

BREEDING, GENETICS, & GENOMICS

Evaluation Methods, Resistant Germplasm, and Breeding for Resistance to Bacterial Blight in Cotton: A Review

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ABSTRACT

Bacterial blight (BB) caused by *Xanthomonas citri* pv. *malvacearum* (Xcm) is an important cotton (*Gossypium* spp.) production problem. In the U.S., BB has been controlled effectively using resistant cultivars and acid-delinted seed since the 1970s; however, resurgence of BB occurred in the early 2010s because of negligence in breeding. This review provides an up-to-date account on the pathogen, resistance evaluation methods, resistant germplasm lines, and breeding methods. Twenty-two Xcm races have been reported worldwide, and race 18 is currently the only one found in production fields in the U.S. To evaluate cotton for BB resistance, a pressure-sprayer-based method with surfactant in the field and a cotyledon-scratching-based method in the greenhouse are most often used. Breeding for BB resistance was highly successful in Sudan between the late 1930s and 1960s, when many resistance genes were transferred to *G. barbadense* from *G. arboreum*, *G. herbaceum*, *G. anomalum*, and *G. hirsutum*. Breeding for BB resistance commenced in the U.S. in the 1940s, leading to development of numerous resistant Upland cultivars. Although backcrossing was often used to transfer resistance genes in early years, forward breeding has been the breeding method of choice. Currently, some and possibly all resistant cultivars in the U.S. possess the resistance gene *B*₁₂, which confers immunity with no water-soaked symptoms. Although *B*₁₂-based resistance has held for a long time, identification of new resistant sources is needed to prevent an epidemic of BB due to evolution or introduction of possible new virulent Xcm races.

Cotton (*Gossypium* spp.) produces the most important natural spinning fiber (lint) for the textile industry in the world and accounts for 85% of the farm-gate value. The remaining production value is provided by cottonseed, which is used in the food industry for extracting vegetable oil for cooking, margarine, and salad dressing and as protein supplement in animal feed.

The genus *Gossypium* comprises approximately 50 species including 45 diploids ($2n = 2 \times = 26$) and five allotetraploids ($2n = 4 \times = 52$) (Wendel and Cronn, 2003). The diploid species are grouped into eight genome groups (A to G and K) according to the pairing affinities of chromosomes (Stewart, 1994), among which only *G. herbaceum* L. (A₁) and *G. arboreum* L. (A₂) are cultivated Old World cotton species, with limited production in India currently. The five allotetraploid species originated from a common ancestor and are assigned to (AD)₁ through (AD)₅ based on their genome organizations (Wendel and Cronn, 2003). Only *G. hirsutum* L. [(AD)₁] and *G. barbadense* L. [(AD)₂] were domesticated in the New World and are cultivated worldwide. *G. hirsutum*, also known as Upland cotton, is high yielding with wide adaptations, accounting for more than 97% of global cotton production. *G. barbadense*, also known as Sea-Island, extra-long staple (ELS), American Pima, or Egyptian cotton, produces superior extra-long, strong, and fine fibers and is grown in a dozen countries. Pima cotton accounts for approximately 3% of global cotton production because of its lower yield potential and narrow adaptation. For example, Pima cotton is only grown in limited areas in four (Arizona, California, New Mexico, and Texas) of the 17 southern states that make up the U.S. Cotton Belt.

There are many biotic stresses affecting cotton growth and reproduction, one of which is bacterial blight (BB) caused by *Xanthomonas citri* pv. *malvacearum* (Xcm). BB is a troublesome disease that plagues global cotton production. In the U.S., BB has been effectively controlled using resistant cultivars and acid-delinted planting seed since the 1970s; however, resurgence of BB occurred in the 2010s because of negligence in breeding effort (Phillips et

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al., 2017; Wheeler, 2018). To fill the knowledge gap, Zhang et al. (2020) provided a comprehensive summary on the genetic and genomic basis of BB resistance in cotton. As a companion paper, this literature review is focused on the Xcm pathogen, germplasm screening methods, resistant germplasm identified or developed, and breeding for Xcm resistance.

BACTERIAL BLIGHT PATHOGEN

Bacterial blight was first reported in the U.S. in Alabama by Atkinson in 1891 (Atkinson, 1892). It is caused by the gram-negative bacterium, *Xanthomonas citri* pv. *malvacearum* (Smith, 1901). Xcm affects cotton that originated in both the Old and New Worlds. Xcm is also aerobic, non-acid producing, and non-spore forming. The bacterial blight cells measure 1 to 1.2×0.7 to $0.9 \mu\text{m}$ in culture. Under the microscope, Xcm is a short, motile rod equipped with a single polar flagellum, formed singly or in pairs (Jalloul et al., 2015; Kale et al., 2012), and infrequently in chains. A chain of Xcm cells forms by connecting each other through bacterial slime (Verma, 1986). This slime layer contains extracellular polysaccharides (EPS). Verma (1986) stated that the number of EPS is directly related to the virulence of Xcm in that the most virulent Xcm has the highest EPS amount and the least virulent Xcm has the lowest. Also, Verma (1986) characterized Xcm strains or races in two groups: lactose utilizing (lac^+) and lactose non-utilizing (lac^-).

Twenty-two Xcm races have been described (Hillocks, 1992; Jalloul et al., 2015; Phillips et al., 2017). A total of 19 physiological races of Xcm have been identified using 11 differential cotton cultivars in the U.S. (Abdo-Hasan et al., 2008; Brinkerhoff, 1970; Hunter et al., 1968; Table 1). To date, races 20, 21, and 22 have been reported only in Central Africa (Abdo-Hasan et al., 2008; Allen and West, 1991; Hunter et al., 1968; Hussain, 1978; Jalloul et al., 2015; Thaxton and El-Zik, 2001; Verma and Singh, 1975). Abdo-Hasan et al. (2008) also illustrated that the spreading of these races varied from region to region. For example, at one time, race 1 was common in Australia, India, and the U.S., whereas races 2 to 5 were documented in the U.S. and India, and race 6 was documented in Nigeria, Zimbabwe, and India. However, race 18 is now the only race found in the U.S. (Phillips et al., 2017; Wheeler et al., 2022). Race 18 also is commonly found in Australia,

West and Central Africa, Brazil, India, Pakistan, and Nicaragua (Allen and West, 1991; Chavhan et al., 2021; de Sousa Braga et al., 2016; El-Zik and Thaxton, 1994; Kumar et al., 2018; Zachowski and Rudolph, 1988). Another highly virulent (HV1) race has been reported in Africa and other regions of the world, which could break the resistance of cotton cultivars to race 18 (Abdo-Hasan et al., 2008; El-Zik and Thaxton, 1994).

Abdo-Hasan et al. (2008) confirmed the diversity and complexity of Xcm using PCR-based marker techniques: randomly amplified polymorphic DNA (RAPD) analysis and inter simple sequence repeats (ISSRs). Other DNA markers have been used to study the genetic diversity of Xcm (e.g., Kumar et al., 2018). DNA polymorphisms can occur due to mutations, such as nucleotide modifications, insertions, and deletions. To date, draft genomes of Xcm from several races, including races 1, 2, 3, 12, 18, and 20, a highly virulent strain, a local strain of unnamed race (likely race 18) in Mississippi, and three African Xcm strains, have been published (Cunnac et al., 2013; Pérez-Quintero et al., 2023; Phillips et al., 2017; Showmaker et al., 2017; Wheeler et al., 2022; Zhai et al., 2013). The genome sequences allowed the development of a TaqMan-based qPCR method to detect and differentiate five Xcm races (1, 2, 3, 12, and 18) in cotton leaves and seeds (Wang et al., 2019). Because type III secreted effector (T3SE) proteins in Xcm play an important role in pathogenicity by interacting with host sugar transporter SWEET genes, one of the most studied T3SEs is the transcriptional-activator-like (tal) effector (TALE) proteins (Cox et al., 2017; Gupta et al., 2021; Haq et al., 2020). Wheeler et al. (2022) recently reported that Xcm race 18 in cotton possesses a unique effector protein XopJ, whereas the other races tested (1, 2, 3, and 12) lacked it.

In cotton, most of the BB resistance *B* genes are dominant (Zhang et al., 2020). It is currently known that, in most cases involving *Xanthomonas* spp. in plants, a dominant host plant resistance *R* gene represents active recognition of a pathogen determinant by an *R* protein or a pattern recognition protein (PRR), whereas non-functional recessive *r* alleles are usually associated with the modulation of pathogen susceptibility genes, such as the SWEET genes (An et al., 2020). However, it is currently unclear how an Xcm TALE protein interacts with a host SWEET gene to induce susceptibility or a host resistance *B* gene to induce an incompatibility reaction in cotton.

The disease caused by BB infection has several names depending on the part of the plant infected such as angular leaf spot, vein blight, blackarm lesion, and boll rot. Several studies have contributed to the recent understanding of the pathogenicity of cotton BB (Jalloul et al., 2015). These studies demonstrated that the influence of BB on cotton yield depended on weather conditions such as rainfall and humidity. The preferable conditions for BB inoculum are 85% humidity, 30 to 40 °C atmospheric temperature, and 28 °C soil temperature. Other factors that raise the chance for BB infection are early seed sowing, poor tillage, and late irrigation (Jalloul et al., 2015), although Showmaker et al. (2017) indicated that the optimal temperature for infection was 25 to 30 °C for a race 18 isolate from Mississippi. The attachment of the bacterium to the cotton leaf surface is the prerequisite for plant infection (Jalloul et al., 2015; Thiers and Blank, 1951). Furthermore, scientists found that injury to plant tissues by blowing

sand, insects, animals, and machines accelerates BB spread and infection on plants. Additionally, seeds have been linked with long-distance spreading of Xcm (Brinkerhoff and Hunter, 1963).

When an acceptable environment is encountered, the pathogen penetrates the leaves through open stomata or wounds, and then symptoms or a hypersensitive reaction (HR) develop in plants (Delannoy et al., 2005). Susceptible plant tissues develop expanding water-soaked lesions (Delannoy et al., 2005). The HR leads to death of a limited number of leaf cells in the inoculated area within two days in resistant plants, which can be used as a marker to detect resistant plants. Cottonseeds are a source of inoculum in the field because Xcm can survive on cotton lint, the seed surface, and within the seed and be transmitted to emerging seedlings (Brinkerhoff and Hunter, 1963; Innes, 1983; Kirkpatrick and Rothrock, 2001; Mijatović et al., 2021; Verma, 1986).

