EVALUATION METHODS, GERMPLASM EVALUATION, GENETICS, AND BREEDING FOR RESISTANCE TO FUSARIUM WILT RACE 4 IN COTTON: PERSONAL KNOWLEDGE AND EXPERIENCES

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Abstract

This presentation reviewed and presented the progress in research on *Fusarium oxysporum* f. sp. *vasinfectum* (FOV) race 4 (FOV4). In our collective efforts between New Mexico and Texas public researchers with support from Cotton Inc., we have screened 5,000 cotton germplasm lines for FOV4 resistance; studied the quantitative genetic basis of FOV4 resistance in a set of Pima cotton genotypes; mapped quantitative trait loci (QTLs) for FOV4 resistance; compared infection processes in the cotton root between susceptible and resistant Pima lines; estimated experimental errors in the field based on a Latin square design; and investigated the effects of cotton cultivar and growth stage, root wounding, planting date, inoculum density and temperature on the FOV4-associated disease development. We showed that high FOV4 inoculum density and uniform FOV4 spore distribution is the key to reliably screen cotton for FOV4 resistance, whether in the field, greenhouse or a hydroponic system. Using root vascular staining alone late in a season would inflate disease resistance level; and plant mortality early in the season is an important criterion to evaluate cotton for FOV4 resistance and should be combined with root staining. Fusarium wilt race 7-resistant Chinese Upland cotton served as an important source of resistance to FOV4. It was used as parental lines in cross breeding and developed three FOV4-resistant cultivars in the New Mexico Cotton Breeding Program.

Introduction

Fusarium wilt caused by *Fusarium oxysporum* f. sp. *vasinfectum* (FOV) race 4 (FOV4) has become an important threat to cotton production in the west and southwest Cotton Belt with a possible expansion to other regions in the US. This presentation represented the collective wisdom from a cooperative project with Texas A&M and Cotton Inc. since 2018. It was focused on evaluation methods, discussing where, when, what and how to evaluate cotton for FOV4 resistance. I then touched on germplasm screening, the genetic basis and breeding for FOV4 resistance.

Experiences in breeding and genetic studies on Fusarium wilt race 7

Previously, I had 15 years of research experience working on race 7 (FOV7) in China between 1985 and 2001. In a FOV7 heavily infested field, we estimated the heritability for FOV7 resistance at higher than 90% in both F_1 and F_2 generations from an 8-parent diallel analysis (Zhang et al., 1994, 1995, 1996; Feng et al., 1996b, c). Once again, under the same FOV7 heavily infested field conditions supplemented with artificial inoculations, we identified two major resistance genes, *Fw₁* and *Fw₂* (Feng et al., 1998), using segregating populations. Furthermore, through a detailed pedigree analysis (Feng et al., 1996a), we showed that more than 100 FOV7 resistant Upland lines and cultivars came from two sources of resistance. Surprisingly, these two sources all came directly from the US Upland cotton. The first source, Chuan 52-128, came from a direct selection in the susceptible Delfos 531, a very old cultivar grown in the US in the 1930s. The second source, Chuan 57-681, came from a selection in the susceptible

Deltapine 15, a very popular cultivar in the US developed in 1947. The two major resistance genes had no deleterious effect on lint yield and fiber quality (Feng et al., 2001).

Characterization of FOV4 in New Mexico and its differences from other states

The breeding work on FOV7 was so successful in China that the disease has been under effective control with the use of resistant Upland cultivars since the mid-1990s. However, almost all publications on FOV7 research were in Chinese. Considering the threats from FOV4 in the US and a new FOV strain in Australia and the close relationship between FOV4 and FOV7, I decided to thoroughly review relevant literature in Chinese and English. In working with my cooperators, we put out two review papers in 2015 and 2016 (Zhang et al., 2015; Sanogo and Zhang, 2016). Then, FOV4 hit home right away. Bob Nichols was instrumental in pushing FOV4 research in New Mexico State University (NMSU). He came to Las Cruces after the Cotton Breeders tour in Arizona in Sept. 2017, and he and I met in my office to talk about it, although there was no official report on identification of FOV4 in New Mexico at that time. In the spring the following year, I was invited to join force with Texas A&M to conduct annual field studies on FOV4 in Fabens, Texas, and we have had a very happy ride since then. In July 2019, Bob came to the New Mexico Cotton Ginners Association annual meeting, where we had a working lunch and talked about FOV4 again. Bob also had direct interactions with others at NMSU including the extension agronomist and plant pathologists. My research has been supported by Tom Wedegaertner and Kater Hake and funded by Cotton Inc.

