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Chapter

Cotton Breeding in the View of Abiotic and Biotic Stresses: Challenges and Perspectives

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Abstract

Global climate change manifested in average annual temperature rise and imbalance of most natural factors, such as changes in annual mean rainfall, air humidity, average temperature of cold and warm months, soil quality, etc., lead to climatic zones displacement. All these have a significant impact on agricultural production in total, including cotton growing. Cotton is one of the most important technical crops in the world. However, it is very sensitive to environmental changes. The influence of abiotic stresses (high temperature, changes in the mean rainfall and soil salinity) causes a dramatic decrease yield of this crop. Moreover, temperature anomalies and climatic zones displacement cause a change in the area of pathogens and pests distribution, which also reduces the cotton yield. One of the possible ways to increase the cotton yield under the influence of abiotic and biotic stresses is the development of new resistant varieties, using both classical breeding methods and genetic engineering achievements.

Keywords: cotton, global climate change, abiotic and biotic stresses, cotton breeding, genetic engineering

1. Introduction

Cotton (*Gossypium* ssp. L.) is the major source of quality natural fiber and widely contributed to textile and seed oil industry [1]. Currently, the annual global cotton fiber production is about 25 million metric tons; the market value estimated is $ 12 billion [2].

Because cotton is a subtropical plant, it is well adapted to survive with dry and hot environment [3]. Despite this, cotton nevertheless reacts to an environmental change such as temperature and rainfall in instance. Long-term exposure of negative factors such as a drought, salinity, and temperature stress causes a significant decrease of yield and fiber quality [4, 5]. Such negative effect on cotton is due to the fact that drought, salinity, and temperature stress cause osmotic imbalance, membrane disorganization, growth decrease, inhibition of cell fission and reproduction; this

also leads to decline of photosynthesis level and hyperproduction of reactive oxygen species (ROS) [6, 7].

In addition to abiotic stresses, the cotton production is greatly influenced by biotic factors, such as pests and diseases that also cause a significant (up to 10–30%) reduction in yield [8]. At the same time, global climate changes responsible for temperature factors and climatic zone displacement also affect their development, geographical distribution, pathogenicity or injuriousness [4].

In this regard to these threats to cotton production, breeders are facing the important task of new cotton varieties resistant to abiotic and biotic stresses. However, this problem-solving by the classical genetics methods has become complicated due to the resistance traits generally having multigenic nature with a complex type of inheritance [9]. Additionally, the breeding oriented on resistance is further complicated by the "bottle-neck" effect such as narrow genetic basis typical for cultivated cotton [10]. Nevertheless, these disadvantages may be successfully overcome by the use of genetic engineering methods: transgenesis, RNA interference, and genome editing approaches.

In this chapter, we would like to analyze and summarize information about increase of cotton resistance to abiotic and biotic factors using genetic engineering approaches.

2. Increasing resistance to abiotic stresses

Abiotic stresses are a direct consequence of climate change. The world increase of temperature is primarily caused by carbon dioxide effect, i.e., its content in the atmosphere. The increase in the average annual temperature is the cause of increase of water evaporation from the soil, which directly leads to osmotic (by drought) and salt stress. One of the features of abiotic stresses is their simultaneous exposure. In other words, they have usually a similar effect on plants and defense mechanisms appearance in plants [11].

Abiotic stresses may affect cotton upon all development stages and lead to significant decrease in both yield and quality of cotton fiber [12, 13]. Thus, an increase of temperature at 2–3°C from the optimum can decrease biomass and yield, as well as increase fiber micronaire [13]. Drought and salinity also cause a decrease in the yield and quality of cotton fiber [6, 14].

In this regard, increase of a cotton resistance to abiotic stresses will reduce a negative effect and can raise the yield and quality of fiber. In this chapter, we consider the impact of abiotic stresses on the morphological and physiological parameters, as well as the mechanisms of resistance development and methods for increasing the adaptive potential of cotton to negative environmental factors.

2.1 Influence of abiotic stresses on morphophysiological parameters in cotton

Influence of abiotic stresses on cotton plants manifested in various forms of morphophysiological and biochemical changes, which reduce yield and fiber quality of cotton [6, 13, 14]. They negatively affect both morphological (seed germination, plant height and architecture, length and area of root system, leaf area, shoot and root biomass, boll development) and physiological parameters (chlorophyll content, photosynthetic efficiency, transpiration rate, stomatal conductance) [6, 13, 14].

