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BREEDING, GENETICS, & GENOMICS

Introgression of Thrips Resistance from Pima Cotton (*Gossypium barbadense* L.) into Upland Cotton (*Gossypium hirsutum* L.)

Navin Shrestha, Matthew Bertone, Daryl T. Bowman, and Vasu Kuraparthy*

ABSTRACT

Thrips are major early season insect pests that cause significant economic damage in Upland cotton in the U.S. Development and deployment of resistant cultivars is the most effective and ecologically sustainable means of reducing thrips damage in cotton. Interspecific hybridization and backcrossing were performed to introgress thrips resistance from Pima cotton (*Gossypium barbadense* L.) accession Coastland 320 into Upland cotton (*Gossypium hirsutum* L.) cultivars Acala Maxxa (AM) and Fiber Max 966 (FM966). Backcross populations were screened for thrips resistance in thrips screening summer field nurseries in North Carolina. Thirty-two BC_2F_2 plants with thrips resistance were identified and backcrossed further to develop BC_3F_2 plants. Eleven AM derived BC_2F_2 resistant plants and 21 FM966 derived BC_2F_2 resistant plants were genotyped using CottonSNP63K array to identify the Pima chromatin in the introgression lines (ILs). In the ILs, introgressed Pima chromatin was detected on chromosomes A01, A08, A09, A10, A11, D10, D11, D12, and D13. Of these, four ILs, two each in AM and FM966 background, showed overlapped introgressed Pima chromatin on chromosomes A10 and D11. Further, four introgression lines, two each in AM and FM966 background, shared a common Pima introgression on chromosome D13. Characterization of thrips species in the screening nursery showed that predominant thrips species were tobacco thrips (*Frankliniella fusca* (Hinds)) followed by western flower thrips (*Frankliniella occidentalis* (Pergande)). The identified ILs with thrips resistance should be a useful source of genetic variability for developing Upland cotton cultivars with pest resistance.

N. Shrestha, D.T. Bowman, and V. Kuraparthy*, North Carolina State University Dept. of Crop & Soil Sciences, Raleigh, NC 27695; and M. Bertone, North Carolina State University Dept. of Entomology & Plant Pathology, Raleigh, NC 27695.
*Corresponding author: vasu_kuraparthy@ncsu.edu

In the U.S., cotton is grown in 17 states, stretching from Virginia to California, covering approximately 12 million acres (USDA-NASS, 2021). Upland cotton (*Gossypium hirsutum* L.) is grown in more than 98% of the cotton acreage while Pima cotton (*G. barbadense* L.) is grown in less than 1.5% of the total cotton acres. Throughout the cotton belt, numerous pests and diseases affect cotton. Among these pests, thrips (Thysanoptera: *Thripidae*) are one of the most problematic early season insect pests in Upland cotton in the U.S. (Quisenberry and Rummel, 1979; Cook et al., 2011; Reay-Jones et al., 2019). Cotton is more vulnerable to thrips attack than most other row crops because the terminal buds of cotton seedlings develop slowly during the first seven to ten days after emergence (Layton and Reed, 2002). Thrips often concentrate their feeding in the terminal bud by piercing it with their mouthparts and sucking the contents, and this damage done to the young growing plant parts results in crinkled and distorted leaves as the plants grow (Layton and Reed, 2002). Prolonged feeding on seedlings causes replacement of plant tissues by air, which results in a silvery appearance of plant tissues (Telford and Hopkins, 1957; Reed and Reinecke, 1990). Gradually the silvery areas become brown. In addition, heavy thrips infestation on young leaves generally produces a crinkled, ragged appearance, and the margins curl upwards and inwards causing 'possum-eared cotton' (Layton and Reed, 2002). Damage caused by thrips on young cotton seedlings has numerous consequences including stunted growth, death of the terminal bud (causing loss of apical dominance leading to excessive vegetative branching referred to as "crazy cotton"), reduced stand, and delayed fruiting and maturity (Gaines, 1934; Layton and Reed, 2002). Thrips damage is prominent during cool and wet periods when the seedlings are growing slowly (Kaur et al., 2018). Other factors such as wind, blowing sand, herbicide injury, nematodes, and rain further compound the plant damage due to thrips (Vyavhare and Kerns, 2017). Cotton seedlings infested by thrips may have reduced plant height

and leaf surface, causing delay in boll formation, development, and maturation, which in turn delays fiber formation and harvest (Cook et al., 2011). In the absence of effective chemical control, thrips can cause moderate to severe damage to seedlings. If not controlled, thrips can cause yield reductions of more than 45.36 kg per 0.40 ha (100 pounds of lint per acre) (Layton and Reed, 2002; Reisig and Huseth, 2019). In 2021, 80% of planted hectares across the U.S. were infested with thrips causing an estimated loss of 102,878 bales (Cook and Threet, 2021).

