 well-established species, only 4 of which are cultivated. In terms of fiber production and quality, the wild cotton relatives are relatively

inferior compared to the cultivated species. Despite this, the wild *Gossypium* germplasm serves as a rich reservoir of novel alleles that can be utilized to improve trait performance in cultivated cotton [7,15]. Interspecific hybridization to broaden the genetic base of the existing cultivars would be an important first step in utilizing the abundant genetic variation from the wild cotton relatives.

This review highlights the useful agronomic traits that have been reported for the different species of wild *Gossypium* during the past decade. Valuable genetic resources that incorporate the genome of wild *Gossypium* into the cultivated cotton by conventional breeding or with the aid of biotechnological techniques, as well as the potential application of these resources for trait improvement are discussed. Investigations toward unlocking the genetic and molecular basis of *Verticillium* wilt resistance and salt tolerance in different wild cotton relatives are presented in brief.

Genetic Diversity in the Genus *Gossypium*

The genus *Gossypium* includes 46 diploid ($2n = 26$) and 7 allotetraploid ($2n = 52$) species representing the AA, BB, CC, DD, EE, FF, GG, KK and AADD genomes (Table 1).

Wild Species	Useful Agronomic Traits	Origin	Genome
<i>G. hirsutum</i>	Widely cultivated	Central America	AD ₁
<i>G. barbadense</i>	Widely cultivated, long and high quality lint, resistance to <i>Verticillium</i> wilt [16]	South America	AD ₂
<i>G. tomentosum</i>	Tolerance to heat, source of the nectariless trait for resistance against tarnished plant bug, fleahoppers, boll rot and bollworm [17], resistance to jassids and thrips [18], high fiber quality, fiber length and fiber fineness [19]	Hawaiian Islands	AD ₃
<i>G. mustelinum</i>	Longer fibers [20,21]	NE Brazil	AD ₄
<i>G. darwinii</i>	Finer fibers, drought tolerance, resistance to <i>Fusarium</i> and <i>Verticillium</i> wilt [22]	Galapagos Islands	AD ₅
<i>G. ekmanianum</i>		Dominican Republic	AD ₆
<i>G. stephensii</i>		Wake Atoll	AD ₇
<i>G. africanum</i>	High fiber strength [23]	Southern Africa	A
<i>G. herbaceum</i> L.	Resistance to hoppers, white flies, thrips, aphids, and leaf curl virus [24]	Southern Africa	A ₁
<i>G. arboreum</i> L.	Resistance to hoppers, white flies, aphids, leaf curl virus [24], thrips [25], drought tolerance, resistance to black root rot, reniform nematodes [26] and spider-mites [27]	Indus valley, Madagascar	A ₂
<i>G. anomalum</i>	Resistance to cotton wilt, angular leaf spot, springtails and aphids, drought tolerance, high fiber quality, cytoplasmic male sterility [28]	Africa (Angola, Namibia)	B ₁
<i>G. triphyllum</i>	Flower color range from blue to purple [29]	Namibia in Africa	B ₂
<i>G. capitis-viridis</i>	High fiber quality, strong resistance to <i>Verticillium</i> and <i>Fusarium</i> wilt [30]	Cape Verde Islands	B ₃
<i>G. trifurcatum</i>		Somalia	B
<i>G. sturtianum</i>	Glandless-seed and glanded-plant [31] Resistance to <i>Fusarium</i> wilt [32]	Australia	C ₁
<i>G. nandewarense</i>		Australia	C _{1N}
<i>G. robinsonii</i>		WA, Australia	C ₂
<i>G. thurberi</i>	Tolerance to mild frost via defoliation, high resistance to <i>Verticillium dahliae</i> [29,33]	Mexico	D ₁
<i>G. armourianum</i>	Resistance to white flies, bacterial blight and jassids [18,29,34]	Mexico	D ₂₋₁
<i>G. harknessii</i>	Cytoplasmic male sterility and fertility restorer [35]	Mexico	D ₂₋₂
<i>G. davidsonii</i>	Salinity tolerance [36]	Mexico	D _{3-d}
<i>G. klotzschianum</i>	Salinity tolerance [37]	Galapagos Islands	D _{3-k}
<i>G. aridum</i>	Salinity tolerance [38] Resistance to reniform nematode [39]	Mexico	D ₄
<i>G. raimondii</i>	Resistance to jassids [34]	Peru	D ₅
<i>G. gossypioides</i>	Resistance to cotton leaf curl disease [40]	Mexico	D ₆
<i>G. lobatum</i>	Resistance to <i>Verticillium</i> wilt [41]	Mexico	D ₇
<i>G. trilobum</i>	Cytoplasmic male sterility and restorer factor. Drought tolerance, resistance to bollworm, pink worm, boll rot, <i>Verticillium</i> and <i>Fusarium</i> wilt [29,42]	Western Mexico	D ₈
<i>G. laxum</i>		Mexico	D ₉