In addition, prolonged exposure to abiotic stresses leads to a decrease in yield and fiber quality. Yield reduction manifested by both a decrease in the number and weight of bolls and fiber yield [6, 13, 14]. At the same time, this negative effect on yield is explained by a decrease in the activity of catabolic processes, including photosynthesis [6, 13, 14]. The fiber quality reduction manifested in a decrease in fiber length and an increase in micronaire. Such influence of abiotic factors on one of the most important agronomic traits of cotton is caused both by reduction of carbohydrate synthesis due to reduction of photosynthesis activity and by disruption of elongation process due to changes of membrane permeability and organization of microtubules and cytoskeleton [13, 14].

Disruption of photosynthesis under abiotic stresses is associated with an increase in ion permeability of chloroplast thylakoids and a decrease in chlorophyll levels, as well as inhibition of the activity of the key enzyme of carbohydrate synthesis 1,5-bisphosphate carboxylase [13–16].

2.2 Mechanisms of resistance to abiotic stresses

To reduce the negative impact of abiotic stresses in plants, including cotton, they have developed some adaptations on physiological and molecular level.

Physiological adaptations include accumulation of soluble substances in vacuoles to maintain cell turgor and decrease of stomatal conductance to reduce transpiration [11, 13, 14].

Molecular defense mechanisms against abiotic stresses include accumulation of osmolytes (proline, betaine, and soluble sugars), changes in activity of antioxidant system reducing level of ROS, regulation of cell ion balance and hormonal activity, as well as changes in activity of heat stress proteins [6, 7, 13, 14, 17]. Let us consider each mechanism separately.

Antioxidant system. One of the aftereffects of abiotic stresses on cotton is an increased level of ROS due to disruption of cell respiration and photosynthesis [6, 7, 13, 14, 17–20]. An increased ROS level leads to oxidative damage to proteins, DNA and lipids, destabilization of membranes, and increase of their permeability [19, 21]. Neutralization of ROS in plants is carried out by antioxidant system that includes nonenzymatic antioxidants (flavonoids, carotenoids, tocopherols, glutathione, etc.) and various antioxidant enzymes (superoxide dismutase, catalase, glutathione peroxidase, peroxidase, ascorbate peroxidase, and glutathione reductase) [21–24]. In most crops, including cotton, the increased activity level of antioxidant enzymes is associated with resistance to abiotic stresses: higher activity of antioxidant enzymes had been seen in more resistance varieties [17, 19, 25].

Ion balance regulation in cell. Ion imbalance and toxicity accompanied by Na^+ accumulation are the main consequences of salt and osmotic stress [6, 7, 11, 14, 18, 26]. To reduce ion toxicity and restore ion balance, plant cells use the Ca^{2+}-dependent salt supersensitive (SOS) regulatory pathway, which regulates ion homeostasis by modulating Na^+/H^+-antiporter activity during salt stress [7, 14, 26, 27]. The SOS pathway consists of plasma membrane Na^+/H^+-antiporter (SOS1), protein kinase (SOS2), and two calcium sensors—SOS3 and SCaBP8 (SOS3-like calcium-binding protein 8) [26, 28].

The excessive accumulation of Na^+ in the cytoplasm also results in the accumulation of Ca^{2+}, which interacts with SOS3/SCaBP8, activating the serine/threonine protein kinase SOS2. Then, SOS2 phosphorylates SOS1, which increases Na^+/H^+-antiporter activity, restoring the ion balance in the cell and enhancing salt tolerance [7, 20, 26]. SOS3/SCaBP8-SOS2 also regulates the activity of other transporters involved in ion

homeostasis: K^+- and Na^+-transporters, vacuolar Na^+/H^+-exchanger (NHX), vacuolar H^+-ATPases, and pyrophosphatases (PPase) [18, 20, 26].

Accumulation of osmolytes. Most abiotic stresses lead to water imbalance and, as a consequence, the induction of osmotic stress, which reduces cell turgor and the activity of many enzymatic systems [7, 11, 14, 18, 20]. To reduce the osmotic stress affects, plant cells accumulated the following osmoprotectors such as proline, betaine, soluble sugars, etc. [7, 11, 14, 18]. These agents protect membrane lipids and proteins from oxidative damage, increase the photosynthesis rate, and restore the osmotic potential of the cell [7, 20, 26, 29, 30].