After limited field surveys in 2017 and 2018 which led to the first report of the detection of FOV4 in New Mexico (Zhu et al., 2020), we conducted a state-wide field survey on more than 500 fields in southern New Mexico in 2019, with a supplementary field survey in 2020. We have identified more than 10 cotton fields with FOV4 (Zhu et al., 2021a), although other *Fusarium* spp. were identified (Zhu et al., 2019a, b; 2021c). We showed that 62% of the FOV4 isolates we collected belonged to the N genotype without a transposon insertion in the *PHO* gene and 38% of them were the T genotype with a large insertion (Zhu et al., 2021a). They were different from the FOV4 isolates we collected from the Fabens area, Texas, which were all MT genotype with a small insertion (Zhu et al., 2021b). The proposition of different FOV4 isolates in New Mexico was different from that in Texas with no N genotype but with MT and T genotypes, from California with a very low percentage of N genotype, and from China with predominantly N genotype but no T genotype in FOV7 (Table 1). We also showed that the ranges of virulence on cotton overlap between the N and T genotype. But on average, the T genotype is more aggressive (Zhu et al., 2021a).

Table 1. FOV4 genotypes and frequencies in different areas

FOV4 genotype	NM	TX*	CA*	China*
N	62	0	6	89
T	38	45	88	0
MT	0	55	0	11
MiT	0	0	6	0

* Based on Bell et al. (2019).

Differences between FOV4 and FOV7

There are eight reported FOV races on cotton worldwide. Most of the races including races 1, 2, 3, 4, and 8 have been reported in the US; race 1, 3, and 5 identified in Africa; race 4 originally reported in India; race 6 in South America including Brazil; and races 7 and 8 in China. Race 1, 2, and 6 belong to the same group. However, race 5 was later found to be the same as race 3, so its race designation is dropped out. Many showed that races 4 and 7 were the same based on limited DNA markers and sequences and belonged to the same race. However, I beg to differ, because there are some distinguished differences between the two races. First, FOV7 was first identified in China, because its responses to the same host differentials including cotton lines and non-cotton species are different from FOV4. Here, I further provide the following three more lines of evidence: (1) the optimal temperatures for both races are different: 23ºC for FOV4 vs. 28ºC for FOV7; (2) FOV4 is an early season pathogen, while FOV7 is a mid-season pathogen; and (3) FOV4 causes high seedling mortality, while FOV7 does not (Table 2). Whole genome sequencing and molecular pathology studies will shed more light on the differences between the two races.

Table 2. Comparison between FOV4 and FOV7.

	FOV4	FOV7
DNA markers	same	same
DNA sequences	same	same
Pathogenicity	different	different
Optimal temperature	$23^{o}C$	$28^{o}C$
Wilt occurrence	early season (seedling)	mid-season (bloom)
Wilt symptoms	high frequency of mortality	low frequency of mortality

Symptoms associated with FOV4 infections and effect of temperature on FOV4

Fusarium wilt caused by FOV4 is an early season disease. Based on our observations in Fabens, Texas since 2018, the first FOV4 disease symptom under the field conditions is mortality, i.e., seedling death right after emergence (Figure 1). Mortality continues at the seedling stage and the square stage (Zhang et al., 2020b). We also see a low percentage of leaf necrosis, chlorosis, defoliation, and dwarf plants at and after this stage. After the square stage, mortality is rare. Fusarium wilt is a vascular disease, so the most reliable diagnostic symptom is root and stem vascular discoloration, also called staining (Zhang et al., 2020b).

Figure 1. Disease symptoms caused by FOV4 at the cotyledon stage (Zhang et al., 2020b).

Plant mortality peaked at around 6 weeks after planting, i.e., the square stage (Zhang et al., 2020b). The two susceptible Pima cultivars Pima S-7 and DP 744 reached more than 80% mortality at this time. On the other hand, the two resistant Pima cultivars Pima S-6 and PHY 841 RF still incurred 20% mortality. Upland cotton DP 1522 B2XF had about 40% mortality. Therefore, mortality occurs in both Pima and Upland cotton and is not Pima specific.