Table 1. Reaction of 19 races of *Xanthomonas citri* pv. *malvacearum* on 11 host differentials (El-Zik and Thaxton, 1994; Hunter et al., 1968)

Host Differentials and Their Response to Races											
Race	A	B	C	D	E	F	G	H	I	J	K
1	+	+	-	-	-	-	-	-	-	-	-
2	+	+	+	-	-	-	-	-	-	-	-
3	+	+	-	-	+	-	-	N/A	N/A	N/A	-
4	+	+	-	-	-	+	-	N/A	N/A	N/A	-
5	+	+	-	-	+	+	-	N/A	N/A	N/A	-
6	+	+	-	+	+	-	-	+	-	-	-
7	+	+	-	+	+	+	-	+	-	-	-
8	+	+	+	+	+	-	-	+	-	-	-
9	+	-	+	-	-	+	-	N/A	N/A	N/A	-
10	+	+	+	+	+	+	-	+	-	-	-
11	+	+	-	-	-	-	-	+	-	-	-
12	+	+	+	-	-	-	-	+	-	-	-
13	+	-	-	-	-	-	-	N/A	N/A	N/A	-
14	+	+	+	-	+	+	-	+	-	-	-
15	+	+	+	-	+	-	-	N/A	N/A	N/A	-
16	+	+	+	+	-	+	-	N/A	N/A	N/A	-
17	+	+	+	-	-	+	-	N/A	N/A	N/A	-
18	+	+	+	+	+	+	-	+	+	+	-
19	+	-	-	-	+	+	+	+	-	-	-

Host differentials: A, Acala 44; B, Stonville 2BS9; C, Stonville 20; D, Mebane B-1; E, 1-10B; F, 20-3; G, 101-102B; H, Gregg; I, Empire B4; J, DP×P4; K, AZZ95 “+” = susceptible reaction and “-” = resistant reaction “N/A” = not available

RESISTANCE SCREENING METHODS AND TECHNIQUES

Bacterial blight resistance is screened either in the field or in controlled environments. There are many different inoculation and evaluation methods for BB resistance in cotton breeding (Thaxton and El-Zik, 1994). Different methods of inoculation and environmental and plant conditions can affect the expression of resistance. Because Xcm needs to enter the leaves through open stomata or wounds to initiate infection (Delannoy et al., 2005), a low-pressure sprayer with organosilicone non-ionic surfactants (Wheeler et al., 2007) or scratching (wounding) the lower surface of cotyledons/leaves with a toothpick (Bird, 1982) are used frequently for artificial inoculations in large scale evaluations. Syringe or vacuum infiltration also can be used in a laboratory setting to infect cotton seedlings (Cox et al., 2017; Wang et al., 2019). Wheeler et al. (2007) improved the inoculation of plant pathogenic bacteria in field plots by using an organosilicone surfactant, and this protocol was used in inoculated field trials between 2000 and 2022. The bacterial blight ratings (race 18) for commercial cultivars tested during this time span are provided in the next section.

Conditions for a Successful Inoculation and Infection of Xcm. Because greenhouse screenings are conducted in a more controlled environment, experimental errors are minimized. Therefore, greenhouse tests standardize screening of cotton for BB resistance in that the environmental conditions are controlled. Greenhouse tests can screen many lines as early as the cotyledon stage in a small area and can control many factors such as inoculum type, inoculation method, temperature, phenological stage of the plant, and minimization of the interference between the pathogen and other diseases. Because environmental conditions can have a significant impact on development of BB symptoms, the preferable conditions for successful inoculations and infections with Xcm are: 85% humidity, 25 to 40 °C atmospheric temperature, and 27.8 °C soil temperature, which raise the chance for infection by Xcm (Cox et al., 2017; Jalloul et al. 2015; Showmaker et al. 2017).

Sources of Inoculum. A reliable inoculation technique should be relatively low cost, simple, and easy to use on bulky plant populations and provide reliable results to determine sources of heritable plant-host resistance and enable selection within a population genetically variable for resistance. The

symptoms of disease induced by artificial inoculation should be such that relatively small differences in the levels of resistance could be detected. Knight (1946) was the first to prepare the Xcm inoculum by soaking dried, infected leaf trash in water for 2 h, and then use the filtrate for spraying. However, Bourland (2018) stated “a breeding program that relies upon using naturally infected leaves for inoculum cannot be sure of the specific race(s) being used and cannot be assured of an ample supply of inoculum each year”. Moosberg (1953) reported that better results were obtained with pure culture inoculation because the low temperature of the tap water used in preparing inoculum from infected trash might have been detrimental to development of the disease and might have contained fewer viable bacteria per unit volume than that prepared from a pure culture.

Comparison of Different Inoculation Methods. Inoculation with Xcm was carried out by various procedures. Weindling (1948) reported that some researchers inoculated by pouring the inoculum over the leaf surface, dipping leaves into the inoculum, atomizing the inoculum, or brushing the inoculum onto the leaf surface with a paint brush. Eddin et al. (2005) also examined various inoculation techniques including: (1) high-pressure sprayers: spraying on the lower surface of the leaves and using a carborundum as an abrasion to help the bacteria to enter the plants (Dizon and Reyes, 1983; Hunter et al., 1968; Verma and Singh, 1975); (2) pin prick method: a fine entomological sterilized needle was used to make small holes on the upper surface of the leaves and then bacteria were applied by using sterile cotton (Verma and Singh, 1970); (3) swabbing with cotton: sterile cotton buds were wetted with Xcm and then rubbed on the abaxial leaf surface (Verma and Singh 1970); (4) hypodermic syringe: using a syringe to inject the bacteria into the midrib and veins of the lower surface of the leaves (Klement, 1963); (5) camel hair brushing: the bacterial suspension was applied on the upper leaf surface by a fine camel hairbrush (Logan, 1958); (6) sandpaper method: gently scratching the leaves with sandpaper and spreading on the bacterial suspension by a hand sprayer on the superior side of the leaves; (7) pressurized spraying: the bacterial suspension was applied to the posterior side of the leaves by pressurization using a small hand sprayer (Verma and Singh, 1970); and (8) clipping with scissors: cutting the leaves with sterilized scissors after dipping in the bacterial suspension.

Eddin et al. (2005) concluded that sandpaper inoculation methods expressed the highest disease incidence, followed by pressurized spraying and hypodermic syringe methods. In another study by Drishak et al. (2014), they applied Xcm by using (1) a toothpick method: a toothpick was dipped in a bacterial slime and scratched the lower surface of the leaves (Bird, 1982); (2) a spray gun method: using hand sprayer to cause wound on the leaves; and (3) a water splash method. Drishak et al. (2014) reported that the toothpick scratching method was most effective for infecting the plants with the highest disease incidence of BB. Inoculations through seeds is another method where the seed surface was sterilized and punctured and then left in bacterial suspension for 8 to 10 h.

Mahmood and Hussain (1993) compared the following methods: (1) hypodermic inoculation by using a sterile plastic syringe (without a needle) to inject the bacteria on the lower surface of leaves; (2) locally made atomizer: bacteria were atomized on the posterior side of leaves; (3) rubbing the lower surface between finger and dipping in inoculum; and (4) a toothpick scratching method. Mahmood and Hussain (1993) concluded that the scratching and hypodermic methods provided more uniform BB infections.

Current Inoculation Practices of Xcm in the U.S. In the U.S., the cotyledon scratching method in the greenhouse (Bird, 1982; Elassbli et al., 2021a, b, c; Wheeler et al., 2022) and spraying Xcm in the field (Bourland, 2004; Wheeler et al., 2007) have been the most frequently used. Since 1978, Bourland has used the modifications of the procedures developed by Bird (1982) in his cotton breeding programs at Mississippi State University and the University of Arkansas (Bourland, 2004, 2013). Field spraying or scratch inoculation techniques are used to inoculate plants. In Arkansas, field spraying is done with a four-row Mud-Master sprayer (Bowman Manufacturing, Newport, AR) equipped with 110-gal tank with nozzles pointed upward to the abaxial side of leaves. Since the early 1990s, a silicon surfactant has been added to the inoculum (mixture of races including races 1, 2, 7, and 18, but always including race 18) to improve inoculation success. Without the aid of the surfactant, Bird and Blank (1951) sprayed at 125 to 150 psi and Brinkerhoff and Hunter (1963) sprayed at approximately 400 psi when inoculating in the field. If a plant is resistant to race 18, it will be resistant to all races in the U.S. Until recent years,

Bourland used a mixture of races 1, 2, 7, and 18. He stated, “the inclusion of other races insures satisfactory inoculation even when race 18 cultures change and/or become less virulent” (Bourland, 2018).

Wheeler et al. (2007) used a silicon surfactant (Silwet L-77[®], Loveland Industries; Greeley, CO) and low pressure (20-30 psi) for field inoculations. With the aid of the surfactant, Bourland kept application pressure below 50 psi. With improved inoculation efficiency, he has been able to confidently spray-inoculate early generation breeding populations in the field. Scratch inoculation of cotyledons in greenhouse plantings is routinely used to evaluate cultivars and breeding lines. Ground powder of dried infected leaves is placed into distilled water (approximately 2 ml of ground tissue per 50 ml of water). Inoculation is done by dipping a modified drafting pen (or toothpick) into the solution, then scratching the abaxial surface of cotyledons. Depending on temperature of greenhouse, cotyledons can be evaluated for resistance after 2 to 3 weeks.

At New Mexico State University (NMSU), Zhang’s lab used the toothpick scratching method and evaluated more than 1,000 germplasm lines for resistance to race 18 between 2016 and 2020 (Elasbly et al. 2021a, b, c; Zhang et al., 2024). However, since 2022, Zhang et al. (2024) have developed a backpack sprayer method to spray Xcm race 18 inoculum with addition of Silwet L-77 to inoculate more than 2,200 Upland and Pima cotton germplasm lines (each with 15 to 30 plants) at the cotyledon to early seedling stage (1-2 true leaves) with high success and efficiency. Wheeler et al. (2022) tested four cultivars with differing levels of resistance to BB with 17 isolates of Xcm (race 18), using the toothpick scratching method, and found excellent agreement between the toothpick method and field spraying method.

Wheeler et al. (2007) inoculated field nurseries with Xcm (race 18) at 10^6 cfu ml⁻¹, at a rate of 468 L ha⁻¹ using the adjuvant Silwet L-77 at 0.2% v/v. The environment in West Texas is often hot and dry in the summer with low relative humidity. The active ingredient of the surfactant Silwet L-77 is a polyalkyleneoxide modified heptamethyltrisiloxane. This product is thought to aid in moving the bacteria efficiently through the stomates. The efficiency of Silwet L-77 was first demonstrated by using bacterial pathogens to infect and control weeds (Johnson et al., 1996; Zidack et al., 1992). Wheeler has been able to successfully inoculate field plots in temperatures

as high as 40 °C and humidity below 30%. Critical factors for successful inoculation include an aggressive isolate of Xcm, water that has not been treated (chlorine or other treatments can kill bacteria), and a tank and pump that is used only for these applications. It is important to avoid putting other products, for example, pesticides, into the tank used for Xcm inoculations. Successful inoculations and symptom development in field nurseries have been made for the previous 23 years by following this method.