Thrips are generally polyphagous and have a wide host range that includes crop and non-crop herbaceous and woody plants (Turina et al., 2012). Although there are as many as 13 species of thrips that infest cotton (Watts, 1937), five major species are prevalent that infest cotton within the U.S. (Wang et al., 2018). Reproduction of thrips is typically haplodiploid (Mound, 2009; Reitz, 2009) and it takes only about 16 days to develop from eggs to adult thrips (Bohmfalk et al., 1996). Because of its short life cycle and high fecundity rate, controlling thrips is arduous. The use of at-planting systemic insecticides has been highly successful in thrips control and is recommended over foliar sprays due to increased persistence, reduced harm to beneficial insects, and occasionally higher yields (Reisig and Huseth, 2022). However, chemical control practices are costly and can lead to the development of resistance to insecticides in pests, outbreak of secondary pests, pest resurgence and greater risk to the environment (Lewis, 1997; Hanson et al., 2017). Further, some predominant thrips species, for example *Frankliniella fusca*, have developed resistance against neonicotinoids, the most commonly used insecticides to treat cotton seeds (Wang et al., 2018).

Researchers have documented the existence of natural variation for thrips resistance among cotton lines. This varied resistance was attributed to morphological traits such as pubescence (Abdel-Bary et al., 1968; Rummel and Quisenberry, 1979; Zareh, 1985; Kaur et al. 2018), thick leaves with a waxy coating (Pandya and Patel, 1964), thicker lower epidermis (Abdel-Gawaad et al., 1973) and higher gossypol levels (Gawaad and Soliman, 1972). Some studies have shown that thrips resistance might not be completely associated with leaf pubescence (Wardle and Simpson, 1927; Watts, 1937; Ballard, 1951; Gawaad and Soliman, 1972; Bowman and McCarty, 1997). Reduced efficacy and economic and environmental impacts of insecticides and varied contribution of cotton morphological features for thrips resistance warrants the need for developing genetic resistance in cotton cultivars to thrips as a long-term solution to reduce infestation and damage in cotton. Evaluation of cotton lines in the field showed differences in the levels of resistance or tolerance to thrips. Upland cotton was generally susceptible to thrips, whereas Pima cotton showed variation for resistance to thrips (Bowman and McCarty, 1997; Kaur et al., 2018). Identification and transfer of genetic resistance to thrips in cotton would be beneficial to growers to reduce dependence on insecticides and to improve the economic viability and sustainability of cotton production in the U.S.

Limited studies have been carried out to understand the genetics of thrips resistance in cotton. Genome wide association studies (GWAS) using a diversity panel of 376 accessions (Tyagi et al. 2014) showed that thrips resistance was quantitatively inherited (Abdelraheem et al., 2021). Studies involving interspecific F_2 mapping populations of *G. hirsutum* x *G. barbadense* crosses indicated that thrips resistance in tetraploid cotton segregated as a single major gene (Zhang et al., 2011). Using similar interspecific segregating mapping populations, Wann et al. (2017) reported the presence of a second major gene (*Thr2*) controlling thrips resistance in cotton suggesting that multiple genes with major effects could be controlling thrips resistance in tetraploid cotton.

In the current study we report on the development of two interspecific backcross populations {(Pima cotton cultivar Coastland 320 x Upland cotton cultivar Acala Maxxa) and (Pima cotton cultivar Coastland 320 x Upland cotton cultivar FiberMax 966)}, which were used to identify and characterize the thrips resistant introgression lines.