Hormonal regulation. Abscisic acid (ABA), ethylene, salicylic acid (SA), jasmonic acid (JA), and brassinosteroids (BR) are the main plant stress hormones [7, 26, 31]. ABA is considered a major stress hormone whose activity increases during drought and salinity [7, 31]. ABA promotes the accumulation of K^+, Ca^{2+}, and osmolytes, reducing the inhibitory effect of abiotic stresses [7, 26, 31]. SA and BR are also involved in plant responses to abiotic stress [7, 26, 31]. An increase in BR under salt stress contributes to the maintenance of ion and osmotic homeostasis, increasing the stress tolerance of plants [7, 26, 31]. In addition, the BR signaling cascade intersects with the SOS pathway. BR leads to calcium accumulation in the cytosol, which activates the SOS pathway through SOS3/SCaBP8 [7, 26, 31]. The protective effect of SA and JA under stress is due to the activation of plant antioxidant system [7, 26, 31].

Heat shock proteins (HSPs). HSPs are molecular chaperones and play an important role in plant resistance to temperature stress [13, 32]. Depending on the molecular weight, the following HSP groups are distinguished: small HSP (sHSP), HSP60, HSP70, HSP90, and HSP100 [13, 32]. sHSP and HSP100 bind to proteins, prevent their denaturation and aggregation, promote their refolding with the participation of ATP-dependent chaperones (ClpB/DnaK) [13, 32]. HSP60 (mitochondrial chaperone or chaperonin 60) contributes to the maintenance of normal mitochondrial and chloroplast functioning under heat stress by keeping the native state of the inner mitochondrial membrane proteins and chloroplast thylakoids [13, 32]. HSP70 is involved in protein folding and prevention of protein aggregation [13, 32]. In addition, inhibition of HSP70 gene expression in cotton leads to oxidative stress by increasing H_2O_2 levels, which suggests the involvement of this chaperone in the regulation of several antioxidant enzymes activity [13, 32]. HSP90 together with HSP70 regulates protein folding by participating in signal transduction through signaling kinases and hormone receptors [13, 32].

Thus, plants have numerous mechanisms to promote abiotic stresses resistance. The genes mediating these defense mechanisms may be potential objects of interest for enhancing the adaptive potential of plants to environmental stress conditions.

2.3 Improving the adaptive potential of cotton to abiotic stresses

A significant decrease in the yield and fiber quality under the influence of abiotic stresses assigns a task for breeders to create cotton varieties resistant to these stresses. To solve this problem, it can use the methods of classical breeding, methods of molecular selection, and genetic engineering. Let us consider the application, advantages, and disadvantages of these methods.

Classical breeding. Inheritance of abiotic stress tolerance traits in cotton is multigenic with complex intergenic interaction including additive and nonadditive, dominant, and epistatic effects [9, 14]. The complex mechanism of trait inheritance

and "bottle-neck" effect make it difficult to use classical breeding methods to obtain cotton varieties resistant to abiotic stress. Moreover, these methods require a lot of time to develop new varieties.

Marker-associated selection (MAS). The use of molecular markers and Quantitative Trait Loci (QTL) mapping made it possible to overcome the disadvantages of classical breeding in developing cotton varieties resistant to abiotic stress [13, 14, 33–35]. Simple sequence repeat (SSR) and single-nucleotide polymorphisms (SNPs) are most commonly used to identify QTL [13, 14, 33–35]. Thus, using SSR markers, 11 QTLs localized on eight chromosomes (c9, c11, c15, c16, c21, c23, c24, c26) associated with salt tolerance traits were identified in the test population from *G. tomentosum* and *G. hirsutum* cross [36]. In the same population, QTLs associated with drought tolerance were also localized on chromosomes c5, c8, c9, and c16 as well as some QTL clusters for same trait on chromosomes c2, c3, c5, c6, c9, c14, c15, c16, and c21 [37]. Additionally, 165 QTLs have been identified in an introgressed population of *G. hirsutum* under abiotic stress conditions using 481 SNPs and 523 SSR markers covered of most cotton chromosomes. In total, 15 of them have been common QTLs of tolerance to abiotic stresses localized in 12 chromosomes: c1, c2, c5, c6, c8, c9, c10, c12, c20, c23, c25, and c26 [14].

Presently, various strategies, including genotyping by sequencing (GBS), SNP arrays, and genome-wide association study (GWAS), as well as populations of recombinant inbred lines (RIL) and backcross inbred lines (BIL), are used to improve the efficiency of QTL mapping [14]. Thus, 95 loci that associated with salt tolerance in *G. hirsutum* were found using GWAS in combination with SSR markers [38]. GWAS in combination with polymorphic SNPs of the CottonSNP63 K array applied to determine resistance of upland cotton has revealed a drought tolerance QTLs on chromosomes c8, c15, c21, c24, c25, and c26 and salt tolerance QTLs on chromosomes c1, c9, c11, c12, c13, c14, c18, c21, and c24 [39]. These data have confirmed using GWAS in combination with SNPs for MAGIC population of *G. hirsutum* including of 550 RILs. It has found that 11 QTLs associated both drought and salt tolerance [40].