Rating of Cotton Plants for Resistance. Ten to 30 days after inoculation, individual plants can be rated for responses to Xcm infections, depending on technique used and environmental conditions. Based on the density and size of water-soaked lesions, the disease severity caused by Xcm can be rated subjectively on a quantitative scale, as practiced by Knight (Zhang et al., 2020) in Sudan and by breeders in the U.S. before the 1990s when a spraying method was used. However, ratings can be only qualitatively done for plants that are inoculated with a toothpick scratching method (susceptible with water-soaked or leaf chlorotic symptoms or resistant in the absence of any symptoms). In addition, because disease severity is affected by numerous factors, including resistance genes and environmental and developmental factors, disease incidence (DI, %) for plants with water-soaked lesions is the most frequently used rating system. Zhang et al. (2024) recently showed that plants in more than 400 susceptible U.S. Upland cotton accessions all possessed the susceptibility associated DNA marker allele for resistance gene *B₁₂* on chromosome D02, regardless of the disease severity. Wheeler et al. (2022) tested 17 isolates of Xcm on four cultivars, chosen with differing levels of resistance to Xcm. The susceptible (DP 1747NR B2XF), partially susceptible (NG 4936 B3XF), partially resistant (DP 1646 B2XF) and resistant (S295) cultivars ranged from an average disease incidence of 73 to 100, 28 to 69, 4 to 40, and 0% incidence with a toothpick method, respectively, depending on the isolate of Xcm used. The four cultivars could be separated significantly ($p = 0.05$) using each of the 17 isolates, but the percentage of plants with symptoms differed, depending on how aggressive the Xcm isolate was. This does point out that isolate aggressiveness will affect a classification system, so it is important to have check cultivars with a range of known responses, so that the germplasm being tested can be assigned to an appropriate classifica-

tion. It is more appropriate to include susceptible, intermediate, and resistant checks within each trial, than use set percentages.

SOURCES OF RESISTANCE TO BACTERIAL BLIGHT

Resistance to BB varied significantly within the genus *Gossypium*. Many cultivars of the diploid *G. arboreum* and *G. herbaceum*, which have been cultivated for centuries, were highly resistant or immune to the disease (Hillocks, 1992; Hunter et al., 1968; Wallace and El-Zik, 1989). The tetraploid genotypes *G. hirsutum* confer the highest range of disease occurrence, ranging from fully susceptible to highly resistant. At the opposite extreme, little resistance occurred naturally in *G. barbadense* (Jalloul, 2015). Table 2 is a summary of cotton cultivars and lines that were reported to be resistant to various Xcm races.

Between 2016 and 2020, Ellassbli et al. (2021a, b, c) evaluated 335 obsolete U.S. Upland cotton accessions, 57 current commercial transgenic Upland cultivars, 66 elite public breeding lines, and 160 advanced breeding lines from NMSU for resistance to Xcm race 18 using a toothpick scratching method (Bird, 1982). The results showed that 50 (14.9%) obsolete Upland cotton accessions were partially to highly resistant. A total of 22 (33.3%) elite public lines and 11 (6.9%) NMSU lines were partially to highly resistant, 11 of which were developed at the University of Arkansas with an active breeding program for BB resistance. One to four lines each of various other public breeding programs were also resistant to race 18, even though no selection for resistance was made during the breeding process. A total of 26 (45.6%) commercial cultivars were partially to highly resistant, thanks to the high success of marker-assisted selection to develop BB-resistant transgenic cultivars by seed companies. However, obsolete Upland cotton germplasm lines were not systematically screened for resistance to BB until recently. Zhang et al. (2024) further evaluated a total of 1,416 non-transgenic Upland cotton accessions deposited in the National Plant Germplasm System. Results showed that 1,198 accessions (84.6%) were highly susceptible with no resistant plants observed, whereas 75 (5.3%) accessions were highly resistant (immune) and did not show any water-soaked symptomatic susceptible plants. Twenty-five (1.8%), 20 (1.4%), 36 (2.5%), and 62 (4.4%) accessions had

susceptible plants at 5 to 30, 30 to 50, 50 to 80, and 80 to 95%, respectively, suggesting their heterogeneous status in responses to Xcm race 18 due to outcrossing or residual variation under non-Xcm selection pressure.

During a testing program that spanned 23 years between 2000 and 2022, Wheeler inoculated numer-

ous commercial cultivars with Xcm race 18. The results of resistant and susceptible cultivars, including many of the various transgenic ones, were reported in annual Proceedings of Beltwide Cotton Conferences (e.g., Wheeler, 2018) and are summarized in Table 3.

Table 2. Cotton cultivars and lines (other than those listed in Tables 3 and 4) that are resistant to *Xanthomonas citri* pv. *malvacearum*

Cultivar or line	Cotton Species	Resistant to Xcm race	Reference
ACALA 1517-88	<i>G. hirsutum</i>	1, 2, & 10	Roberts et al. (1988)
ACALA 1517-99	<i>G. hirsutum</i>	1, 2, & 10	Cantrell et al. (2000)
ACALA 1517-88	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
Acala 1517-95	<i>G. hirsutum</i>	2 & 10	Cantrell et al. (1995)
ACALA 1517-SR2	<i>G. hirsutum</i>	1, 2, & 10	Malm et al. (1987)
ACALA 1517-SR3	<i>G. hirsutum</i>	1, 2, & 10	Cantrell et al. (1992)
ACALA 3080	<i>G. hirsutum</i>	?	Singh et al. (2007)
ACALA BR-110	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
AJEET 133	<i>G. hirsutum</i>	?	Shastry and Tomar (2006)
ARBB-1301	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARBB1302	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARBC 19	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARBC-1301	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARBC-1302	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARBD 27	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARBH 2040	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
ARBHB-1301	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARBHB-1302	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARBHH 351	<i>G. hirsutum</i>	?	Shastry and Tomar (2006)
ARBHH 51	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
ARBHH-1301	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARBHH-1302	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARCH 3244	<i>G. hirsutum</i>	18	Patole et al. (2016)
ARCH 5640	<i>G. hirsutum</i>	?	Shastry and Tomar (2006)
ARCHH 9191	<i>G. hirsutum</i>	18	Patole et al. (2016)
AUB BR10	<i>G. hirsutum</i>	1, 2, 6, 7, 10, & 18	Shepherd and Kappelman (1987)
AUB BR3	<i>G. hirsutum</i>	1, 2, 6, 7, 10, & 18	Shepherd and Kappelman (1987)
AUB BR4	<i>G. hirsutum</i>	1, 2, 6, 7, 10, & 18	Shepherd and Kappelman (1987)
AUB BR5	<i>G. hirsutum</i>	1, 2, 6, 7, 10, & 18	Shepherd and Kappelman (1987)
AUB BR6	<i>G. hirsutum</i>	1, 2, 6, 7, 10, & 10	Shepherd and Kappelman (1987)
AUB BR7	<i>G. hirsutum</i>	1, 2, 6, 7, 10, & 18	Shepherd and Kappelman (1987)
AUB BR8	<i>G. hirsutum</i>	1, 2, 6, 7, 10, & 18	Shepherd and Kappelman (1987)
AUB BR9	<i>G. hirsutum</i>	1, 2, 6, 7, 10, & 18	Shepherd and Kappelman (1987)
BGDHH 807	<i>G. hirsutum</i>	18	Patole et al. (2016)
BGDHH 821	<i>G. hirsutum</i>	18	Patole et al. (2016)

Table 2. Continued

Cultivar or line	Cotton Species	Resistant to Xcm race	Reference
BHH24	<i>G. hirsutum</i>	18	Patole et al. (2016)
BLLCABS-3-86	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1997)
BPCH-1101	<i>G. hirsutum</i>	18	Patole et al. (2016)
BPHB-1207	<i>G. hirsutum</i>	18	Patole et al. (2016)
BRONCO 625	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
BS 39	<i>G. hirsutum</i>	18	Patole et al. (2016)
BS 79	<i>G. hirsutum</i>		Chattannavar et al. (2010)
BSSCH 489	<i>G. hirsutum</i>	?	Shastry and Tomar (2006)
BSSCH 918	<i>G. hirsutum</i>	?	Shastry and Tomar (2006)
C221-91	<i>G. hirsutum</i>	?	Cook et al. (1997)
C224-91	<i>G. hirsutum</i>	?	Cook et al. (1997)
C300-91	<i>G. hirsutum</i>	?	Cook et al. (1997)
C306-91	<i>G. hirsutum</i>	?	Cook et al. (1997)
CABCHUS-2-86	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1997)
CABD3CABCH-1-89	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1998a)
CAHUGARPIH-1-88	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1998a)
CASCOT 2910	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
CASCOT 5910	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
CASCOT C-13	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
CASCOT L-7	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
CB 1135	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
CB 232	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
CB 407	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
CCB 30	<i>G. hirsutum</i>	18	Patole et al. (2016)
CCCHH07-1	<i>G. hirsutum</i>	?	Vimala (2011)
CCH 03-23	<i>G. hirsutum</i>	?	Vimala (2011)
CD3HCABCUH-1-89	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1998a)
CD3HCAHUGH-2-88	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1998a)
CD3HCHULBH-1-88	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1998a)
CD3HHARCIH-1-88	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1998a)
CDP37HPIH-1-86	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1997)
CENCOT	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
CNDTS 55	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
CNH 3	<i>G. hirsutum</i>	18	Patole et al. (2016)
CNH121	<i>G. hirsutum</i>	18	Patole et al. (2016)
CNHO 12	<i>G. hirsutum</i>	18	Patole et al. (2016)
Coker 320	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
Coker 4360	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
CSH-3178,	<i>G. hirsutum</i>	18	Patole et al. (2016)
CSHG-1729	<i>G. hirsutum</i>	18	Patole et al. (2016)
CSHH-2012	<i>G. hirsutum</i>	18	Patole et al. (2016)
CSHUG2BES-2-87	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1997)
DB 16	<i>G. hirsutum</i>	18	Patole et al. (2016)