MATERIALS AND METHODS

Plant Materials and Phenotyping in the Field. From a multi-year germplasm screening study, Pima cotton cv. Coastland 320 (CL320) (PI 608213) (Figures 1a and 1b) was identified as a good source of thrips resistance in cotton (Bowman and McCarty, 1997; Kaur et al., 2018). To transfer thrips resistance of CL320 into Upland cotton, two different Upland cotton cultivars (Acala Maxxa (AM)) (PI 540885) (Figures 1c and 1d), and FiberMax 966 (FM966)) (PI 619097) (Figures 1e and 1f) were used as female parents to cross with CL320 in the summer of 2017. Segregating backcross populations were developed by using AM and FM966 as recurrent parents. The F_1 plants of AM x CL320 and FM966 x CL320 were crossed

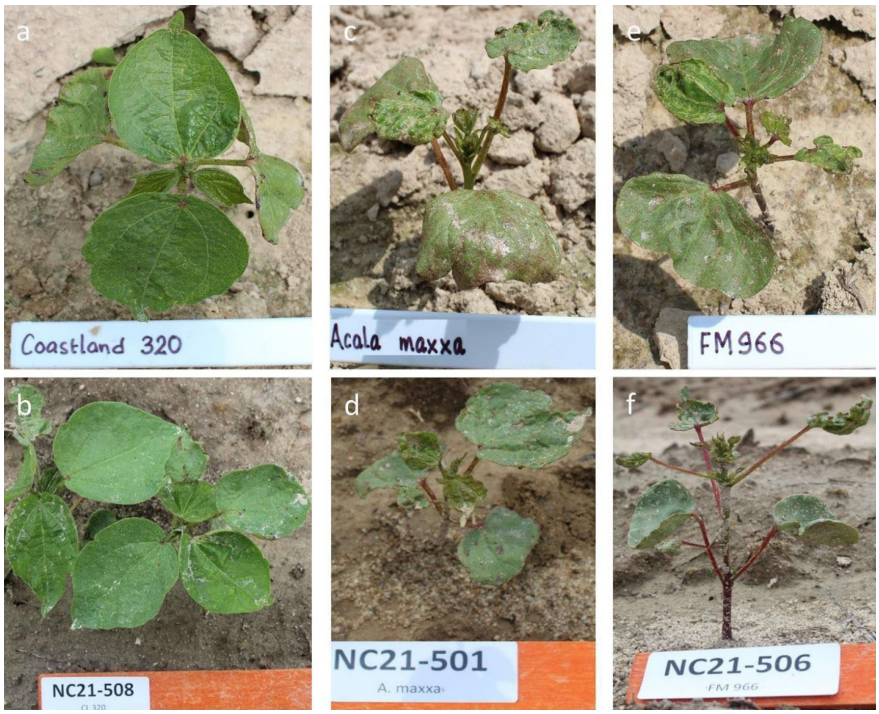

Figure 1. Phenotypes of parental accessions infested by thrips at two to three true leaf stages in the field. Pima cotton cultivar Coastland 320 displaying resistance to thrips infestation in the year 2020 (Figure 1a) and 2021 (Figure 1b). Upland cotton cultivar Acala Maxxa showing damage caused by thrips infestation in the year 2020 (Figure 1c), and 2021 (Figure 1d). Upland cotton cultivar Fiber Max 966 displaying susceptible phenotype due to damage caused by thrips in the year 2020 (Figure 1e), and 2021 (Figure 1f).

as male parents to their respective recurrent parents AM and FM966 to develop BC_1F_1 plants. The BC_1F_1 plants were crossed as males to the recurrent parents to develop BC_2F_1 plants. In subsequent years, for each generation, the backcross plants along with the parental and susceptible control accessions were planted and evaluated in a thrips screening summer nursery at Upper Coastal Plain Research Station (UCPRS), Rocky Mount, NC. Susceptible parents were planted in three replicates at random in the field. Insecticide seed treatments were not used, and sprays were performed after the cotton reached flowering stage. Thrips damage on the plants was visually scored at the third to fourth true leaf stage. Phenotyping was done as described in Bowman and McCarty (1997) and Kaur et al. (2018). Plants with no obvious thrips damage with a score of zero (0), were selected as resistant plants (Figure 2). In all years, the selected plants were manually selfed by bagging the flower buds using glassine bags (Uline, Buford, GA) during flowering and/or crossed to their respective recurrent parents AM and FM966. Along with the crossed bolls, at least four selfed bolls were separately harvested from each plant.