<i>G. turneri</i>	Caduceus involucels [43]	Mexico	D ₁₀
<i>G. schwendimanii</i>		Mexico	D ₁₁
<i>G. stocksii</i>	Strong fibers, resistance to leaf curl virus [44], resistance to reniform nematode [45]	East Africa, Arabia	E ₁
<i>G. somalense</i>	Resistance to reniform nematode [45] Extra fiber strength, resistance to Egyptian bollworm and pink bollworm, arid tolerance [46]	Northeastern Africa	E ₂
<i>G. areysianum</i>		Arabia	E ₃
<i>G. incanum</i>		Arabia	E ₄
<i>G. benadirensis</i>		Somalia, Ethiopia, Kenya	E
<i>G. bricchettii</i>		Somalia	E
<i>G. vollesenii</i>		Somalia	E
<i>G. longicalyx</i>	Resistance to reniform nematode [45,47]	Africa	F ₁
<i>G. bickii</i>	Glandless-seed and glanded-plant [48]	Central Australia	G ₁
<i>G. australe</i>	Glandless-seed and glanded-plant, resistance to aphids and spider-mites [49] Resistance to <i>Fusarium</i> and <i>Verticillium</i> wilts, drought tolerance [50]	Australia	G ₂
<i>G. nelsonii</i>		Australia	G ₃
<i>G. costulatum</i>		Australia	K ₁
<i>G. populifolium</i>		WA, Australia	K ₂
<i>G. cunninghamii</i>		Northern NT, Australia	K ₃
<i>G. pulchellum</i>		WA, Australia	K ₄
<i>G. pilosum</i>		WA, Australia	K ₅
<i>G. anapoides</i>		Australia	K ₆

Table 1: Origin, genome assignment and useful agronomic traits of *Gossypium* species.

The genus diverged from its closest relatives, *Kokia* and *Gossypoides*, approximately 5-10 million years ago, whereas speciation was estimated to have occurred 1-5 million years ago. Long-distance, transoceanic dispersal was proposed to have driven the evolution of the diploid species, whereas wide hybridization between species having the A and D genomes and subsequent polyploidization gave rise to the allotetraploids (Figure 1) [7,51,52,53]. Species within the genus are geographically distributed in the arid and semi-arid regions of the tropics and sub-tropics, with new exotic species still being discovered in Australia and in the isolated islet chain in the West Pacific [7,28,50,54].

Out of the more than 50 *Gossypium* species, only the allotetraploids *G. hirsutum* and *G. barbadense*, and the diploids *G. arboreum* and *G. herbaceum* are cultivated for their spinnable fibers. *G. hirsutum*, which is also known as Upland cotton, Long Staple cotton or Mexican cotton, occupy over 90% of the world cotton cultivation whereas *G. barbadense*, otherwise known as Sea Island cotton, Pima cotton or Egyptian cotton, contributes to 8% of the global cotton production. The cultivated diploid species provide approximately 2% of the world's cotton and are cultivated in the more traditional growing areas of India, Pakistan, China, Bangladesh and Iran [24,51].

Based on genetic hybridization properties, *Gossypium* species are further grouped into the primary, secondary and tertiary gene pools. Both the cultivated (*G. hirsutum* and *G. barbadense*) and wild allotetraploids (*G. tomentosum*, *G. mustelinum* and *G. darwinii*) comprise the primary gene pool of cotton. The secondary gene pool includes the diploids having the A, B, D and F genomes, whereas the tertiary gene pool is composed of species with C, E, G and K genomes [7,55]. Genetic diversity studies using random amplified polymorphism DNA (RAPD), amplified fragment length polymorphism (AFLP), simple sequence repeats (SSR) and/or single nucleotide polymorphisms (SNPs) indicate the availability of a tremendous amount of genetic variation among the different wild species, as well as among exotic subspecies

of *Gossypium* [9,56-60]. This genetic diversity is reflected in the extensive variation in the gross morphology, maturity, photoperiodicity, yield potential, fiber quality, environmental adaptability and tolerance to pests and diseases that has been reported for the wild species of *Gossypium* (Table 1) [55,61]. To efficiently utilize this natural variation in cotton improvement, the genetic and molecular basis of phenotypic variations observed across the wild *Gossypium* germplasm need to be unlocked.