Table 2. Continued

Cultivar or line	Cotton Species	Resistant to Xcm race	Reference
DB-1301	<i>G. hirsutum</i>	18	Patole et al. (2016)
DB-1302	<i>G. hirsutum</i>	18	Patole et al. (2016)
DCH 32	<i>G. hirsutum</i>	18	Patole et al. (2016)
DELTAPINE 45	<i>G. hirsutum</i>	?	Vimala (2008)
DES 119	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
DHB-1301	<i>G. hirsutum</i>	18	Patole et al. (2016)
DHB130	<i>G. hirsutum</i>	18	Patole et al. (2016)
DHH 1201	<i>G. hirsutum</i>	18	Patole et al. (2016)
DHH 852	<i>G. hirsutum</i>	?	Bhattiprolu (2011)
DHH-1301	<i>G. hirsutum</i>	18	Patole et al. (2016)
DHH-1302	<i>G. hirsutum</i>	18	Patole et al. (2016)
DP 20	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
DP 50	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
DP 5415	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
DP 5690	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
DP 77	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
DP 77	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
DP 77	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
DP Acala 90	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
DP Acala 90	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
DP Acala 90	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
DP SR-383	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
DP SR-482	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
DSC-1301	<i>G. hirsutum</i>	18	Patole et al. (2016)
DSC-1302	<i>G. hirsutum</i>	18	Patole et al. (2016)
F2617	<i>G. hirsutum</i>	18	Patole et al. (2016)
FHH 231	<i>G. hirsutum</i>	18	Patole et al. (2016)
FHH 234	<i>G. hirsutum</i>	18	Patole et al. (2016)
G. Cot. 100	<i>G. hirsutum</i>	18	Patole et al. (2016)
GISV 103	<i>G. hirsutum</i>	?	Vimala (2011)
GISV 267	<i>G. hirsutum</i>	18	Patole et al. (2016)
GISV272	<i>G. hirsutum</i>	18	Patole et al. (2016)
GJHV 514	<i>G. hirsutum</i>	18	Patole et al. (2016)
GP 3755	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
GP 3774	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
GP1005	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
GP1005A	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
GP74+	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
GSB 21	<i>G. hirsutum</i>	18	Patole et al. (2016)
GSB-44	<i>G. hirsutum</i>	18	Patole et al. (2016)
GSGHH-412	<i>G. hirsutum</i>	18	Patole et al. (2016)
GSH-4	<i>G. hirsutum</i>	18	Patole et al. (2016)
GSHB 989	<i>G. hirsutum</i>	18	Patole et al. (2016)
GSHH 2599	<i>G. hirsutum</i>	18	Patole et al. (2016)

Table 2. Continued

Cultivar or line	Cotton Species	Resistant to Xcm race	Reference
GSHH 2646	<i>G. hirsutum</i>	18	Patole et al. (2016)
GSHV 162,	<i>G. hirsutum</i>	18	Patole et al. (2016)
GTHH 193	<i>G. hirsutum</i>	18	Patole et al. (2016)
GTHH 194	<i>G. hirsutum</i>	18	Patole et al. (2016)
GTHH 208	<i>G. hirsutum</i>	18	Patole et al. (2016)
GTHV 04/13	<i>G. hirsutum</i>	18	Patole et al. (2016)
H 1465	<i>G. hirsutum</i>	18	Patole et al. (2016)
H1330	<i>G. hirsutum</i>	1, 2, 7, & 18	Bourland (1996)
HAG 1015	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
HAGHH 2064	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
HHH 455	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
HHH 494	<i>G. hirsutum</i>	18	Patole et al. (2016)
HOLLAND 1919	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
HOLLAND 4002	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
HOLLAND 4002	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
HOLLAND 4002	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
HOLLAND 850	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
HS 23	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
HURDT'S 700	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
HURDT'S 700	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
HURDT'S 700	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
INDAM 1020	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
JKCH 2516	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
KC311	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
KDCH 42	<i>G. hirsutum</i>	?	Shastry and Tomar (2006)
KDCH 9821	<i>G. hirsutum</i>	?	Shastry and Tomar (2006)
KHH 445	<i>G. hirsutum</i>	?	Shastry and Tomar (2006)
KU 07	<i>G. hirsutum</i>	a mixture of Xcm races	Pkania et al. (2014)
LANKART 142	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
LANKART 511	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
LANKART LX 571	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
LANKART PR-75	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
LBBCABCHUS-1-87	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1997)
LBBCD3H-1-87	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1997)
LBBCDBOAKH-1-90	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1998a)
LBBCHU2GS-I-87	<i>G. hirsutum</i>	?	El-Zik and Thaxton (1997)
LC	<i>G. hirsutum</i>	?	Chattannavar et al. (2010)
LH 2298	<i>G. hirsutum</i>	18	Patole et al. (2016)
LMSH 263	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
Lockett 77	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
MAR-7B	<i>G. hirsutum</i>	multiple races	Thaxton and El Zik (2004a)
MCU 3	<i>G. hirsutum</i>	?	Vimala (2008)
MRC 7091	<i>G. hirsutum</i>	18	Patole et al. (2016)
MRC 7361	<i>G. herbaceum</i>	?	Bhattiprolu (2011)

Table 2. Continued

Cultivar or line	Cotton Species	Resistant to Xcm race	Reference
MRC 7388	<i>G. hirsutum</i>	18	Patole et al. (2016)
NCHH 565	<i>G. hirsutum</i>	?	Shastry and Tomar (2006)
NCMDR 1	<i>G. hirsutum</i>	?	Dhoke et al. (2010)
NCMDR 10	<i>G. hirsutum</i>	?	Dhoke et al. (2010)
NCMDR 11	<i>G. hirsutum</i>	?	Dhoke et al. (2010)
NCMDR 15	<i>G. hirsutum</i>	?	Dhoke et al. (2010)
NCMDR 16	<i>G. hirsutum</i>	?	Dhoke et al. (2010)
NCMDR 18	<i>G. hirsutum</i>	?	Dhoke et al. (2010)
NCMDR 3	<i>G. hirsutum</i>	?	Dhoke et al. (2010)
NCMDR 5	<i>G. hirsutum</i>	?	Dhoke et al. (2010)
NCMDR 6	<i>G. hirsutum</i>	?	Dhoke et al. (2010)
NDL 762	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
NDLH 1905	<i>G. hirsutum</i>		Chattannavar et al. (2010)
NDLH 1938	<i>G. hirsutum</i>		Chattannavar et al. (2010)
NH 633	<i>G. hirsutum</i>	?	
NSCH 111	<i>G. hirsutum</i>	?	Shastry and Tomar (2006)
NSPL 423	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
P 5430	<i>G. hirsutum</i>	18	Patole et al. (2016)
P1752	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
PA 532	<i>G. arboreum</i>	?	Jagtap et al. (2012)
Paig 265	<i>G. hirsutum</i>	?	Jagtap et al. (2012)
PHH 177	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
Phule 492	<i>G. hirsutum</i>	18	Patole et al. (2016)
PM 145	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
PM 147	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
PM 404	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
PM 505	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
PM 893	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
PM HS 26	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
PM HS200	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
PR80	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
RAB 8	<i>G. hirsutum</i>	18	Patole et al. (2016)
RAH 61	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
RAHB 302	<i>G. hirsutum</i>	?	Vimala (2011)
RAHH 138	<i>G. hirsutum</i>	?	Vimala (2011)
RAHH 138	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
RAHH 255	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
RHB-0922	<i>G. hirsutum</i>	18	Patole et al. (2016)
RHB-1005	<i>G. hirsutum</i>	18	Patole et al. (2016)
RHB-1014	<i>G. hirsutum</i>	18	Patole et al. (2016)
RHH – 0917	<i>G. hirsutum</i>	18	Patole et al. (2016)
RHH – 0924	<i>G. hirsutum</i>	18	Patole et al. (2016)
RHH 0707	<i>G. hirsutum</i>	18	Patole et al. (2016)
RHH-1007	<i>G. hirsutum</i>	18	Patole et al. (2016)

Table 2. Continued

Cultivar or line	Cotton Species	Resistant to Xcm race	Reference
RHH-1014	<i>G. hirsutum</i>	18	Patole et al. (2016)
RHH-1015	<i>G. hirsutum</i>	18	Patole et al. (2016)
RS 2527	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
SCHH 23	<i>G. hirsutum</i>	?	Shastri and Tomar (2006)
SCS 1206	<i>G. hirsutum</i>	18	Patole et al. (2016)
SCS 404	<i>G. hirsutum</i>	?	Chattannavar et al. (2010)
SHH 801	<i>G. hirsutum</i>	18	Patole et al. (2016)
SHH 808	<i>G. hirsutum</i>	18	Patole et al. (2016)
SHH 818	<i>G. hirsutum</i>	18	Patole et al. (2016)
ST 324	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
ST 453	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
ST 506	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
Suvin	<i>G. hirsutum</i>	18	Patole et al. (2016)
SVPR 3	<i>G. hirsutum</i>	?	Vimala (2008)
SVPR3	<i>G. hirsutum</i>	?	Vimala (2011)
T 09	<i>G. hirsutum</i>	multiple races	Pkania et al. (2014)
T 11	<i>G. hirsutum</i>	multiple races	Pkania et al. (2014)
T 15A	<i>G. hirsutum</i>	multiple races	Pkania et al. (2014)
T 16B	<i>G. hirsutum</i>	multiple races	Pkania et al. (2014)
T 16C	<i>G. hirsutum</i>	multiple races	Pkania et al. (2014)
T 24A	<i>G. hirsutum</i>	multiple races	Pkania et al. (2014)
T 24B	<i>G. hirsutum</i>	multiple races	Pkania et al. (2014)
T 26	<i>G. hirsutum</i>	multiple races	Pkania et al. (2014)
TAM 88G-104	<i>G. hirsutum</i>	?	Smith (2001)
TAMCOT CAMD-E	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
TAMCOT SP21S	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
TAMCOT SP37H	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)
TAMCOT 22	<i>G. hirsutum</i>	?	Thaxton et al. (2005)
TAMCOT CAB-CS	<i>G. hirsutum</i>	18	Bird et al. (1986)
TAMCOT CAB-CS	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
TAMCOT CAMD-E	<i>G. hirsutum</i>	1, 2, 7, & 14	Bird (1979b)
TAMCOT CD3H	<i>G. hirsutum</i>	18	Bird et al. (1988)
TAMCOT CD3H	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
TAMCOT HQ95	<i>G. hirsutum</i>	1, 2, & 18	El-Zik and Thaxton (1990)
TAMCOT PYRAMID	<i>G. hirsutum</i>	?	Thaxton and El Zik (2004b)
TAMCOT SP21S	<i>G. hirsutum</i>	1, 2, 7, & 14	Bird (1979a)
TAMCOT SP37H	<i>G. hirsutum</i>	1, 2, 7, & 14	Bird (1979c)
TCH 1705	<i>G. hirsutum</i>	18	Patole et al. (2016)
TCH 1716	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
TCHB 13526	<i>G. hirsutum</i>	18	Patole et al. (2016)
TCHH 52	<i>G. hirsutum</i>	?	Shastri and Tomar (2006)
TCHH-2	<i>G. herbaceum</i>	?	Bhattiprolu (2011)
TCHH160161	<i>G. hirsutum</i>	18	Patole et al. (2016)