In addition, the use of meta-analysis allows improving the accuracy of QTL mapping associated with abiotic stresses. For example, this approach has identified 23 stress tolerance QTL clusters on 15 different cotton chromosomes: c3, c4, c5, c6, c7, c11, c14, c15, c16, c19, c20, c23, c24, c25, and c26 [41].

Summarizing the above, the use of molecular markers and associative mapping data can significantly reduce the time to breed resistant cotton varieties.

Transgenic approaches. These approaches are widely used to increase cotton resistance to abiotic stresses. Thus, overexpression of *AVP1* and *OsSIZ1* genes in cotton enhances its resistance under both drought and heat shock stresses [42]. Overexpression of *HSP101* gene also increases resistance of cotton to temperature stress [13]. Further, transformation of cotton by *AsHSP70* gene from *Agave sisalana* resulted in improvement of a number of physiological parameters under heat stress [43].

Application of transgenic approaches also allows increasing cotton resistance to drought and salinity. Many transcription factors, regulating the activity of functional genes, can influence drought and salt tolerance in cotton [13]. Thus, overexpression of transcription factor *GhABF2* increases both drought and salt tolerance in cotton through regulation of ABA cascade genes [44]. Overexpression of other transcription factor genes (*AtRAV1/2*, *AtABI5,* and *SNAC1*) also increases cotton resistance to drought and salinity [13].

Increase in defense capacity of cotton due to increase level of osmoprotectants and activity of antioxidant enzymes and ion antiporters also enhance the adaptive resistance of the crop to abiotic stresses [13]. Overexpression in cotton of *AtEDT1/HDG11* gene from *A. thaliana* led to the increase of proline level and activity of antioxidant enzymes, increasing the resistance to salt and osmotic stress [45]. Moreover, transformation of cotton by the H^+-phosphatase gene (*TsVP*) from *Thellungiella halophile* allowed to reduce the negative effect of salt stress on photosynthetic activity [13]. Individual and coexpression of H^+-pyrophosphatase (*AVP1*) and vacuolar Na^+/H^+-antiporter (*AtNHX1*) genes from *A. thaliana* led to the increase of cotton salt tolerance due to more efficient regulation of ion balance [13].

Regulation of hormonal status by overexpression of their biosynthesis genes can also increase the adaptive potential of cotton resistance to salt and osmotic stress. Thus, overexpression of isopentenyltransferase (*IPT*) gene, one of cytokinin biosynthesis genes, increased cotton resistance to drought and salinity [13, 46]. Furthermore, cotton transformation with AtLOS5 gene (involved in ABA biosynthesis) from *A. thaliana* increased drought tolerance of the crop [13].

In this way, the application of transgenic methods makes it possible to effectively increase cotton resistance to abiotic stresses. However, those approaches are limited by the legislative regulation of GMO in many countries, according to this all transgenic crops obliged to undergo a full cycle of biosafety assessment [47].

Modern methods of genetic engineering. To overcome the biosafety constraints of transgenic cotton, researchers use modern genetic engineering methods including RNA interference (RNAi) and genome editing (GE) approaches.

RNAi is one of promising approaches both for studying of resistance genes and developing new cotton varieties resistant to abiotic stresses [10, 48]. For example, the use of VIGS-mediated RNAi revealed that R2R3-type *GbMYB5* transcription factor increases cotton resistance to abiotic stresses due to proline accumulation and increase antioxidant enzymes activity [10]. It has been also found that the expression levels of several miRNAs in leaves (miR156, miR157, miR162, miR172, miR397, miR398, miR399) and roots (miR172, miR397, miR398, miR399) change under salt and osmotic stress [49]. In addition, RNAi of phytochrome A1 gene increased the resistance of cotton to salt stress by activation of antioxidant enzymes [17].

Application of GE approaches to increase the adaptive potential of cotton in accordance to abiotic stresses is currently quite limited. However, there are successful applications of GE in cotton. For example, the target editing of *GhRDL1* and *GhPIN1–3* genes by the use of CRISPR/Cas9 system has allowed to obtain drought-resistant cotton lines [50].