Genotyping of the Introgression Lines (ILs). Two different backcross derivatives were used for genotyping using the CottonSNP63K array (Hulse-Kemp et al., 2015). In the year 2021, 39 BC_2F_2 thrips resistant lines, four susceptible plants (two each from AM and FM966 derived lines) and three parental accessions were genotyped whereas in the year 2022, BC_2F_3 families (six AM and five FM966 derived) and BC_3F_1 families (five AM and two FM966 derived) were used along with three parental accessions and two susceptible lines for genotyping. Leaf tissue samples were collected in 2 ml centrifuge tubes in liquid nitrogen. Genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen USA, Germantown, Maryland) quantified using a NanoDrop ND – 1000 spectrophotometer (Thermo Fisher Scientific, Massachusetts, USA). Genotyping with the CottonSNP63K array was done at Texas A&M Institute for Genome Sciences and Society as described in Hulse-Kemp et al. (2015).

From the 63,058 SNPs used in genotyping, polymorphic SNPs between parental combinations AM and CL320, and FM966 and CL320 were identified. To identify non-redundant markers for the analyses for each parental combination, different steps used to filter the marker numbers included: 1) removal of missing markers and heterozygous markers from parental lines,

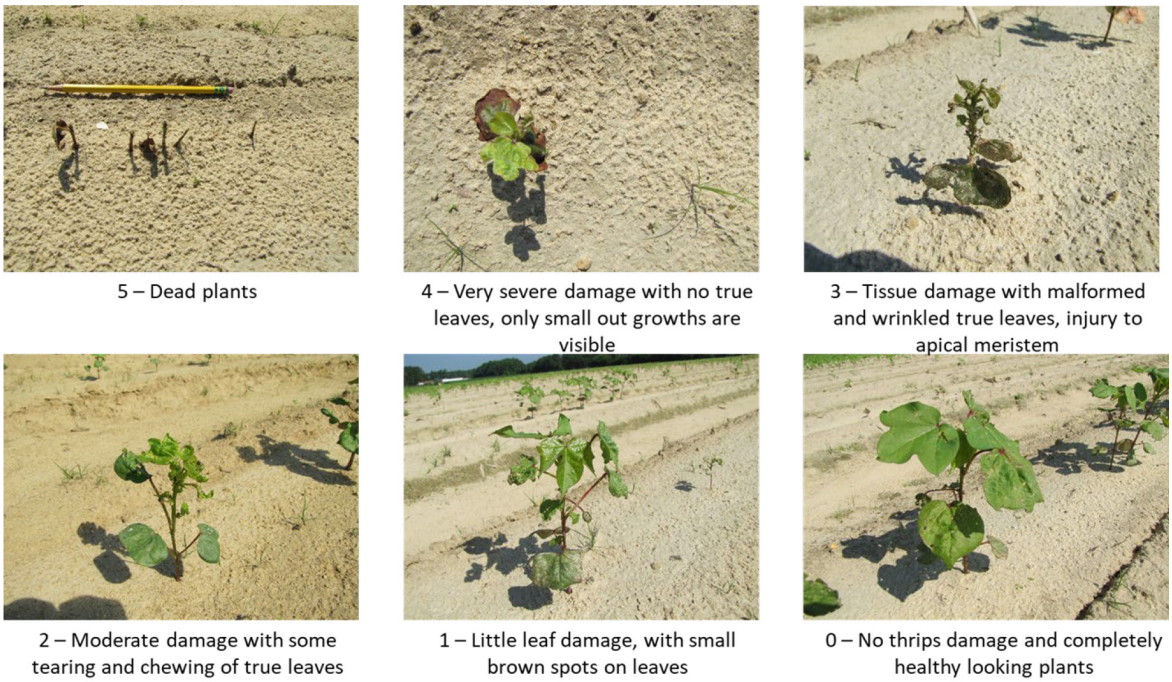

Figure 2. Phenotypic rating used for screening thrips resistance in cotton. On a scale of 0-5, score zero (0) indicates healthy plants with no visible thrips damage, and a score of 5 represents dead plants due to severe thrips damage.

2) removal of monomorphic markers and heterozygous markers from BC_2F_2s with missing values more than 30% and 3) the removal of markers without any chromosomal information when aligned to the *G. hirsutum* cv. TM1 CRI_v1.0 reference genome (Yang et al., 2019). Linkage maps developed by Zhang et al. (2019), Zhu et al. (2021), and Shrestha et al. (2022) were used to assign the markers on specific A and D sub-genome chromosomes. Introgressions from Pima cotton were determined based on the polymorphic marker pattern.