So, why FOV4 causes seedling mortality? Through a growth chamber study, we showed that $23^{o}C$ is the optimal temperature for FOV4 growth and disease development on cotton, as compared to 20, 26 and $29^{o}C$ (Zhang et al., 2021a). When we looked at the local temperatures, the conditions were favorable to FOV4 infections from mid-April to June in terms of low and mean temperatures in 2020 and 2021. Only when daily temperatures reached $35^{o}C$ or higher, did mortality or disease severity ratings decline. Our planting date study supported this conclusion. In fact, the late April to mid-June plantings caused higher disease severity or mortality than the mid-April planting in both 2020 and 2021.

Relationships among mortality, root and stem staining

Root vascular staining (RVS) has been extensively and almost exclusively used to screen cotton for resistance to FOV4 since its identification in California. We set out to understand if mortality and RVS both could be used under field conditions. We set up an 8 x 8 Latin square design study in two fields with one in Fabens, Texas and another in La Union, New Mexico, and in the greenhouse in Las Cruces, New Mexico. In each of the three locations, we had two tests- Tests 1 and 2. In addition, we also had two progeny-row tests, Tests 3 and 4 in Fabens, Texas.

We used 8 cultivars including 2 Pima and 6 Upland with different responses to FOV4 infections. Because it is an 8 x 8 Latin square design, we had 8 replications in each of the two directions based on planting row (column) and the tier or range (row). Mortality data were taken at 20, 30 and 36 days after planting (DAP) in Fabens, Texas; 36 DAP in New Mexico, and 48 DAP in the greenhouse. RVS and stem vascular discoloration (SVD) were taken at maturity in late October. The analysis of variance (ANOVA) showed that there was a significant difference among tiers in the Fabens field only, suggesting that randomized completed block design with replications based on tier can estimate and remove systematic experimental error due to tier. However, a genotypic variation was detected in all the three locations. Overall across all the tests, FM 2334GLT and Pima PHY 881 RF had the lowest mortality among the 8 cultivars tested, followed by FM 2448GLT, and then other four Upland cultivars (Acala 1517-08, Acala 1517-18 GLS, Acala Daytona RF, and PHY 480 W3FE). And Pima S-7 was highly susceptible. More detailed results can be found in Zhang et al. (2021c).

Here, I would like to focus on the coefficient of variation (CV) in mortality. In Fabens, when we screened the plots early at 20 DAP, it was very high (45-50%), because variable seed germination and seedling emergence. And it then went down to 33-37% at 30 DAP and further reduced to 22-29% at 36 DAP. However, the CV was too high (60-70%) in La Union, NM for the field results to be reliable, due to low and uneven FOV4 spore counts. So, the Fabens study was further analyzed. As expected, the CV from the greenhouse study was the lowest (17-28%) due to high and uniform inoculum density from artificial inoculations. However, when both mortality and RVS are included in the Fabens study, the CV was the lowest (11-15%). See Zhang et al. (2021c) for more details. MR or RVS alone would inflate disease resistance, because some of the plants that survived early might be from escapes and needed more time for FOV4 infections. Therefore, continuing screening plants using RVS at the adult or mature stage will minimize the chance of escapes. So, both MR and RVS should be used in combination.

The results from RVS are similar to MR. Results between the two tests in each location were significantly correlated for mortality and root staining. Interestingly, the mortality results from the three locations were also significantly and positively correlated. Zhang et al. (2021c) reported the results.

Because root staining requires uprooting plants, it is labor intensive and timely consuming. So, we decided to look at SVD, primarily focused on the stem at the soil line. We developed a rating system from 0 for no stem discoloration to 5 for 90% xylem discoloration or dead plants. We took some of the stems to the lab and did FOV4 isolation. The results indicate that SVD was significantly and positively correlated with the FOV4 isolation frequency, especially between 0 with very low isolation frequency (<10%) and 3 (with 90% isolation frequency). So, we dug lots of plants and looked at the root and stem in Tests 1 and 2 each with 64 plots in Fabens. We also cut lots of stems in Tests 3 and 4 with a total of 838 plots. The results show that MR was highly significantly correlated with RVS in Tests 1 and 2, and both were also highly significantly correlated with the combined disease severity rating (DSR) based on both parameters (Figure 2). We obtained the same results between MR and SVD (Figure 3). In the two progeny-row tests- Tests 3 and 4, we confirm that MR was significantly correlated with SVD.