Summarizing the above, it should be noted that presently, marker-associated selection and transgenic methods have the greatest importance in breeding of cotton resistant to abiotic stresses.

3. Improving resistance to biotic factors

Biotic factors (insect pests and pathogens) are among the most important factors that reduce cotton productivity [4, 8, 51]. For example, losses of cotton yield from pests may be up to 84% [51] and due to pathogens up to 30% [8]. As in the case of abiotic factors, global climate change leads to a shift of climatic zone, affecting the growth, development, and spread of insect pests and pathogens [4]. As results, this leads to the emergence of new pests and pathogens in these areas.

In this regard, improving plant resistance to biotic factors allows effectively control of pests and pathogens to reduce yield losses. In this part, we are looking at the characteristics of the main pests and pathogens, as well as a natural defense mechanisms and methods of improving cotton resistance to them.

3.1 Characteristics of major pests and pathogens of cotton

Insect pests. Cotton pest insects can be divided into two groups according to the mechanism of plant damage: chewing and piercing-sucking [52]. The first group includes insects that feed the plant biomass: cotton bollworm (*Helicoverpa armigera*), fall armyworm (*Spodoptera frugiperda*), pink moth (*Pectinophora gossypiella*), spotted bollworm (*Earias vittella*), and cotton leafworm (*Alabama argillacea*). The pests of this group of insects are larvae (caterpillars) that feed on immature bolls and leaves [8, 52].

The second group includes sap feeding insects that damage phloem: boll weevil (*Anthonomus grandis*), cotton aphid (*Aphis gossypii*), thrips (*Frankliniella spp*, *Thrips tabaci*, *Neohydatothrips variabilis*, and *Scirtothrips dorsalis*), cotton seed bug (*Oxycarenus hyalinipennis*), tarnished plant bug (*Lygus lineolaris*), cotton fleahopper (*Pseudatomoscelis seriatus*), and two-spotted spider mite (*Tetranychus urticae*) [8, 52]. The pests in this group are adults and/or nymphs [52].

In addition, soil nematodes can also cause a significant cotton yield reduction [8]. Nematodes parasitizing on cotton include the root-knot nematode (*Meloidogyne incognita*), reniform nematode (*Rotylenchulus reniformis*), and sting nematode (*Belonolaimus longicaudatus*) [8].

Phytopathogens. Cotton pathogens include viruses, bacteria, and fungi [8, 53]. Fungi of genera *Fusarium*, *Rhizoctonia*, *Pythium,* and *Thielaviopsis* affect cotton seedlings causing seedling root rot [53]. Blackspot causes with fungus of *Alternaria macrospora* Zimm, leading to leaves damage. *Ramularia areola* causes Ramularia blight of cotton [53]. Cotton boll rot is a complex disease caused by several fungal pathogens such as *Fusarium moniliforme*, *Calletotrichum gossypii*, *C. capsici*, *Aspergillus flavus*, *A. niger*, *Rhizopus nigricans*, *Nematospora nagpuri,* and *Botryodiplodia sp*. This disease affects the bolls, spreads to inner tissues, and leads to rotting of the seeds and fibers [53]. The most dangerous form of boll-rot is anthracnose, caused by *Calletotrichum gossypii* Southw. Anthracnose in cotton can occur in all growth stages of the plant, and it can affect all tissues, causing seedling or young plants to wilt and die, as well as a severe reduction in fiber and seed yields [53].

F. oxysporum f. sp. *vasinfectum* causes development of cotton Fusarium wilt at seedling stage with cotyledon lesions [53]. Verticillium wilt is caused by *Verticillium dahliae* Kleb, which affects cotton leaves in the budding or immature bolls stages [53].

The viral diseases include cotton leaf curl disease (CLCuD) and (CLCrD) [53]. CLCuD is caused by begomoviruses that lead to leaf injury (swollen veins, leaf curl, enation, and stunting). When affected in the early stages of development, there is a significant reduction in yield [53]. The cotton leaf curl virus (CLCrD) affects the leaves resulting in leaf discoloration and vein hypertrophy, leaf curl, shortening of internodes, and growth stunting. The infestation degree depends on the stage of plant development [53].

Bacterial blight of cotton is one of the most serious diseases causing significant yield losses [8, 53]. Disease results from infection by *Xanthomonas citri* pv. *malvacearum* [8, 53]. Affected plants show the following symptoms such as defoliation, swelling and darkening of stems, bolls detachment. By severely affecting, the fiber quality is decreased due to coloration and the plant death [53].