Identification of Thrips Species in the Screening Nursery. Thrips species identification was done by selecting the four most severely infested plants of susceptible parents (AM and FM966) at 30 days after planting from each replication in the year 2022. Insect sample collection was conducted as described in Rummel and Arnold (1989). Four highly susceptible plants from each replicate were cut using a pair of scissors at the ground level. Shoots along with the leaves of each susceptible genotype from each replication were immersed immediately in 1-liter mason jars containing soapy water. Jars were vigorously shaken to dislodge the thrips. Soapy water with insect samples were poured into a 230-mesh testing sieve (U.S. Standard Sieve Series No. 230, 8 inches diameter, 63 microns, 0.0025 inches opening; Dual Manufacturing Co., Chicago, IL 60618), and washed with running tap water. The dislodged thrips and their larvae were stored in 70% ethyl alcohol in scintillation vials. A buchner funnel was used under vacuum with filter paper to separate thrips from the ethanol. Larval thrips were not identified to species but were counted using a dissecting microscope. Slide-mounted adult specimens were viewed under a compound microscope to count the thrips number (adult and larvae) and the species were identified as described in Palmer et al. (1989).

RESULTS

Transfer of Thrips Resistance from Pima Cotton into Upland Cotton. In summer 2019, 196 AM derived BC_1F_1 plants and 161 FM966 derived BC_1F_1 plants along with the two parental accessions (AM and FM966 as three replicates) were planted at the Central Crops Research Station (CCRS), Clayton, NC. The BC_1F_1 plants were backcrossed as females to the respective recurrent parents. In total, we harvested the seed of 357 BC_2F_1 families. From these, seeds of six families were discarded due to immature, unviable seeds and/or insufficient seeds (< 15) required for machine planting. This resulted in obtaining seed of 351 BC_2F_1 families (192 families in AM background and 159 BC_2F_1 families in FM966 background) for machine planting in the following summer.

Development and Evaluation of Backcross Families. In the summer of 2020, 357 BC_2F_1 fami-

lies along with 25 plots of parental accessions (AM, FM966 and CL320) were planted in the thrips screening nursery at the Upper Coastal Plain Research Station (UCPRS), Rocky Mount, NC. Recurrent parents AM and FM966 showed clear susceptibility responses to thrips. Symptoms of these responses ranged from moderately to severely damaged to dead plants (score 2-5; Figure 2). Based on visual observation of plants with thrips damage, 321 BC_2F_1 plants were categorized as thrips resistant (phenotypic score 0; Figure 2). Of these selected resistant plants, 159 plants were from the AM cultivar background (Figures 3 & 4a), and 162 plants from the FM966 background (Figures 3 & 4a). These 321 BC_2F_1 families along with parental accessions and susceptible controls (AM, FM966, and CL320) were selected for thrips screening in UCPRS, Rocky Mount, NC in summer 2021. Phenotyping for thrips response at three to four true leaf stage resulted in the selection of 139 resistant BC_2F_2 plants (70 plants were from AM background and 69 were from FM966 background). Most of the plants in two BC_2F_2 families (NC21-522- AM derivative and NC21-727- FM966 derivative) showed strong resistance against thrips. Resistant plants were manually selfed to advance them to generation BC_2F_3 stage and backcrossed to their respective recurrent parents to obtain BC_3F_1 generation. This resulted in the development of 18 AM derived BC_2F_3 families, 26 FM966 derived BC_2F_3 families, 12 AM derived BC_3F_1 families, 16 FM966 derived BC_3F_1 families.

In the summer of 2022, field evaluation of backcross derivatives showed significantly higher thrips pressure, where resistant parent CL320 often displayed the phenotypic score of one (Figure 2) while susceptible recurrent parents showed the highest mortality rate. Interestingly, CL320 showed quick recovery to normal seedling growth. Phenotypic screening of BC_2F_3 and BC_3F_1 families for thrips resistance identified 34 resistant plants. These included 15 BC_2F_3 plants of AM background, six BC_2F_3 plants of FM966 background and nine BC_3F_1 families of AM background and four BC_3F_1 plants of FM966 background (Figure 4c). Distribution of thrips-resistant introgressed lines by generation and year is summarized in Table 1.