Development of Exotic Genetic Resources towards the Utilization of Wild Cotton Relatives in Trait Improvement

The wild cotton germplasm has been recognized as a rich reservoir of genes underlying traits of agronomic importance and to some extent, has been tapped to improve the productivity and fiber quality of cultivated cotton. Wide hybridizations using exotic subspecies of *G. hirsutum* has successfully transferred *Verticillium* wilt resistance and salinity tolerance from *G. hirsutum* subsp. *mexicanum* var. *neruosum* to elite upland cotton cultivars [62]. Similarly, quantitative trait loci (QTLs) controlling fiber quality and yield potential have been identified from interspecific hybrids developed between *G. hirsutum* and the wild allotetraploids *G. darwinii*, *G. mustelinum* and *G. tomentosum* [15,20,63]. The use of genetic bridges to facilitate crossing between the two tri-species hybrids *G. hirsutum* × *G. longicalyx* × *G. armourianum* and *G. hirsutum* × *G. longicalyx* × *G. herbaceum* has successfully introgressed the reniform nematode (*Rotylenchus reniformis*) resistance from *G. longicalyx* to *G. hirsutum* [64].

Despite the successful transfer of useful genes from a few wild species and subspecies into the cultivated cotton by conventional means, the extent of wide hybridizations within species of *Gossypium* has been limited. Interspecific hybridization between the cultivated *G. barbadense* and *G. hirsutum* via conventional crosses has

so far been unsuccessful [65,66]. Failure to develop interspecific hybrids between these two species may be attributed to the numerous genomic incompatibilities that result in sterility, cytological abnormalities, distorted segregation, hybrid breakdown, limited recombination between homologous chromosomes, and linkage drag that transfers undesirable traits along with the genes of interest in the wide hybrids [67-69].

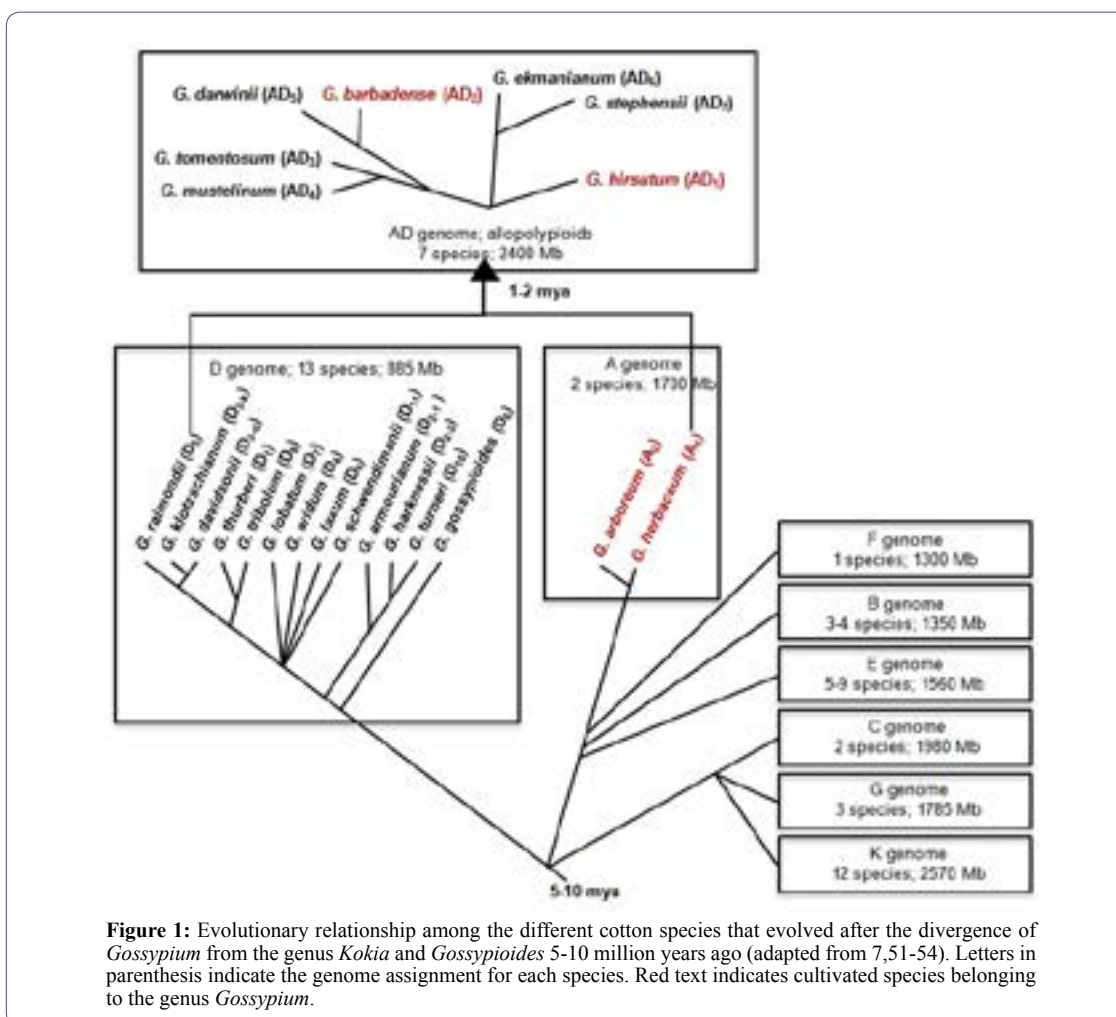
As an alternative to conventional gene introgression, exotic libraries that provide opportunities to break up disadvantageous associations between traits so that beneficial genes can be moved across *Gossypium* species from different gene pools have been generated. Chromosome segment substitution lines (CSSLs), monosomic alien addition lines (MAALs) and multi-parent advanced generation inter-crosses (MAGIC) are only few of the powerful genetic tools that can be used to identify and quantify the effects of specific alleles from wild relatives.