3.2 Mechanisms of resistance to biotic factors

The long coevolution of cotton and insect pests and pathogens has resulted in mechanisms to reduce the damage from biotic factors. Molecular mechanisms of pathogen resistance include the activation of resistance genes (R-genes) in response to exposure. R-gene activation triggers a large number of intracellular cascades leading to the synthesis of protective substances that reduce the damage by pathogens [54, 55]. Morphological and chemical defense mechanisms have been developed in cotton to reduce the pest influence degree [56, 57]. Let us in more detail consider mechanisms of resistance to insect pests and pathogens correspondingly.

Resistance to pests. Morphological defenses and chemicals (secondary metabolites) of cotton directly influence the insect (imago or larvae) affecting important parameters of their life cycle [56]. Trichomes are considered as the major morphological adaptation of cotton that increases its insect resistance. These provide protection by forming a physical barrier or excreting chemical repellents, toxins, or adhesive substance [56].

Terpenoids, flavonoids, tannins, and anthocyanins are among the secondary metabolites providing direct protection of cotton plants from insects [56]. Terpenoids are the most studied protectors of cotton. Terpenoids synthesized in cotton include gossypol, hemigossypol, hemigossypolone, and heliocides H1, H2, H3, and H4 contained in small subepidermal and intracellular pigment glands [56]. Cotton terpenoids have direct toxic effect on insect pests including *H. virescens*, *H. zea*, *H. armigera*, *P. gossypiella*, *Estigmene acrea*, *E. insulana*, and *E. vitella*. In addition, gossypol and gossypol-like compounds are toxic to the gall nematode *Meloidogyne incognita* [56].

It should also be noted that damage of cotton by pests and pathogens causes induction of terpenoid biosynthesis by activation of JA-, SA-, and ethylene-dependent signaling pathways [56, 58]. These pathways activation occurs due to elicitors, which, interacting with specific receptors, lead to an increase in intracellular Ca^{2+}. This in turn activates calcium-dependent proteins, including Ca^{2+}-dependent protein kinases (CDPKs) [58]. CDPK, by phosphorylating proteins and changing gene expression patterns, activates mitogen-activated protein kinases (MAPK), leading to JA and SA formation, on the one hand, and the ethylene pathway, on the other [58].

Resistance to pathogens. Plant resistance to pathogens (plant immunity) is controlled by resistance genes (R-genes) [54]. R-genes encode surface (receptor-like kinases—RLK) or intracellular receptors (nucleotide-binding proteins with leucine-rich repeats—NLR) activating a various mechanism under interaction with them [54, 59–61]. One consequence of receptor activation is an increase intracellular Ca^{2+} concentration, leading both to the activation of the Ca^{2+}-dependent signaling cascade and an increase in ROS levels [59–61]. At the same time, ROS play the function of an intracellular signaling molecule contributing to the development of systemic acquired resistance (SAR). It should also be noted that both Ca^{2+}- and ROS-dependent signaling cascades by activation of JA-, SA-, and ethylene-dependent signaling pathways lead to synthesis of phytoalexins (mainly gossypol and gossypol-like terpenes), which play an important role in cotton resistance to pathogens [59–61]. For example, induction of gossypol synthesis in cotton has been proved by infestation with *Verticillium dahlia*, *Fusarium oxysoporum* f.sp. *vasinfectum*, *Rhizoctonia solani*, *Rhizobium rhizogenes,* and *Xanthomonas spp* [56].

Thus, plants have a various mechanisms that provide resistance to pests and pathogens. Genes mediating these defense mechanisms may be potential genes for improving cotton resistance to biotic factors. In addition, the control of genes of the

causative agents themselves, playing an important role in their life activity, may also be of potential interest.

3.3 Improving cotton resistance to biotic factors

Biotic factors (pathogens and pests) are one of the main reasons for significant yield losses (up to 84% due to insects and up to 30% for pathogens) in agriculture [4, 8, 51]. At the same time, strategies to control infestations are an increase in the internal defense mechanisms of plants or introduction of pathogen-targeted constructs into the genome [62, 63]. Methods of classical breeding, molecular breeding, and genetic engineering are used to develop new varieties that are resistant to the impact of biotic factors. Let us consider the application, as well as advantages and disadvantages of each of these methods.

Classical breeding. Classical breeding methods increase the internal defense mechanisms of the plants and use the cotton germplasm reserves to produce new resistant varieties. For example, among all cultivated cotton species (*G. hirsutum* L., *G. barbadense* L., *G. arboretum* L., and *G. herbaceum* L.), only *G. barbadense* has sufficient resistance to *Verticillium dahlia*. However, transgenesis of the resistance into upland cotton by classical breeding methods has so far not been successful [59].