Table 2. Continued

Cultivar or line	Cotton Species	Resistant to Xcm race	Reference
Tropical 205	<i>G. hirsutum</i>	1, 2, & 18	Bayles and Verhalen (2007)
TSHH23-7	<i>G. hirsutum</i>	?	Vimala (2011)
Westburn M	<i>G. hirsutum</i>	1, 2, 7, & 10	Bayles and Verhalen (2007)

Table 3. Ratings of commercial Upland cotton cultivars (*Gossypium hirsutum*) after inoculation with *Xanthomonas citri* pv. *malvacearum* (race 18) in field trials, Lubbock, Texas, from 2000 to 2022 (by T. Wheeler)

Cotton cultivar ^z	Rating ^y	Cotton cultivar	Rating
AFD 5062LL	R	AR 3885 B2XF	S
AFD 5064 F	S	AR 9371 B3XF	R
AFD 5065 B2F	S	AR 9598 B3XF	R
All-Tex 317 RR	S	AR 9831 B3XF	R
All-Tex Apex B2RF	S	BCG 245	R
All-Tex Arid B2RF	S	BCG 24R	S
All-Tex Atlas	S	BCG 28R	S
All-Tex Atlas Plus	S	BCG 295	R
All-Tex Atlas RR	S	BCG 30R	PS
All-Tex Concho B2XF	R	BSD 224	PR
All-Tex Dinero B2RF	S	BSD 4X	S
All-Tex Edge B2RF	S	BSD 9X	PR
All-Tex Epic RF	S	BSD TAMCOT 73	S
All-Tex Excess	R	BSD Ton Buster Elite	S
All-Tex Excess Plus	S	BSD Ton Buster Magnum	S
All-Tex Magnum RR	S	BW 2038 B2F	S
All-Tex Marathon B2RF	R	BW 3220 B2F	S
All-Tex Max-9	PS	BW 3255 B2RF	R
All-Tex Nitro-44 B2RF	R	BW 3552 B2F	S
All-Tex Orbit RF	S	BW 4021 B2RF	R
All-Tex Patriot RF	S	BW 4630 B2F	S
All-Tex Patriot RR	S	BW 8391 B2RF	R
All-Tex Summitt B2RF	R	BW 9775 B2RF	R
All-Tex Titan B2RF	R	BXN 16	PS
All-Tex Top-Pick	S	CG 3020 B2RF	R
All-Tex Warrior RR	S	CG 3035 RF	S
All-Tex Xpress	PR	CG 3156 B2RF	S
All-Tex Xpress RR	PR	CG 3220 B2RF	S
Americot 1504 B2RF	R	CG 3226 B2XF	S
Americot 1521 B2RF	R	CG 3475 B2XF	MS
Americot 1532 B2RF	PS	CG 3520 B2RF	S
Americot 1550 B2RF	S	CG 3527 B2XF	S
Americot 1622 B2RF	R	CG 3787 B2RF	R
Americot 1664 B2RF	S	CG 3885 B2XF	S
Americot 427R	S	CG 4020 B2RF	S
Americot 8120	S	Concho 287	PS
AR 3475 B2XF	MS	Cotton States 010001G:	R

Table 3. Continued

Cotton cultivar ^z	Rating ^y	Cotton cultivar	Rating
Cotton States 170001G:	R	DP 1553 B2XF	S
Cotton States 370001G:	R	DP 1555 B2RF	S
Cotton States 450001G	S	DP 1558NR B2RF	S
Cotton States 530001G:	S	DP 161 B2RF	S
DG 2100 B2RF	R	DP 1612 B2XF	PS
DG 2215 B2RF	R	DP 1614 B2XF	MS
DG 2242 B2RF	S	DP 1639 B2XF	R
DG 2520 B2RF	S	DP 164 B2RF	S
DG 2615 B2RF	PR	DP 1646 B2XF	PR
DG 3109 B2XF	S	DP 167 RF	S
DG 3385 B2XF	S	DP 1725 B2XF	S
DG 3445 B2XF	R	DP 174 RF	S
DG 3544 B2XF	R	DP 1747NR B2XF	S
DP 0912 B2RF	S	DP 1820 B3XF	R
DP 0920 B2RF	R	DP 1822 XF	R
DP 0924 B2RF	S	DP 1823NR B2XF	S
DP 0935 B2RF	S	DP 1835 B3XF	S
DP 0949 B2RF	S	DP 1840 B3XF	R
DP 1028 B2RF	S	DP 1845 B3XF	R
DP 1032 B2RF	PR	DP 1851 B3XF	R
DP 1034 B2RF	S	DP 1908 B3XF	R
DP 104 B2RF	S	DP 1909 XF	R
DP 1044 B2RF	MS	DP 1948 B3XF	R
DP 1048 B2RF	S	DP 2012 B3XF	R
DP 1050 B2RF	S	DP 2020 B3XF	R
DP 110 RF	S	DP 2022 B3XF	R
DP 1133 B2RF	R	DP 2038 B3XF	R
DP 1137 B2RF	S	DP 2044 B3XF	R
DP 117 B2RF	S	DP 2115 B3XF	MS
DP 121 RF	S	DP 2123 B3XF	PS
DP 1212 B2RF	S	DP 2127 B3XF	S
DP 1219 B2RF	S	DP 2141NR B3XF	S
DP 1252 B2RF	S	DP 2143NR B3XF	S
DP 1311 B2RF	S	DP 2239 B3XF	S
DP 1321 B2RF	S	DP 2379	S
DP 1359 B2RF	PR	DP 393	PR
DP 141 B2RF	S	DP 424 B2R	S
DP 1410 B2RF	R	DP 432 RR	S
DP 1441 RF	S	DP 444 BG/RR	R
DP 1454NR B2RF	S	DP 445 BG/RR	S
DP 1518 B2XF	R	DP 448 B	S
DP 1522 B2XF	S	DP 454 BG/RR	R
DP 1538 B2XF	S	DP 455 BG/RR	S
DP 1538 B2XF	S	DP 455 BG/RR	S

Table 3. Continued

Cotton cultivar ^z	Rating ^y	Cotton cultivar	Rating
DP 515 BG/RR	PS	FM 9063B2F	R
DP 543 BG/RR	R	FM 9068F	R
DP 555 BG/RR	R	FM 9101GT	R
DP 655 BG/RR	S	FM 9160B2F	R
FM 1320GL	PS	FM 9170B2F	R
FM 1621GL	S	FM 9180B2F	R
FM 1730GLTP	R	FM 9250GL	R
FM 1735LLB2	R	FM 955LLB2	R
FM 1740B2F	R	FM 958	R
FM 1773LLB2	S	FM 958LL	R
FM 1830GLT	R	FM 960B2	R
FM 1835LLB2	PR	FM 960B2R	R
FM 1845LLB2	PR	FM 960BR	R
FM 1880B2F	R	FM 960RR	R
FM 1888GL	R	FM 965LLB2	R
FM 1900GLT	PR	FM 966	R
FM 1911GLT	R	FM 966LL	PR
FM 1944GLB2	S	FM 981LL	PR
FM 1953GLTP	R	FM 988LLB2	R
FM 2007GLT	PR	FM 989	R
FM 2011GT	R	FM 989 BR	R
FM 2031 LL	R	FM 989B2R	R
FM 2202 GL	R	FM 989RR	R
FM 2322 GL	S	FM 991B2R	R
FM 2334GLT	R	FM 991BR	R
FM 2398 GLTP	R	FM 991RR	R
FM 2484B2F	R	H&W GeneTex 520R	PS
FM 2498GLT	R	H&W GeneTex 521	PR
FM 2574GLT	R	H&W GeneTex 522	PR
FM 2989GLB2	R	H&W GeneTex-512	PS
FM 5013	S	NG 1511 B2RF	MS
FM 5024	S	NG 1551 RF	S
FM 5035LL	S	NG 1553 R	S
FM 800B2R	R	NG 1556 RF	S
FM 800BR	R	NG 1572 RF	R
FM 800RR	R	NG 2051 B2RF	PR
FM 819	R	NG 2448 R	R
FM 819RR	R	NG 2501 B2RF	PR
FM 8270GLB2	R	NG 2549 B2RF	S
FM 832	R	NG 3195 B3XF	S
FM 832LL	R	NG 3273 B2RF	R
FM 840B2F	R	NG 3306 B2RF	S
FM 9058F	R	NG 3348 B2RF	PR
FM 9060F	R	NG 3405 B2XF	S

Table 3. Continued

Cotton cultivar ^z	Rating ^y	Cotton cultivar	Rating
NG 3406 B2XF	S	PHY 333 WRF	S
NG 3410 RF	R	PHY 339 WRF	R
NG 3500 XF	R	PHY 340 W3FE	R
NG 3517 B2XF	MS	PHY 350 W3FE	R
NG 3522 B2XF	S	PHY 355	S
NG 3538 RF	S	PHY 367 WRF	S
NG 3539 BR	R	PHY 375 WRF	R
NG 3550 RF	S	PHY 390 W3FE	R
NG 3640 XF	R	PHY 394 W3FE	R
NG 3699 B2XF	R	PHY 400 W3FE	R
NG 3729 B2XF	S	PHY 410 R	S
NG 3780 B2XF	S	PHY 411 W3FE	R
NG 3930 B3XF	R	PHY 417 WRF	S
NG 4010 B2RF	R	PHY 425 RF	S
NG 4012 B2RF	R	PHY 427 WRF	S
NG 4098 B3XF	R	PHY 430 W3FE	R
NG 4111 RF	R	PHY 440 W	S
NG 4190 B3XF	S	PHY 440 W3FE	R
NG 4545 B2XF	R	PHY 443 W3FE	R
NG 4601 B2XF	MS	PHY 444 WRF	MS
NG 4689 B2XF	R	PHY 450 W3FE	R
NG 4777 B2XF	R	PHY 470 WR	S
NG 4792 XF	R	PHY 480 W3FE	R
NG 4936 B3XF	MS	PHY 480 WR	S
NG 5007 B2XF	S	PHY 485 WRF	S
NG 5150 B3XF	S	PHY 487 WRF	S
NG 5315 B2RF	S	PHY 490 W3FE	R
NG 5711 B3XF	R	PHY 495 W3RF	S
PHY 125 RF	S	PHY 499 WRF	S
PHY 14512	S	PHY 519 WRF	S
PHY 205 W3FE	R	PHY 545 W3FE	R
PHY 210 W3FE	R	PHY 565 WRF	S
PHY 220 W3FE	PS	PHY 569 WRF	S
PHY 222 WRF	S	PHY 575 WRF	R
PHY 223 WRF	R	PHY 580 W3FE	R
PHY 230 W3FE	R	PHY 745 WRF	S
PHY 243 WRF	PR	PHY 952	S
PHY 250 W3FE	R	PHY GA 894	S
PHY 300 W3FE	R	PHY GA161	S
PHY 308 WRF	S	PHY HS-12	S
PHY 312 WRF	PS	PM 1218 BG/RR	R
PHY 315 RF	S	PM 183	S
PHY 330 W3FE	R	PM 2145 RR	PS
PHY 332 W3FE	R	PM 2167 RR	R