CSSLs are developed by hybridizations between an elite or adapted crop cultivar with a wild donor parent. Chromosome introgressions from the wild donor to the cultivated parent genome are commonly monitored using molecular markers. Each CSSL is selected to carry only a single chromosome introgression in a known locus within the genome. The whole genome of a wild donor parent is typically

represented in a set of CSSLs composed of several lines [70]. The uniform genetic background of CSSLs provides the advantage of easily associating a phenotype with the introgressed chromosome segment, as well as identifying genes/QTLs using only simple statistical analysis [71].

In cotton, CSSL sets representing the whole genome of *G. barbadense* in the background of *G. hirsutum* have been developed by various groups of researchers and have been used to identify and map QTLs controlling fiber yield and quality [72-76]. To date however, no other *Gossypium* species has been used as a donor in the development of CSSLs.

MAALs are also important genetic stocks that are derived from crosses between a crop and its wild ancestor. Development of MAALs usually requires embryo rescue of the interspecific hybrid before it aborts. A distinct characteristic of MAALs is the presence of a single chromosome from the wild ancestor in addition to the normal chromosome complement of a given crop. MAALs not only provide a convenient way of dissecting wild genomes into individual chromosome in a functional genomics background but also serve as bridges to transfer favorable genes from the wild to the cultivated species [77].



Morphological, cytological and molecular analysis using microsatellite markers have aided in the development of MAALs for *G. anomalum*, *G. australe*, *G. sturtianum* and *G. somalense* in the background of the upland cotton. *G. hirsutum*, *G. australe* and *G. somalense* have been reported to possess tolerance to drought, whereas all four wild species have been documented to have resistance to a range of pests (reniform nematode, Egyptian and pink bollworm, springtails, aphids and/or mites) and diseases (*Fusarium*, *Verticillium*, cotton wilt and/or angular leaf spot) [28,46,50,78,79]. Although these MAALs have already been characterized morphologically and to some extent, physiologically, screening of these exotic libraries under a range of biotic and abiotic pressures would allow the identification of lines that can be used for the improvement of disease resistance and drought tolerance in cotton.

In contrast to CSSLs and MAALs which are based on bi-parental crosses, MAGIC populations involve intercrossing a number of parental lines for several generations to combine the genomes of all parents in the progeny lines [80]. The use of multiple parents to develop the population effectively increases the genetic variation within the population as a result of greater mixing of diverse alleles. Because the population undergoes a greater number of recombination events, MAGIC populations can provide higher resolution for QTL mapping [81].

MAGIC populations have also been developed in cotton by intercrossing 10 cultivars and one non-commercial variety of *G. hirsutum* in a half-diallel design. Molecular characterization of the MAGIC population using SSRs and SNP markers showed introgressions coming from the 11 parents used in the crosses. Genome-wide association studies using this MAGIC population identified a QTL cluster controlling four fiber quality traits [82,83].