Such interspecific crossing for the purpose of transfer wilt resistance genes is complicated by different type of these traits inheritance in *G. hirsutum* and *G. barbadense* L. Studies of interspecific crossing show dominant or partially dominant inheritance of resistance traits, while by intraspecific crossing of *G. hirsutum*, the traits inheritance is more complex [59]. A number of studies report wilt resistance control by a single dominant gene, while others state that resistance is a quantitative trait [59, 64]. An additional difficulty is the fact that varieties with high wilt resistance have low fiber yield and quality, as well as crop yield [59]. In addition, it should be noted that classical breeding methods are time-consuming, which reduces the effectiveness of this approach in breeding pathogen-resistant cotton varieties.

Marker-associated selection (MAS). MAS and QTL mapping have been widely used in the development of cotton varieties resistant to Verticillium and Fusarium wilt. For example, more than 400 QTL of resistances to both kind of wilt have been identified, which are distributed over all 26 pairs of chromosomes [34, 59, 64]. These data were obtained both using mapping of chromosome-substituted and RIL populations with the help of various markers type and GWAS [59, 64–68].

Furthermore, a meta-analysis of the consensus map of Cotton Marker Database (CMD) based on *G. hirsutum* × *G. barbadense* cross, five mutagenesis "hot spots" of wilt resistance were identified on c16 and c23 chromosomes [69]. Same meta-analysis revealed that 74 QTLs of nematode resistance are localized on all chromosomes. Thus, 71 QTLs of them are associated with resistance to root-knot nematode, and three remains with resistance to reniform nematode. Especially, the greatest number of QTLs for this trait was identified on chromosomes c7 and c11. The mutagenesis hotspot of nematode resistance is also located on chromosome c7 [69, 70]. Additionally, this study shown that two QTLs of resistance to *Xanthomonas campestris* pv. *Malvacearum* are localized on chromosomes c5 and c14 [69].

The obtained data of a QTL mapping can be successfully used in further MAS and genomic breeding programs.

Transgenic approaches. These approaches are currently the most effective method for creating cotton varieties resistant to insect pests [8]. According to ISAAA, transgenic cotton occupies about 79% of the total cultivated area of this crop [71]. Despite

the existence of various strategies to develop insect-resistant transgenic crops (use of several genes with insecticidal properties such as inhibitors of insect's digestive proteases, α-amylase, lectin, etc.), most transgenic insect-resistant (IR) crops, including cotton, are based on insertion of *cry* genes encoding *Bacillus thuringiensis* (Bt) toxin in the host plant genome [8, 72]. Bt (or Cry) toxins have specific activity against insect from orders such as *Lepidoptera*, *Coleoptera*, *Hymenoptera,* and *Diptera*, as well as for nematodes [8, 72]. The cultivation of Bt-cotton has significantly reduced the use of insecticides in cotton-growing countries [72]. The use of transgenic cotton plants with Bt-gene sets further expands the potential of transgenic cotton and reduces the emergence of resistant insect populations [8, 72].

Thus, vegetative insecticidal proteins (*Vip*s) from *B. thuringiensis* with insecticidal activity against *Gossypium spp*. pests are promising for the creation of transgenic IR-cotton [8]. The proteins *Vip1* and *Vip2* are binary toxins, which are very toxic to some representatives of *Coleoptera* and *Hemiptera*. The action mechanism of *Vip3* is similar to that of Bt-toxins [8].

In order to create varieties resistant to fungal pathogens (*Rhizoctonia solani*, *Alternaria alternata*, *Alternaria macrospora,* and *Fusarium oxysporum*), transformation of cotton with genes encoding chitinases has been used [8]. Glucose oxidase genes were introduced into the cotton genome to improve resistance to *V. dahliae*, while the harpin encoding gene (*hpa1Xoo*) from *Xanthomonas oryzae* pv. *oryzae* is used to provide resistance to various pathogens [8]. Transformation of cotton with the antisense movement protein (*AV2*) and antisense coat protein (*ACP*) genes from CLCuV results in resistance to CLCuD [8].

In accordance with above, the application of transgenic technology is currently the most used and commercially successful for creating pest and pathogen resistant crops. However, the most serious disadvantage of this technology is the need for long-term biosafety assessment of transgenic cotton to minimize risks of human health and the environment [47].