Table 3. Continued

Cotton cultivar ^z	Rating ^y	Cotton cultivar	Rating
PM 2200 RR	PS	ST 474	S
PM 2266 RR	S	ST 4747GLB2	S
PM 2280 BG/RR	PS	ST 4848GLT	S
PM 2326 BG/RR	S	ST 4892BR	PS
PM 2326 RR	S	ST 4946GLB2	S
PM 2344 BG/RR	S	ST 4949GLT	S
PM 2379 RR	S	ST 4990B3XF	S
PM 280	R	ST 4993B3XF	R
PM 330	S	ST 5007B2RF	R
PM HS-26	S	ST 5020GLT	R
SG 215 BR	R	ST 5032GLT	S
SG 501 BG	PS	ST 5115GLT	R
SG 521 RR	PR	ST 5122GLT	S
ST 239	R	ST 5242BR	S
ST 2448 R	R	ST 5288B2F	R
ST 2454 R	PS	ST 5289GLT	R
ST 3539 BR	R	ST 5303R	S
ST 4145LLB2	S	ST 5458B2F	S
ST 4288B2F	S	ST 5471GLTP	R
ST 4357B2RF	S	ST 5517GLTP	R
ST 4427B2F	S	ST 5599 BR	PR
ST 4480B3XF	R	ST 5600B2XF	S
ST 4498B2F	S	ST 5707B2XF	PR
ST 4550GLTP	S	ST 6182GLT	S
ST 4554B2RF	S	ST 6448GLB2	R
ST 4664RF	S	ST 6611B2RF	S
ST 4700B2RF	S	ST 6622RF	S
ST 4550GLTP	S	ST 6182GLT	S
ST 4554B2RF	S	ST 6448GLB2	R
ST 4664RF	S	ST 6611B2RF	S
ST 4700B2RF	S	ST 6622RF	S

^z Names of companies or seed brands include Armor (AR), Associated Farmers Delinting (AFD), Beltwide Cotton Genetics (BCG), Brownfield Seed and Delinting (BSD), Beltwide (BW), Croplan Genetics (CG), DynaGro (DG), Deltapine (DP), FiberMax (FM), NexGen (NG), Phytogen (PHY), Paymaster (PM), SureGrow (SG), and Stoneville (ST). Transgenic traits include original glyphosate tolerance only to the 4-leaf stage (R, RR), glyphosate tolerance all season (RF, F, G), glufosinate tolerance (L, LL), Bollgard with 1 gene (BG, B), Bollgard with 2 genes (B2, T,W), Bollgard with 3 genes (B3, TP, W3), dicamba, glufosinate, and glyphosate tolerance (XF), and 2,4-D choline, glufosinate, and glyphosate tolerance (FE).

^y Blight ratings were susceptible (S), moderately susceptible (MS), partially susceptible (PS), partially resistant (PR), and resistant (R). Because trials were done over a long-time span, in some cases only resistant or susceptible were used. In some years, the susceptible rating was broken into more categories. Generally, susceptible were 50% or more plants with symptoms in the field plots. Statistical analyses and mean separations were used to determine categories. Partially resistant were often 15-45% susceptible, and resistant were often < 10% susceptible.

RESISTANCE BREEDING

Resistance breeding is achieved by crossing a desirable but disease-susceptible plant to another plant that is a source of resistance and generating genetic populations that segregate for the traits of the parents. Therefore, identification of resistant breeding sources is the first step for breeders. Breeding methods include selection, introduction, marker-assisted selection, genetic engineering, and hybridization including backcross, pedigree, and bulk methods. Breeding for cotton resistance to Xcm could be done under natural or artificial infection conditions. Artificial inoculation methods give more reliable information and improve selection efficiency in breeding programs than the natural infection method; however, these methods demand time and require controlled environments (Hillocks, 1992).

Backcrossing Breeding. Backcrossing was the most often used method in breeding cotton for resistance to Xcm in early years. Breeding of cotton plants for Xcm resistance started in Africa after 1939 and in the U.S. and rest of the world in the 1950s (Verma, 1986). *G. hirsutum* and *G. barbadense* were used to produce cultivars with resistance for BB. In Sudan, Knight (for a review, see Zhang et al., 2020) identified and transferred many BB-resistant *B* genes. These genes include *B*₁, *B*₂, and *b*₇ from Upland; *B*₂, *B*₃ and *B*₁₀ from *G. hirsutum* race punctatum; *B*₄ and *B*₆ from *G. arboreum*; *B*₅ from a perennial *G. barbadense*; recessive gene *b*₈ from *G. anomalum* Wawr. & Peyer; and *B*₉ from *G. herbaceum* into the susceptible cultivar ‘Sakel’ (*G. barbadense*) by backcrossing. Many strains of Sakel were generated and were homozygous for genes *B*₁ to *b*₇ (Knight, 1957). ‘Bar XLI’, which is homozygous for *B*₂ gene, was the initial commercial resistant *G. barbadense* cultivar. Large cotton growing regions grew these resistant cultivars (with the *B* genes transferred to Sakel and Upland cultivars) in Sudan in 1962 to 1963 (Knight, 1963). A *B*₆ gene was added to cultivar ‘Barakat’ which replaced the Bar XLI cultivar in the 1970s (Verma, 1986). After Knight’s retirement, the breeding effort for BB resistance in Africa was continued by N. L. Innes until the 1970s (Innes, 1974, 1983; Innes et al., 1974).

Upland cotton cultivar ‘Albar51’, established in Uganda from a Nigeria cotton cultivar ‘Allen’, formed the source for blight-resistant cultivars in Africa (Akello and Hillocks, 2002). Cultivar Sea Is-

land (*G. barbadense*) had polygenic resistance to BB of cotton, but its resistance could not be transferred to Sakel by backcrossing (Brinkerhoff, 1970). In the U.S., an immune line 101-102B also was developed from backcrossing Empire WR containing a polygenic resistance with Bar 4/16 carrying Knight’s *B*₂ *B*₃ resistance genes and then crossing the end product of the backcross with an Upland line, MVW (Bird, 1960, as cited by Brinkerhoff et al., 1984). This line was resistant to all Xcm races that occupied America at that time. Innes et al. (1974) proposed that there was a strong modifier gene complex, *B*_{Sm}, in 101-102B. However, Brinkerhoff et al. (1984) proposed that the BB immune line 101-102B was susceptible to the new isolates, HV1, HV3, and HV7 discovered in Upper Volta and Sudan after being resistance for more than 20 years.

Similarly, Brinkerhoff et al. (1984) developed a BB immune line, Im 216 (Bayles and Johnson, 1985), by backcrossing between genotype containing *B*₂, *B*₃, and *b*₇ genes as the donor parent and a genotype carrying the resistance polygene, *B*_{Sm}, as the recurrent parent in Oklahoma. Bird (1982) summarized several experiments that were used to develop cultivars to be resistant to several diseases in the Multi-Adversity Resistance (MAR) program. He thought that high resistance to the disease can be transferred successfully if segregating populations carry three major or more suitable modifying genes. To find these genes, these populations were screened with a mix of at least four races of Xcm because the known major genes acted quantitatively with the existence of several races of the pathogen (Brinkerhoff et al., 1984). When HV1, HV3, and HV7 isolates (an African Xcm) were existent, the MAR cultivars were used to reselect resistance to these new isolates. As a result, the developed MAR lines were resistant to all Xcm races and isolates but the HV1 isolate (Bush, 1983).

In 1984, S295 (*G. hirsutum*), a progeny of the cross Pan 575 × (J193 × SR1 F4), was identified as a resistant cultivar to the new Xcm isolate HV1 in Africa (Girardot et al., 1986). Wallace and El-Zik (1989) investigated the inheritance of the resistance to the Xcm race 18 and isolate HV1 in S295 and showed the resistance to race 18 and HV1 was conferred by the same dominant gene, designated *B*₁₂, or two tightly linked resistance genes in S295. However, no follow-up work appears to have been conducted because the virulent African Xcm strain

was not detected in the U.S. Therefore, it is unknown if S295 was used as a parent to develop resistant cultivars and breeding lines in the U.S. and elsewhere.

Forward Breeding. Since the 1980s, cross or forward breeding has been the method of choice in breeding for cotton with resistance to Xcm, unless resistance genes were transferred through backcrossing from another species such as *G. barbadense* to Upland cotton. Examples to illustrate the success in the U.S. are listed below.

Texas A&M University's MAR Program: L.S. Bird started his genetic studies and breeding for BB resistance in the 1950s, which was then extended to include breeding for resistance to two other seedling pathogens including *Rhizoctonia solani* and *Pythium ultimum* and slow rate of radicle elongation during cold germination. This formed the foundation of the MAR system (Bird, 1982, 1986). The earliest BB-resistant cultivars were 'Tamcot SP 21', 'Tamcot SP 23', and 'Tamcot SP 37' released by Bird (1976), which were later found to be resistant to Xcm race 18 (Elassbli et al., 2021a; Zhang et al., 2024). These cultivars were derived from a composite cross involving eight parental lines and possessed $B_2B_3b_7$ resistance genes. The B_2B_3 genes were transferred to an Empire WR strain (*G. hirsutum*) from Knight's *G. barbadense* Sakel strain 4/16 through four generations of backcrossing, whereas b_7 was from 'Blightmaster' and was identified originally in 'Stoneville 20' (Zhang et al., 2020). However, resistance genes B_2 and B_3 were identified originally in African Upland cotton (also some U.S. Upland cotton) and a race stock of *G. hirsutum* var. *punctatum*, respectively, and were transferred into *G. barbadense* Sakel by Knight in Sudan (Zhang et al., 2020). It appears that these early BB-resistant cultivars carried the $B_2B_3b_7$ combination (which were originally from Upland cotton) and became some of the founder parents for the MAR germplasm pools from MAR-1 to MAR-8, which led to the release of more than 10 Tamcot cultivars including 'Tamcot Sphinx' (El-Zik and Thaxton, 1996) and 'Tamcot Pyramid' (Thaxton and El-Zik, 2004b) and more than 360 elite MAR breeding lines (El-Zik and Thaxton, 1998b). Many of those lines were found to be resistant to Xcm race 18 (Elassbli et al., 2021a; Zhang et al., 2024). After Bird's retirement, the MAR program was continued by K. M. El-Zik and then P. Thaxton until it was terminated in the early 2000s.