Despite the potential of MAGIC populations in moving genes from multiple wild cotton species into progeny lines, this type of genetic resource in cotton is still in its infancy. The value of utilizing wild MAGIC populations in the elucidation of genetic determinants underlying complex traits and in delivering solutions to current challenges in crop production is yet to be realized [80]. The potential use of wild MAGIC populations in actual breeding programs would also depend on the successful evaluation of the genetic diversity at the DNA level and linking these variations with observable phenotypic performances.

Aside from developing exotic libraries, biotechnological methods such as haploid induction, interspecific cell fusion and somatic hybridization have been proven effective in overcoming sexual incompatibilities between the wild and the cultivated cotton [42,84]. Symmetric electrofusions between the tetraploid *G. hirsutum* and the diploids *G. trilobum*, *G. klotzschianum*, *G. bickii*, *G. davidsonii* and *G. stocksii* have successfully generated viable somatic hybrids containing novel genetic combinations coming from the allotetraploid and the diploid parents [42,85-89]. The results of such studies indicate the feasibility and the efficiency of somatic hybridization in incorporating divergent genomes into breeding programs for cotton [42,44,45].

Understanding the Genetic Basis of Disease Resistance and Salt Tolerance in Wild *Gossypium* Species Towards their Utilization in Breeding

Verticillium wilt resistance

Verticillium wilt is an important disease in cotton caused by the

soil-borne fungus *Verticillium dahliae*. One of the salient features of this fungus is its ability to remain viable in the soil for extended periods, allowing the build-up of pathogen inoculum over time. Successful colonization of the host cotton plants by the fungal pathogen leads to systemic infection which can eventually result in leaf wilting, chlorosis and necrosis. Infection by the pathogen during the later stages of plant growth development can lead to floral organ abscission [90-92].

Cultural management, as well as application of fungicides and other soil amendments has been widely used to control *Verticillium* wilt in cotton. To date however, breeding and cultivation of resistant cultivars remain the most efficient, cost-effective and environmentally benign means to manage the disease [91].

G. barbadense has been reported to have higher levels of resistance to *Verticillium* wilt compared to the upland cotton *G. hirsutum*. Backcross inbred lines developed between the two allotetraploids successfully introgressed disease resistance mechanisms from Pima to the upland cotton, along with improved fiber quality. Commercial cotton cultivars developed by major seed companies in the US have also been reported to benefit from *Verticillium* wilt resistance from *G. barbadense* [16]. The widespread deployment of cultivars with *Verticillium* wilt resistance that is based only on the genetic variation provided by Pima cotton risks the breakdown of such resistance mechanism with the emergence of a new or more virulent pathotypes or races of the pathogens. For a broader spectrum and more durable form of resistance to *Verticillium* wilt, the wild *G. thurberi*, *G. trilobum*, and *G. capitata-viridis* can be tapped for novel genetic variation conferring resistance to the disease.

The wild species, *G. thurberi* (DD genome) has been identified to harbor genes conferring resistance to *Verticillium* wilt [28,33]. Proteomic studies on *G. thurberi* plants infected with *V. dahliae* identified 52 up-regulated proteins that are involved in stress and disease resistance, transcriptional regulation, signal transduction, protein processing and degradation, photosynthesis, production capacity and basic metabolism. While the result of the study indicates that disease response in *G. thurberi* is a function of the expression of multiple genes, it is important to note that five of the up-regulated proteins are products of disease resistance genes [33]. A reverse-genetics approach to identify the genes coding for the up-regulated proteins will provide basis for further investigation on the mechanisms underlying *Verticillium* wilt resistance in *G. thurberi*, towards practical applications in cotton improvement.

Like *G. thurberi*, *G. trilobum* (DD genome) and *G. capitata-viridis* (BB genome) have been reported to have resistance to *Verticillium* wilt [30,42]. Initial efforts to utilize the important agronomic traits of *G. trilobum* and *G. capitata-viridis* in breeding for *G. hirsutum* improvement have not been successful due to reproductive barriers between the two wild species and the upland cotton. To circumvent difficulties in producing wide hybrids due to fertility barriers, protoplast fusion was used to obtain symmetric somatic hybrids between *G. trilobum* and *G. hirsutum*. Flow cytometry in combination with the use of molecular markers such as RAPDs, SSRs, AFLPs and sequence-related amplified polymorphic markers confirmed the somatic hybridity of the regenerated plants. The hexaploid fusion plants exhibited morphological stability throughout generations, as well as strong vegetative growth and photosynthetic capacity [42]. Although the somatic hybrids have yet to be screened for *Verticillium* wilt resistance, the success by which protoplast fusion was able to incorporate the genetic material of *G. trilobum* together with that of *G. hirsutum*

opens up possibilities of introducing disease resistance from wild *Gossypium* species to elite cotton cultivars.