RNA interference (RNAi). The host-induced gene silencing (HIGS) approach, in which a construct is introduced into the host genome that induces posttranslational suppression of gene expression in pathogen or pest through dsRNA upon infection, is most commonly used to achieve resistance to biotic factors with RNAi [8, 10, 59]. Thus, introduction of RNAi construct to hygrophobins1 (*VdH1*) gene of *V. dahliae* into cotton genome provides resistance to this pathogen [73]. A similar effect is achieved by HIGS to *V. dahliae VdRGS1* gene mediated by tobacco rattle virus [74].

The use of HIGS to the genes encoding proteins that play an important role in the life maintenance of insect allows the development of cotton IR lines. Thus, silencing of cytochrome P450 gene of insect monooxygenase (*CYP6AE14*) involved in gossypol detoxification leads a significant increase in cotton resistance to cotton bollworm (*Helicoverpa armigera*) [10, 75].

Another approach to improve cotton resistance to biotic stresses is virus-induced gene silencing (VIGS) of the host genome [10]. Thus, VIGS-mediated suppression of *GhNDR1*, *GhMKK2,* and *GbVE1* gene expression in cotton increased its resistance to *V. dahliae* [10].

Summarizing these, RNAi is a promising approach to develop cotton varieties resistant to biotic stresses. However, the application of this approach is limited by high probability of effect on nontarget organisms and complexity of cotton genome, due to tetraploidy [10].

Genome editing approaches. GE methods are also promising for developing pathogen and pest-resistant cotton varieties. For example, CRISPR/Cas9-mediated editing

of Gh14–3-3d gene, which is a negative regulator of disease resistance, has allowed obtaining cotton lines with high resistance to *V. dahliae* [50, 76]. However, despite the promise of GE methods, their application is limited by the complexity of the genome of cultivated tetraploid cotton species, needing to edit both homologs in A- and D-subgenomes.

Thus, summarizing the data above, transgenic methods are currently the most used and commercially successful strategy for developing of new insect pest and pathogen-resistant varieties.

4. Conclusion and future perspectives

Global climate change has a significant impact on cotton production through the complex impact of abiotic and biotic factors, reducing yields and fiber quality [4, 8, 13, 14, 51]. This poses a task to breeders of developing new cotton varieties that are resistant to abiotic and biotic stresses. To challenge it, breeders use both classical and molecular breeding methods and genetic engineering.

By developing cotton varieties resistant to abiotic stresses, molecular breeding methods are more often used, while genomic transgenomic methods improve resistance to insect pests and pathogens [8, 14]. However, the use of modern genetic engineering approaches, including cis- and intragenesis methods, is limited by the complexity of the genome of cultivated tetraploid cotton species. Therefore, the application of RNAi and GE methods to obtain cotton varieties resistant to abiotic and biotic stresses is currently insignificant [8, 14].

In addition, the insignificance of using molecular breeding methods to create pest and pathogen-resistant cotton varieties should be noted. This is due to the insignificant number of mapped insect and pathogen resistance loci in the cotton genome [59–70].

Fundamental understanding of molecular and genetic mechanisms underlying cotton resistance to abiotic and biotic stresses will allow application of cis- and intragenesis methods as well as RNAi and GE technologies in new resistant varieties development. Thus, the genes encoding DRE-binding protein 1 (*GhDBP1*), Na^+/H^+-antiporter (*SOS1*; *GhNHX1*), and H^+-pyrophosphatase (*AVP1*) are promising genes for improving drought and salt tolerance [14]. Overexpression of own heat shock genes can be used to improve resistance to heat stress [13]. RNAi and GE technologies can also be used to reduce the expression level of negative regulators of resistance to abiotic stresses.

Studying the mechanisms of interaction between the host plant and insect pests or pathogens, as well as the molecular and genetic basis of life support functions of causative agents, will allow more successful use of the HIGS, RNAi, and GE technologies to suppress key genes and cisgenesis technologies to enhance the host plant defense mechanisms. Genes encoding Vacuolar-type ATPase (*V-ATPaseE*), tubulin-folding cofactor D (*TBCD*), choline acetyltransferases, receptor for activated C kinases (*RACK*), and zinc finger transcription factor (*HUNCHBACK*) are promising for HIGS approach application. Overexpression of key genes of stress hormone biosynthesis (SA, JA, and ethylene) can be used to enhance the protective properties of cotton. In addition, pyramiding the genes for different resistance traits to develop varieties with combined resistance to stresses is promising.

Thus, modern molecular biology technologies have great potential to reduce the negative effect of global climate changes on cotton yield and fiber quality.

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