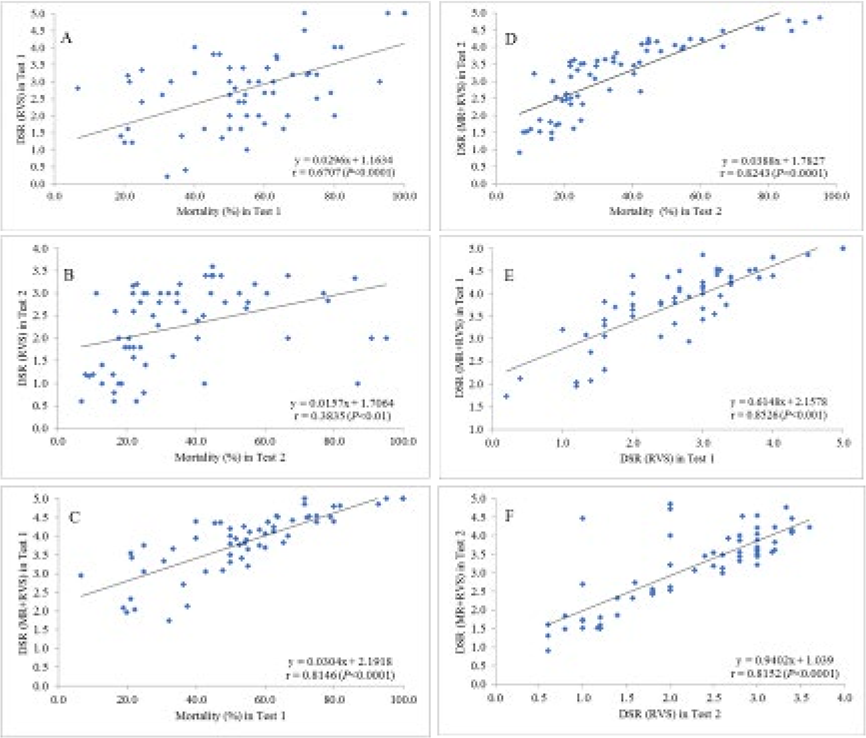

Figure 2. Relationship among mortality rating (MR), root vascular staining (RVS) and disease severity rating (DSR) based on both MR and RVS, i.e., DSR (MR+RVS), in Tests 1 and 2.

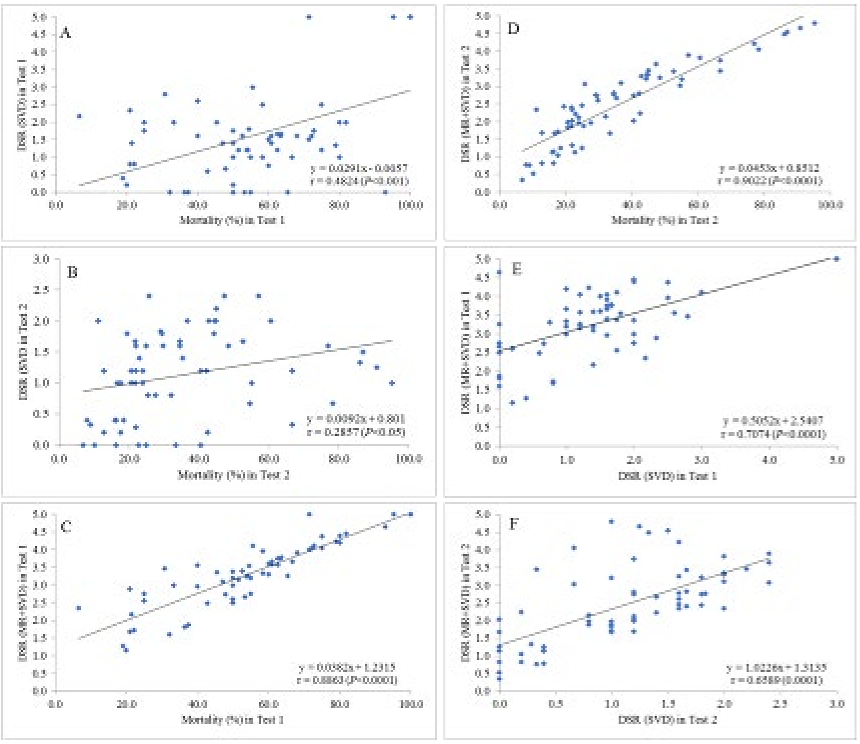

Figure 3. Relationship among mortality rating (MR), stem vascular discoloration (SVD) and disease severity rating (DSR) based on both MR and SVD, i.e., DSR (MR+SVD), in Tests 1 and 2.