To tap into the genetic variation present in *G. capitis-viridis*, tri-species hybridization followed by chromosome doubling was used. The tetraploid *G. hirsutum* cv. TM1 was initially crossed with *G. australe* (GG genome), creating a triploid F₁ hybrid which was then treated with colchicine to generate an allohexaploid. Crossing the allohexaploid with *G. capitis-viridis* using the pseudophyletic introgression method generated an allopolyploid which has genetic contributions from the three *Gossypium* species. Field evaluations showed that the trihybrid has an intermediate morphology compared to the three wild species used to generate the hybrid, as well as higher resistance to insect pests [30]. Screening of the tri-hybrid against *Verticillium* wilt will determine the utilization of this novel germplasm in breeding programs to improve the resistance of cotton to the disease.

Salinity tolerance

The wild species of *Gossypium* serve as a treasure trove of genetic variation not only for resistance to pests and diseases but also for tolerance to a range of abiotic stresses including mild frost, drought and salinity. Due to the reproductive barriers that impede the interspecific hybridization among genetically distant species within the genus *Gossypium*, wild cotton relatives have not been largely used in breeding programs. Despite this constraint, studies have been conducted to examine the complexity of salt tolerance mechanisms in wild cotton using various 'omics' strategies. Understanding the genetic and molecular mechanisms that regulate salt tolerance in the wild cotton species will provide the necessary first step in exploiting natural variation within *Gossypium* in breeding for salinity tolerance in cotton.

The wild species *G. davidsonii* (DD genome), *G. klotzschianum* (DD genome) and *G. aridum* (DD genome) have been reported to exhibit tolerance to salinity stress. Next-generation RNA-sequencing in *G. davidsonii* from Baja, California identified 4744 and 5337 differentially expressed genes in the roots and leaves, respectively, of plants subjected to salt stress. Functional annotation of these genes elucidated the role of the Salt Overly Sensitive (SOS) and Reactive Oxygen Species (ROS) signaling pathways in salt tolerance in *G. davidsonii* [36]. In *G. klotzschianum* plants subjected to high salt stress (300 mM NaCl), transcriptome analysis showed the differential expression of 8312 and 6732 genes in the roots and leaves, respectively. Similar to *G. davidsonii*, functional annotation of genes that were differentially expressed in *G. klotzschianum* under high salt stress were involved in ROS and SOS signaling pathways, with the addition of genes involved in hormone biosynthesis and signal transduction [37]. In both wild species, differential expression was also observed in the transcription factor families of *AP2/EREBP*, *bZIP*, *bHLH*, *MYB*, *NAC*, and *WRKY*. Transcriptome analysis of *G. aridum* plants subjected to salt stress (200 mM NaCl) detected differential expression of genes involved in transport, hormone-stimulus response and signaling [38].

Although the molecular basis of salt tolerance in wild cotton relatives are far from being understood, results of 'omics' studies to dissect the complexity of salt tolerance in these wild species will provide basis for further investigations towards the identification and validation of genes/quantitative trait loci conferring salt tolerance in cotton.

Conclusion

Crop failures due to generations of utilizing a narrow genetic base for various crops have been documented throughout the history of agriculture. The wild species of *Gossypium* offers a tremendous amount of genetic variation that can be exploited to create and select for novel gene combinations that can give the highest productivity under a wide range of agricultural environments. The initial hurdle in developing interspecific cotton hybrids due to cross incompatibilities has been overcome using a suite of conventional and biotechnological tools that facilitated the effective incorporation of genetic materials from the wild *Gossypium* germplasm into existing cotton cultivars. Despite this major accomplishment, a large portion of the natural variation in the wild species of cotton remains unexploited. A requisite in the effective utilization of the rich diversity present in the wild cotton germplasm is the elucidation of the genetic basis of important agronomic traits. Recent advances in genomic technologies including the advent of high throughput sequencing technologies and genotyping platforms will allow rapid gene discovery towards a more precise utilization of natural genetic variation in cotton improvement.

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