The University of Arkansas: Fred Bourland (2004, 2013, 2018) has used the basic procedures

developed and summarized by Bird (1982) in his cotton breeding programs at Mississippi State University and the University of Arkansas. Over the past 45 years, he has developed and released 109 cotton germplasm lines and eight cultivars, 97 of the germplasm lines and all eight cultivars were selected for resistance to Xcm. During the early years of his work, he primarily crossed Xcm-resistant lines from Bird's program to lines that were better adapted to the Mississippi Delta region. As his program progressed, he began using Xcm-resistant lines developed in his program as parents and has introduced lines (mostly Xcm susceptible) from other public breeders to increase genetic diversity. Consequently, most of his crosses have included at least one Xcm-resistant parent. Bourland annually inoculates all plants in his F_2 through F_4 populations and discards plants showing susceptible reactions. Individual plants are selected from the F_4 populations. Seed from the individual plants are evaluated as progeny in the F_5 and F_6 generations, where they are again screened for response to BB. Progeny rows having susceptible plants are normally discarded. Selected progenies are promoted to strains and evaluated in replicated strain tests for up to five years. All seed increase of Xcm-resistant strains are inoculated, and any susceptible plants are removed. Thus, most lines released from this program are highly resistant to this disease (Table 4).

New Mexico State University: Breeding for BB resistance was established in the 1950s and continued until the early 2000s (Zhang, 2018). As a result, at least 8 BB-resistant cultivars, including 'Acala 1517BR' (BR was used to indicate BB resistance by the breeder), 'Acala 1517BR-1', 'Acala 1517BR-2', 'Acala 1517-70', 'Acala 1517-77BR', 'Acala 1517-88', 'Acala 1517-95', and 'Acala 1517-99', were developed. Acala 1517BR received its BB resistance from the resistant donor parent Stoneville 20 possessing resistance gene b_7 (Zhang et al. 2020), and its cross with 'Acala 1517C' resulted in Acala 1517BR-1. Both were resistant to race 1 but susceptible to race 2. Acala 1517BR-2 was resistant to both races with its resistance to race 2 derived from Upland NM8738, an introgression line from Arizona Long Staple 120 (*G. barbadense*). Acala 1517-70 was resistant to races 1, 2, and 10 with resistance from the Acala 9136 parent being derived from *G. barbadense* cv. Tanguis. Acala 1517-77BR was a selection from 'Acala 1517-77', which was also derived from a single plant selection in Acala 1517-70. Its cross with 'Deltapine 70' yielded Acala

1517-88 also with resistance to races 1, 2, and 10. Acala 1517-95 was resistant to races 2 and 10, and Acala 1517-99 was resistant to races 1, 2, and 10, with resistance also derived from Acala 9136. However, because BB was not a serious cotton production issue in New Mexico after the 1990s, breeding for BB resistance was discontinued until 2015, when BB again became a problem.

Direct selection for race 18 resistance during a breeding process is highly successful. However, because of the nature of resistance to race 18 by the major resistance gene B_{12} , selection during a breeding process might not be necessary if one of the parents used in creating breeding populations is resistant. For example, Ellassbli et al. (2021a) evaluated 66 elite public breeding lines and 160 advanced breeding lines from NMSU for resistance to Xcm race 18 and showed that 22 (33.3%) elite public lines and 11 (6.9%) NMSU lines were partially to highly resistant. One to four lines from each of the other public breeding programs were also resistant to race 18, even though no selection for resistance was made during the breeding process. Because

sources of resistance for race 18 are readily available and often used as parents for breeding in New Mexico and many other breeding programs, some cultivars and elite breeding lines developed through the traditional pedigree selection might be resistant to race 18 or might carry resistance gene(s) for race 18 even if not homogeneous (Ellassbli et al., 2021a).

Marker-Assisted Selection (MAS). Since the 2000s, MAS has been used by several seed companies to select and develop commercial transgenic Upland cotton cultivars for resistance to race 18, based on several closely linked SSR and SNP markers to B_{12} (Xiao et al. 2010; Zhang et al. 2020). Zhang et al. (2020) listed the primer sequences for these markers. It appears that MAS for breeding commercial transgenic Upland cotton cultivars for resistance to race 18 has been highly successful (Table 3). With assistance from public breeders and/or plant pathologists, several private companies have for many years periodically screened their germplasm for BB resistance. Now, these private companies are using MAS to identify and select cotton for BB resistance.

Table 4. Bacterial blight resistant Upland cotton cultivars and germplasm lines (*Gossypium hirsutum*) released by Fred Bourland

Cultivar or line	Resistant to Xcm race	Reference	GP	PI
Cultivars				
‘H1330’	1, 2, 7, & 18	Bourland (1996)	CV-108	583875
‘UA48’	1, 2, 7, & 18	Bourland and Jones (2012a)	CV-129	660508
‘UA222’	1, 2, 7, & 18	Bourland and Jones (2012b)	CV-130	664929
‘UA103’	1, 2, 7, & 18	Bourland and Jones (2013)	CV-131	664928
‘UA107’	1, 2, 7, & 18	Bourland and Jones (2018a)	CV-136	685638
‘UA114’	1, 2, 7, & 18	Bourland and Jones (2018b)	CV-137	685639
‘UA212ne’	1, 2, 7, & 18	Bourland and Jones (2020)	CV-143	692970
‘UA248’	1, 2, 7, & 18	Bourland and Jones (2021a)	CV-145	693756
Lines				
Miscot 7813	1, 2, 7, & 18	Bourland (1987)	GP-303	607312
Miscot 7841	1, 2, 7, & 18	Bourland (1987)	GP-304	607313
Miscot 7913-51	1, 2, 7, & 18	Bourland (1988)	GP-316	511348
Miscot 7913-83	1, 2, 7, & 18	Bourland (1988)	GP-317	511349
Miscot 7913-84	1, 2, 7, & 18	Bourland (1988)	GP-318	511350
Miscot T8-27	1, 2, 7, & 18	Bourland and Bridge (1988)	GP-353	518655
Miscot 7918	1, 2, 7, & 18	Bourland and White (1989a)	GP-362	520750
Miscot 7803-51	1, 2, 7, & 18	Bourland and White (1989b)	GP-363	520751
Miscot 7803-52	1, 2, 7, & 18	Bourland and White (1989b)	GP-364	520752
Miscot 7853	1, 2, 7, & 18	Bourland et al. (1990)	GP-421	536525
Miscot 7824	1, 2, 7, & 18	Bourland and White (1992)	GP-507	556979

Table 4. Continued

Cultivar or line	Resistant to Xcm race	Reference	GP	PI
Arkot 8110	1, 2, 7, & 18	Bourland et al. (1997a)	GP-663	595850
Arkot 8303	1, 2, 7, & 18	Bourland et al. (1997b)	GP-664	595851
Arkot 8102	1, 2, 7, & 18	Bourland et al. (1997c)	GP-665	595852
Arkot 8506	1, 2, 7, & 18	Bourland et al. (1997c)	GP-666	595853
Arkot 8514	1, 2, 7, & 18	Bourland et al. (1997c)	GP-667	595854
Arkot 8606	1, 2, 7, & 18	Bourland and Benson (2002a)	GP-740	628634
Arkot 8710	1, 2, 7, & 18	Bourland and Benson (2002b)	GP-741	628635
Arkot 8717	1, 2, 7, & 18	Bourland and Benson (2002b)	GP-742	628636
Arkot 8727	1, 2, 7, & 18	Bourland and Benson (2002c)	GP-743	628637
Arkot 8918	1, 2, 7, & 18	Bourland and Benson (2002d)	GP-744	628638
Arkot 9103	1, 2, 7, & 18	Bourland and Benson (2002d)	GP-745	628639
Arkot 8712	1, 2, 7, & 18	Bourland et al. (2005)	GP-791	636101
Arkot 9111	1, 2, 7, & 18	Bourland and Jones (2005a)	GP-798	638506
Arkot 9101	1, 2, 7, & 18	Bourland and Jones (2005b)	GP-799	638507
Arkot 9108	1, 2, 7, & 18	Bourland and Jones (2005b)	GP-800	638508
Arkot 9203-03	1, 2, 7, & 18	Bourland and Jones (2006a)	GP-853	641157
Arkot 9203-17	1, 2, 7, & 18	Bourland and Jones (2006a)	GP-854	641158
Arkot 9202	1, 2, 7, & 18	Bourland and Jones (2006b)	GP-858	641159
Arkot 9208	1, 2, 7, & 18	Bourland and Jones (2006b)	GP-859	641160
Arkot 9406ne	1, 2, 7, & 18	Bourland and Jones (2006c)	GP-863	641704
Arkot 9605ne	1, 2, 7, & 18	Bourland and Jones (2006c)	GP-864	641705
Arkot 9631ne	1, 2, 7, & 18	Bourland and Jones (2006c)	GP-865	641706
Arkot 9315	1, 2, 7, & 18	Bourland and Jones (2006d)	GP-866	641707
Arkot 9409	1, 2, 7, & 18	Bourland and Jones (2006d)	GP-867	641708
Arkot 9304a	1, 2, 7, & 18	Bourland and Jones (2007b)	GP-870	643438
Arkot 9304b	1, 2, 7, & 18	Bourland and Jones (2007b)	GP-871	643439
Arkot 9308	1, 2, 7, & 18	Bourland and Jones (2007b)	GP-872	643440
Arkot 9314	1, 2, 7, & 18	Bourland and Jones (2007b)	GP-873	643441
Arkot 9506	1, 2, 7, & 18	Bourland and Jones (2007a)	GP-874	643442
Arkot 9513	1, 2, 7, & 18	Bourland and Jones (2007a)	GP-875	643443
Arkot RM24	1, 2, 7, & 18	Bourland and Jones (2007c)	GP-881	643444
Arkot 9608ne	1, 2, 7, & 18	Bourland and Jones (2008a)	GP-888	651854
Arkot 9610	1, 2, 7, & 18	Bourland and Jones (2008b)	GP-891	651856
Arkot 9620	1, 2, 7, & 18	Bourland and Jones (2008b)	GP-892	651857
Arkot 9623	1, 2, 7, & 18	Bourland and Jones (2009a)	GP-908	651858
Arkot 9625	1, 2, 7, & 18	Bourland and Jones (2009a)	GP-909	651859
Arkot 9704	1, 2, 7, & 18	Bourland and Jones (2009b)	GP-914	654509
Arkot 9706	1, 2, 7, & 18	Bourland and Jones (2009b)	GP-915	654510
Arkot 9721	1, 2, 7, & 18	Bourland and Jones (2009c)	GP-918	654511
Arkot 9811	1, 2, 7, & 18	Bourland and Jones (2010)	GP-919	658215
Arkot 9815	1, 2, 7, & 18	Bourland and Jones (2010)	GP-920	658216
Arkot 0008	1, 2, 7, & 18	Bourland and Jones (2011a)	GP-932	660502
Arkot 0009	1, 2, 7, & 18	Bourland and Jones (2011a)	GP-933	660503