The next question is: how about the relationship between root staining and stem staining? So, our analysis further shows that both parameters were highly correlated (Figure 4). Especially when we included the mortality data, the correlation was the highest between DSR (MR+RVS) and DSR (MR+SVD). Therefore, under field conditions with high FOV4 inoculum density and relatively uniform inoculum, mortality, stem rating and root rating can all be used, but the combined use of MR with RVS or MR with SVD is the most reliable.

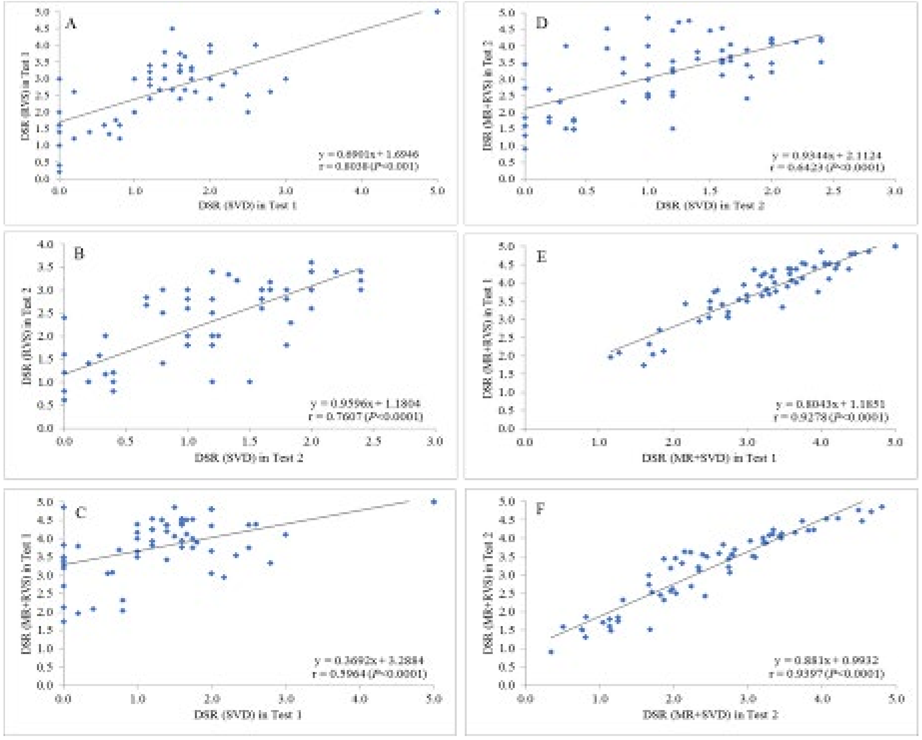

Figure 4. Relationship between root vascular staining (RVS) and stem vascular discoloration (SVD) and disease severity rating (DSR) based on both MR and SVD, i.e., DSR (MR+SVD), and DSR (MR+SVD) in Tests 1 and 2.

Seed germination tests for FOV4 resistance

It is also known that FOV4 causes root rot. However, we have to dig up roots from adult or mature plants when rating root rot or staining. Root infection by FOV4 during seed germination may reduce seedling emergence, but it is hard to take the data, and there have been no published results. So, we asked: can we look at the root during seed germination? We set up many seed germination tests. The results will be discussed in the next presentation (Zhu et al., 2022). Here, I just want to say that root rot was in fact observed. Roots from the control without inoculation had no root rot. Both Pima PHY 881 RF and Pima DP 359 RF had significantly lower root rot than other 6 cultivars 7 days post inoculation after seed germination for 7 days. Therefore, FOV4 resistance in cotton can be evaluated at the seed germination stage.

Evaluating cotton for FOV4 resistance in a hydroponic system

When evaluating cotton for resistance to FOV4, we have mostly used potting soil to grow cotton. We also used a hydroponic system to infect the root to compare the infection process among different cotton cultivars. We achieved 100% disease incidence and the disease severity rating as high as 4 in Pima S-7 within 14 days post inoculation, as compared to 60% incidence and 1.6 severity rating in Pima PHY 841 RF (Zhu et al., 2021d). The results were consistent with these from the field and greenhouse evaluations. Therefore, an infested farm soil, a commercial potting soil, and a hydroponic system can be also used for evaluating cotton for FOV4 resistance.