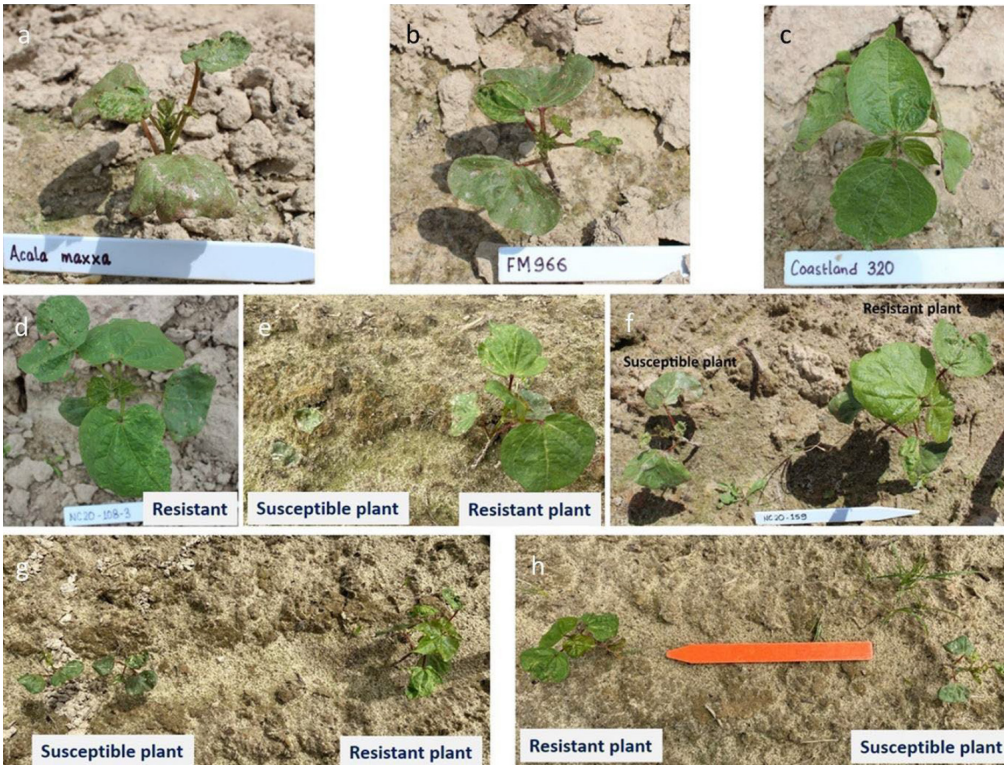

Figure 3. Screening of parental accessions Pima cotton cultivar Coastland 320, and Upland cotton cultivar Acala Maxxa and Fiber Max 966 along with their BC_2F_1 derivatives for thrips response at Upper Coastal Plain Research Station (UCPRS), Rocky Mount, NC in summer 2020. Acala Maxxa (Figure 3a), and Fiber Max 966 (Figure 3b) displaying susceptible phenotype, and Coastland 320 (Figure 3c) exhibiting resistant phenotype in the field condition. Some BC_2F_1 lines exhibited resistant phenotype (Figure 3d), and some lines segregated for resistant and susceptible phenotypes in response to thrips infestation (Figures 3e, 3f, 3g, & 3h).