Table 4. Continued

Cultivar or line	Resistant to Xcm race	Reference	GP	PI
Arkot 0012	1, 2, 7, & 18	Bourland and Jones (2011a)	GP-934	660504
Arkot 0015a	1, 2, 7, & 18	Bourland and Jones (2011b)	GP-935	660505
Arkot 0015b	1, 2, 7, & 18	Bourland and Jones (2011b)	GP-936	660506
Arkot 0016	1, 2, 7, & 18	Bourland and Jones (2011b)	GP-937	660507
Arkot 0111	1, 2, 7, & 18	Bourland and Jones (2014a)	GP-974	664925
Arkot 0113	1, 2, 7, & 18	Bourland and Jones (2014a)	GP-975	664926
Arkot 0114	1, 2, 7, & 18	Bourland and Jones (2014a)	GP-976	664927
Arkot 0219	1, 2, 7, & 18	Bourland and Jones (2014b)	GP-972	668533
Arkot 0222	1, 2, 7, & 18	Bourland and Jones (2014b)	GP-973	668534
Arkot 0305	1, 2, 7, & 18	Bourland and Jones (2015a)	GP-983	669971
Arkot 0306	1, 2, 7, & 18	Bourland and Jones (2015a)	GP-984	671966
Arkot 0309	1, 2, 7, & 18	Bourland and Jones (2015a)	GP-981	669969
Arkot 0316	1, 2, 7, & 18	Bourland and Jones (2015a)	GP-982	669970
Arkot 0403ne	1, 2, 7, & 18	Bourland and Jones (2015b)	GP-996	674469
Arkot 0409	1, 2, 7, & 18	Bourland and Jones (2015b)	GP-997	674470
Arkot 0410HG	1, 2, 7, & 18	Bourland and Jones (2015b)	GP-998	674471
Arkot 0502ne	1, 2, 7, & 18	Bourland and Jones (2017)	GP-1007	677330
Arkot 0504ne	1, 2, 7, & 18	Bourland and Jones (2017)	GP-1008	677331
Arkot 0506ne	1, 2, 7, & 18	Bourland and Jones (2017)	GP-1009	677332
Arkot 0517HG	1, 2, 7, & 18	Bourland and Jones (2017)	GP-1010	677333
Arkot 0705	1, 2, 7, & 18	Bourland and Jones (2018c)	GP-1033	685636
Arkot 0711	1, 2, 7, & 18	Bourland and Jones (2018c)	GP-1034	685637
Arkot 0611	1, 2, 7, & 18	Bourland et al. (2019)	GP-1035	687864
Arkot 0617	1, 2, 7, & 18	Bourland et al. (2019)	GP-1037	687866
Arkot 0712	1, 2, 7, & 18	Bourland et al. (2019)	GP-1036	687865
Arkot 0822	1, 2, 7, & 18	Bourland and Jones (2021b)	GP-1088	697030
Arkot 0908-52	1, 2, 7, & 18	Bourland et al. (2021)	GP-1091	697035
Arkot 0908-56	1, 2, 7, & 18	Bourland et al. (2021)	GP-1090	697034
Arkot 0908-60	1, 2, 7, & 18	Bourland et al. (2021)	GP-1089	697033
Arkot 0912-18	1, 2, 7, & 18	Bourland and Jones (2022)	GP-1098	697032
Arkot 0912-41	1, 2, 7, & 18	Bourland and Jones (2022)	GP-1097	697031
Arkot 0902	1, 2, 7, & 18	Bourland et al. (2023)	GP-1130	700940
Arkot 1005	1, 2, 7, & 18	Bourland and Jones (2023a)	GP-1127	700852
Arkot 1015	1, 2, 7, & 18	Bourland and Jones (2023)	GP-1128	700853
Arkot 1019	1, 2, 7, & 18	Bourland and Jones (2023a)	GP-1129	700854
Arkot 1112	1, 2, 7, & 18	Bourland and Jones (2023b)	GP-1139	702559
Arkot 1114	1, 2, 7, & 18	Bourland and Jones (2023b)	GP-1140	702560
Arkot 1115	1, 2, 7, & 18	Bourland and Jones (2023b)	GP-1141	702561
Arkot 1102ne	1, 2, 7, & 18	Bourland and Jones (2024)	GP-1142	702558
Arkot 1202	1, 2, 7, & 18	Bourland et al. (2024)	GP-1143	702793
Arkot 1207	1, 2, 7, & 18	Bourland et al. (2024)	GP-1144	702794
Arkot 1208	1, 2, 7, & 18	Bourland et al. (2024)	GP-1145	702795
Arkot 1214	1, 2, 7, & 18	Bourland et al. (2024)	GP-1146	702796

PERSPECTIVE

Since the 1970s, BB in cotton has been under effective control using resistant cotton cultivars and acid-delinted planting cottonseed. However, resurgence of BB has periodically occurred in the U.S. when breeding for resistance was ignored and scouting of cotton production fields is relaxed. The development of BB in major seed production areas and subsequent infection in planting seed can result in a resurgence of BB across large cotton growing regions, as was seen in the U.S. from 2011 to 2017. Once introduced in regions, BB was perpetuated until sufficient acreage of resistant cultivars was grown.

Breeding for BB resistance in the U.S. has been highly successful because of the extensive efforts from several public cotton breeding programs (based on field and greenhouse selections) and major seed companies more recently in using both field screening and marker-assisted selection to introduce BB resistance into insect-resistant and herbicide-tolerant Upland cotton cultivars. As a result, the number of resistant commercial Upland cotton cultivars has increased in recent years. It appears that resistance is conferred by the resistance gene B_{12} with no obvious deleterious effects in most, if not all, of the current breeding lines and cultivars. The single resistant genetic source has been a cause for concern, although the available resistance to race 18 has not yet broken down, which seems to confirm that “immunity” is available to Xcm. If a more virulent strain does not evolve, BB will likely become a non-issue unless screening and breeding for resistance is again relaxed.

There are more than 20 major resistance genes including B_1 to B_{12} identified through segregation analyses and allelic tests (Zhang et al., 2020). However, many of the resistant germplasm lines carrying those genes are currently inaccessible or lost. It is also unclear what race(s) were present when most of these resistance genes were identified in Sudan. In addition, the early inoculation and evaluation methods in resistance genetic studies need to be revisited based on current knowledge and techniques in screening. Although a molecular mapping study on a few B genes including B_2 , B_3 , and B_{12} was reported by Wright et al. (1998), the exact genetic relationships among those and other B genes and their chromosomal locations except for the fine-mapped B_{12} are currently unknown. Zhang et al. (2024) identified new sources of resistance (possible

new alleles or new genes but tightly linked to B_{12}) to race 18 in Long Star and early Acala, Coker, and Deltapine germplasm lines, although all possessed a B_{12} -linked marker. Gowda et al. (2022) recently suggested a different resistance QTL (BB-13) in close proximity to B_{12} on chromosome D02 (Xiao et al., 2010; Yang, 2013), through a genome-wide association study (GWAS) of 380 Upland cotton accessions and linkage mapping using 104 recombinant inbred lines (RILs) from a cross of resistant Arkot 8102/susceptible ‘Maxxa’. These studies suggest that the B_{12} locus and its neighboring region on D02 likely carry more than one resistance gene against Xcm race 18 and other isolates (such as HV1, Wallace and El-Zik, 1989), but further studies are needed to delineate this region.

There are 22 pathogenic Xcm races reported in cotton production worldwide using a set of host differentials. Based on the gene-for-gene theory, there is an avirulence gene (*avr*) in a pathogen for a resistance R gene in the host. Relationships between several pairs of resistance B genes and *avr* genes have been established (De Feyter and Gabriel, 1991; De Feyter et al., 1993; Delannoy et al., 2005; Essenberg et al., 2002, 2014). However, *avr* genes for most Xcm races including race 18 have not been identified. Although race 18 is the dominant and most virulent race in the U.S., a more virulent race was reported in Africa in the late 1980s. Evolution or introduction of a new and more virulent race than race 18 could break down the resistance provided by B_{12} . However, at present, some of the lines in the established set of host differentials are apparently lost or unavailable, rendering it difficult to ascertain what specific races will be present across the U.S. Cotton Belt. Surveys in the 1990s and 2000s indicated that race 18 is the only one present in production fields.

A related concern is the availability (purity and virulence) of races, which cannot be confirmed without race differentials. Bourland (2018) stated: “the question then arises of whether new races will evolve over time. The ‘immunity’ described by Bird (1982) and Brinkerhoff et al. (1984) appears to be standing. Access to cultures of multiple, virulent races is essential for establishing BB resistance”. In cotton, there are cases where one B gene confers resistance to multiple Xcm races (i.e., one R gene-several *avr* genes), and one race can infect plants with multiple B genes (i.e., one *avr* gene-several B genes). In the past, a mixture of multiple races was often used to inoculate cotton for resistance to

multiple races. However, it is currently known that a plant resistant to race 18 is also resistant to all other races in the U.S. Inoculation of an aggressive race 18 isolate is more common in evaluation of cotton for resistance, because the fitness or selection pressures over the last 40 years have shown that other known races are not detected in cotton production fields, as shown by a number of surveys conducted by Peggy Thaxton (Thaxton et al., 1992, 2001), using the race differentials. Another advantage of using this singular race strategy is that there is no need for the old set of host differentials and to separately maintain and culture different races, unless a new, more virulent race arises. However, to prevent such a scenario from occurring, there is a need to identify new genetic sources of resistance to be deployed as an alternative to or in combination with the *B₁₂* gene. Because the virulence determinants *avr* genes in *Xcm* belong to the *avrBs3/pthA* gene family and encode type III effectors, sequencing of the type III effectors-coding genes in *Xcm* populations from producer fields can also provide an alternative of closely monitoring possible changes of pathogenicity and aggressiveness of the pathogen across cotton production regions over time (Phillips et al., 2017; Wheeler et al., 2022).

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