Effect of growth stage on FOV4 disease development

We further asked: which cotton growth stage is most sensitive to FOV4 and should be used in evaluation? Based on several studies, we show that the cotyledon stage is the most susceptible to FOV4 infections, and root wounding makes all cotton lines including resistant ones susceptible. As seedlings become older, they are less susceptible with less mortality.

Germplasm screening for FOV4 resistance

Using artificial inoculation at the cotyledon stage or the 1-true leaf stage, we have screened more than 5,000 lines since 2018 (Abdelraheem et al., 2021a, b; Zhang et al., 2020a, b; 2021b). We show that half of the Upland, Pima and cultivated diploid Asiatics (mostly *Gossypium arboreum* with a few *G. herbaceum* accessions) had 100% mortality. Very few Pima accessions (1.4%) had mortality below 50%. A few more Asiatic (2.2%) accessions had less than 50% mortality. This number was as high as 19.2% in Upland cotton (Table 3). So, repeated selection within Upland cotton is important to identify resistant germplasm.

Table 3. Germplasm screening for FOV4 resistance.

Mortality (%)	Upland (%)	Pima (%)	Asiatics (%)
Total accessions	n=1204	n=152	n=372
0	6 (0.5%)	0 (0%)	0 (0%)
1-10	18 (1.5%)	0 (0%)	1 (0.3%)
10-20	27 (2.2%)	0 (0%)	1 (0.3%)
20-30	19 (1.6%)	1 (0.7%)	1 (0.3%)
30-40	71 (5.9%)	0 (0%)	2 (0.5%)
40-50	90 (7.5%)	1 (0.7%)	3 (0.8%)

Genetic basis of resistance to FOV in cotton

There are more studies on the genomic basis for resistance to FOV7, together with a few reports on FOV4 (Abdelraheem et al., 2017). Here, we put together all reported quantitative trait loci (QTLs) for FOV resistance by chromosomes, with about 40 on the A-subgenome and 60 on the D-subgenome. Some chromosomes have more QTLs, while others have a few or none.

Table 4. Quantitative trait loci (QTLs) reported for FOV resistance in cotton.

Chromosome	No. QTLs	Chromosome	No. QTLs
c1/A01	3	c15/D01	6
c2/A02	3	c14/D02	4
c3/A03	6	c17/D03	10
c4/A04	0	c22/D04	3
c5/A05	0	c19/D05	8
c6/A06	8	c25/D06	3
c7/A07	2	c16/D07	6
c8/A08	8	c24/D08	4
c9/A09	2	c23/D09	3
c10/A10	1	c20/D10	0
c11/A11	0	c21/D11	4
c12/A12	6	c26/D12	6
c13/A13	0	c18/D13	5
A-subgenome	39	D-subgenome	62

Through a genome-wide association study (GWAS) on 367 US Upland cotton accessions using more than 20,000 SNP markers, we identified QTLs for FOV4 resistance on chromosomes 8 (A08), 14 (D02), 16 (D07), 17 (D03), 18 and 19 (Abdelraheem et al., 2020). Through another GWAS analysis on 550 recombinant inbred lines derived from intermating 11 Upland parents, we confirmed that there is a major QTL on chromosome 14 (D02).

We also put together major results on genetics of resistance to FOV in cotton (Table 5; Zhang et al., 2015). Major resistance genes for different races are reported. There are major resistance genes for difference FOV races, including a major resistance gene on chromosome 16 (D07) for race 1, a major gene on 14 (D02) for FOV4, and a major gene on 17 (D03) for FOV7.

Table 5. Major FOV resistance genes identified in cotton.