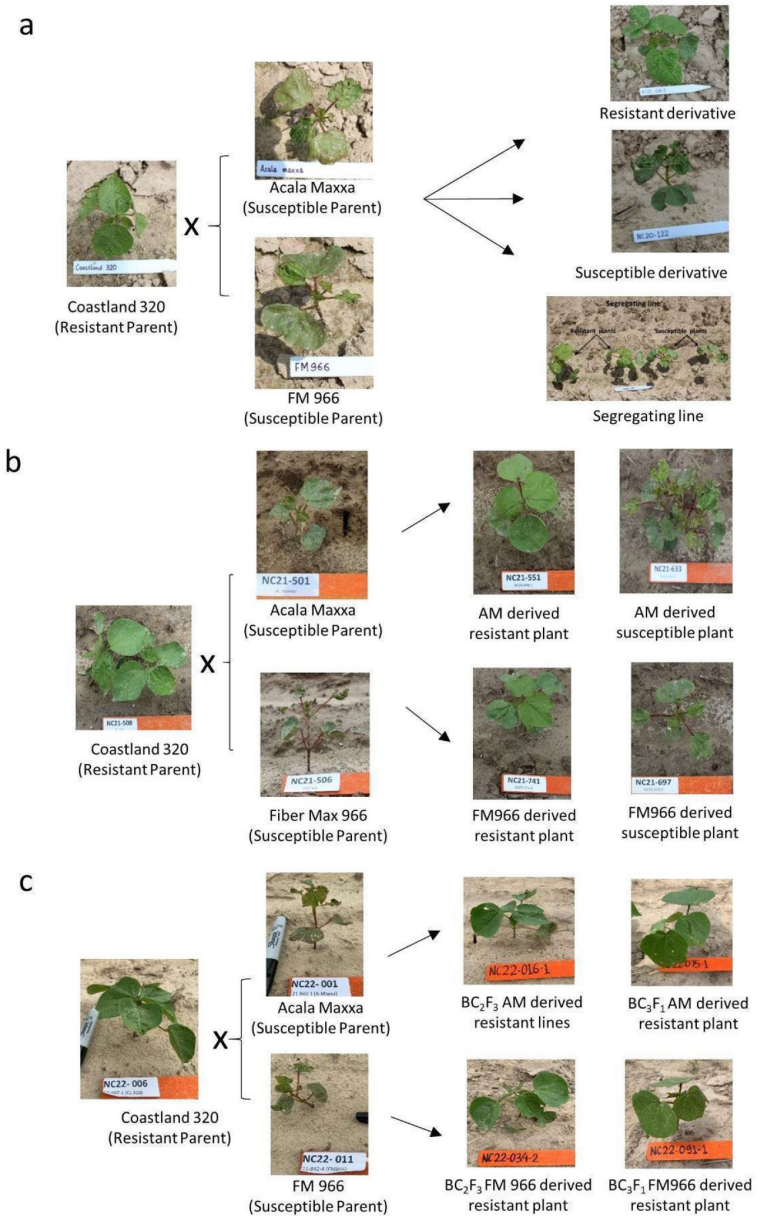

Figure 4. Response to thrips infestation exhibited by parental accessions and their back cross derivatives evaluated in the thrips screening nursery at Rocky Mount, NC. Phenotypes of the BC_2F_1 derivatives [{(CL320 x AM & FM966) x AM & FM966} x AM & FM966] evaluated in summer nursery at Rocky Mount, NC in the year 2020 (Figure 4a). Phenotypes of parents and BC_2F_2 plants evaluated in the year 2021 (Figure 4b). Phenotypes of parents and BC_3F_1 and BC_2F_3 plants evaluated in the year 2022 (Figure 4c.).

Table 1. Summary of thrips resistant introgressed lines selected in the screening nurseries.

Year	No. of AM derived introgressed lines[a]	No. of FM966 derived introgressed lines[b]	Total no. of selected thrips resistant introgressed lines[(a + b)]	Generation
2020	159	162	321	BC_2F_1
2021	70	69	139	BC_2F_2
2022	15	6	21	BC_2F_3
2022	9	4	13	BC_3F_1

Characterization of Thrips Resistant Introgressed Region(s) with SNP Markers. Genotyping of 11 BC_2F_2 AM derived ILs and 21 BC_2F_2 FM966 derived ILs along with the parental accession using 63K SNP array (Hulse-Kemp et al., 2015) resulted in the identification of 13,378 non-redundant polymorphic markers between parents AM and CL320 and 12,966 non-redundant polymorphic markers between parents FM966 and CL320. Using cut-off values of 300 Kb and 100 Kb genomic region size, for interstitial and telomeric (terminal) introgressed regions, respectively, a total of 201 introgressed regions were identified in 11 Acala Maxxa derived BC_2F_2 ILs. Among these, 127 were interstitial introgressions, while 74 were terminal CL320 introgressions (unpublished results). Most of the introgressed regions were identified in nine chromosomes, namely A01, A08, A09, A10, A11, D10, D11, D12, and D13, based on the frequency of presence of these regions in an individual. The smallest Pima introgressed segment identified was 138.74 Kb in size located in the telomeric region of chromosome A03 in IL NC21-630-1, which was defined by flanking markers i54615Gb and i62755Gt (unpublished results). The largest introgressed region identified was 125.15 Mb in size, located in the interstitial region of chromosome A06 in IL NC21-581-1. This introgression was defined by flanking markers i52154Gb and i11460Gh (unpublished results). Chromosomes A11 and A12 of IL NC21-551-1, chromosome A08 of IL NC21-581-1, chromosome D08 of IL NC21-630-1, chromosome A08 of IL NC21-641-1, and chromosome D05 of IL NC21-661-1 each possessed three introgressed segments, which were the highest number of Pima introgressions observed within a chromosome in these ILs (unpublished results). Chromosomes revealing introgressed segments from Pima cotton into Upland cotton in the eleven AM derived BC_2F_2 introgressed lines is presented in Table 2.