Group	FOV	Distribution	Resistant line	Chromosome	Authors
1	Race 1	US, Africa	Upland	1 recessive gene	Jones (1953)
	Race 1	US, Africa	Upland	1 dominant gene	Smith and Dick (1960)
	Race 1	US, Africa	Pima Seabrook	2 dominant genes	Smith and Dick (1960)
	Race 1	US, Africa	Pima S-7	*FOV1*- D07 (c16)	Wang & Roberts (2006)
	Race 1	US, Africa	Pima S-7	*FOV1*- D07 (c16)	Ulloa et al. (2011)
	Race 2	US, more virulent on soybean than race 1			
	Race 6	Brazil	Upland IAC17	1 major gene	Gridi-Papp et al. (1977)
2	Race 3	Egypt	*G. barbadense*	1 dominant gene	Fahmy (1927)
	Race 3	Israel	Acala SJ-2	1 dominant gene	Netzer et al. (1985)
	Race 3	Uzbekstan	Upland	1 recessive gene	Abdullaev et al. (2015)
	Race 5	Sudan, same as race 3. Its race designation was withdrawn			
3	Race 4	India	Asiatic diploid	2 genes	
	Race 4	US	Pima S-6	*FOV4*- D02 (c14)	Ulloa et al. 2013
	Race 4	US	Nem-X	Major QTL- D02	Wang et al. (2018)
	Race 7	China	Chinese Upland	Fw_1 and Fw_2	Feng et al. (1998)
	Race 7	China	Chinese Upland	Fw^R- D03 (c17)	Wang et al. (2009)
	Race 7	China	Chinese Upland	*FOV7*- *Gh_D03G0209*	Liu et al. (2021)
	Race 7	China	Chinese Pima	D11 (c21)	Zhu et al. (2010)
	Race 7	China	*G. arboreum*	A11- *Ga11G2353*	Du et al. (2018)
4	Race 8	China, US		?	

Breeding for FOV4 resistance in Upland cotton

Interestingly, FOV4 resistance has been identified from FOV7-resistant Chinese Upland cotton. Further selection has enhanced the resistance. So, they have become the most important source of resistance for FOV4 resistance in Upland. For example, U1 was selected from FOV7-resistant Liaomin 7 by Jim Olvey (based on a presentation at Beltwide Cotton Conferences in 2021). In the New Mexico Cotton Breeding Program, I have extensively used Chinese Upland cotton in cross breeding. As a result, three FOV4-resistant cultivars- NuMex COT 15 GLS, NuMex COT 17 GLS, and Acala 1517-20 (Zhang, 2020c; Zhang and Wedegaertner, 2021; Zhang et al., 2016, 2020c) were developed and released. Two of them and Liaomin 7 were further used by Mauricio Ulloa in cross breeding to develop 17 new lines with resistance to FOV4 (Ulloa et al., 2021).

Summary

1. On FOV4, we have identified FOV4 in more than 10 fields which are still confined in south of Las Cruces, NM, with 62% N and 38% T genotypes. There is no field with a mixture of the two genotypes. The genotype composition is different from that in TX, CA, and China (FOV7). FOV4 is different from FOV7 in terms of optimal temperature requirement for growth and infections, cotton growth stage, mortality, and pathogenicity on a set of differential hosts. There is a wide range of virulence within each FOV4 genotype, which appears unrelated to virulence.
2. On evaluation methods, seedling mortality is an important criterion to measure FOV4 resistance early in the

season. However, combining mortality with root rating or stem rating late in the season is the most reliable. Evaluation in a field with high and uniform FOV4 inoculum density and in greenhouse with artificial inoculation can be used. When evaluating cotton for FOV4 resistance under control conditions, low temperature (21-23^{o}C) should be used. Seed germination and seedlings up to the 1st-true leaf stage can be inoculated with FOV4. One can use infested farm soil, un-infested potting soil, or hydroponics, but the key is effective and uniform FOV4 inoculum density.

3. On germplasm evaluation, more than 5,000 lines and cultivars were evaluated. Upland cotton appears to have more accessions with resistance to FOV4 than Pima cotton and Asiatic diploid cotton.
4. On the genetic basis, more than 100 quantitative trait loci (QTLs) for FOV resistance have been reported. A major FOV4-resistance gene or QTL on D02 and a major FOV7-resistance gene on D03 are identified. Our FWAS analysis on an association mapping panel of 367 Upland accessions and another set of 550 RILs confirmed the existence of the QTL on D02 for FOV4 resistance. A major FOV7-resistance gene on A11 is identified in Chinese Asiatic cotton, but no resistance QTL or gene is reported on A11 of the tetraploid cotton.
5. On breeding, repeated selection within resistant germplasm lines can enhance resistance to FOV4. FOV7 resistant Chinese Upland serves as an important source of resistance to FOV4. Cross breeding can transfer FOV4 resistance to progeny.

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