Similarly, the twenty-one FM966 derived BC_2F_2 ILs consisted of 198 introgressed regions, including 120 interstitial introgressions and 78 telomeric Pima introgressions (unpublished results). The smallest introgressed region identified was 110.77 Kb in size, located in the telomeric region of chromosome D13 in IL NC21-686-1, and is defined by flanking markers i13873Gh and i13885Gh (unpublished results). The largest introgressed region of 120.71 Mb was situated in the interstitial region of chromosome A06 in IL NC21-834-1 and it was defined by flanking markers i22405Gh and i11403Gh (unpublished results). The maximum number of introgressed regions (three) was found on chromosome D11 in IL NC21-733-1 (unpublished results). Chromosomes displaying the introgressed segments from Pima cotton into Upland cotton in twenty-one FM966 derived introgressed lines is presented in Table 3.

The AM derived BC_2F_2 IL NC21-644-1, and FM966 derived BC_2F_2 IL NC21-738-1, have overlapping segments of Pima introgressions (443,409 bp - 61,670,428 bp) flanked by markers i39966Gh and i40279Gh in chromosome A10, whereas the other AM derived BC_2F_2 IL NC21-581-1 and FM966 derived IL NC21-733-1 share introgressions (193,350 bp – 1,364,656 bp) flanked by SNPs i06647Gh and i06714Gh on chromosome D11 (unpublished results). Interestingly, ILs NC21-652-2 (AM derived) and NC21-727-5 (FM966 derived) shared the Pima (CL320) introgressions (84,627 bp and 2,048,145 bp) flanked by markers i12952Gh and i52924Gb on chromosome D13, which were similar to the common introgressions on the same chromosome in ILs NC21-661-1 (AM derived) and NC21-758-1 (FM derived) (unpublished results). This suggests that these four introgression lines have Pima introgressions located in identical regions. Furthermore, we observed there were overlapping regions of introgression in the FM966 derived ILs NC21-727-3 and NC21-733-1, spanning from 136,055 bp to 4,762,380 bp on chromosome A08, flanked by the markers i03696Gh and i50019Gb (unpublished results), whereas lines NC21-733-1 and NC21-750-2 share introgressed regions from 443409 bp to 61670428 bp, flanked by SNPs i39966Gh and i40279Gh markers (unpublished results). Similarly, ILs NC21-727-3 and NC21-750-2, both derived from FM966, have a common introgressed region from 115,087,207 bp to 119,033,140 bp on chromosome A11, bounded by markers i00811Gh and i53639Gb (unpublished results).

Identification of Thrips Species. Thrips samples from field collections in the year 2022 were counted and analyzed, resulting in a total of 114 thrips samples. The most predominant thrips species in the screening nursery at Rocky Mount in North Carolina were tobacco thrips (*Frankliniella fusca* (*Hinds*)), western flower thrips (*Frankliniella occidentalis* (*Pergande*)), and flower thrips (*Frankliniella tritici* (*Fitch*)). *Frankliniella fusca* was the dominant species (96.49%) followed by *F. occidentalis* (3.5%), and *F. tritici* (0.01%) (unpublished results; Figure 5). Collected samples consisted of 1,078 unidentified larvae, which were excluded from the current results (unpublished results).

Table 2. Chromosomes showing introgressed regions from Pima cotton transferred to Upland cotton in 11 Acala Maxxa derived BC_2F_2 introgressed lines.

Chromosome	NC21-551-1	NC21-557-1	NC21-568-1	NC21-571-1	NC21-581-1	NC21-610-2	NC21-630-1	NC21-641-1	NC21-644-1	NC21-652-2	NC21-661-1
A01	Y[z]	N[y]	Y	Y	Y	Y	Y	Y	Y	Y	Y
A02	Y	Y	N	N	Y	Y	Y	Y	N	N	N
A03	Y	N	N	N	Y	N	Y	N	Y	Y	Y
A04	N	N	N	N	Y	N	N	N	N	N	Y
A05	Y	N	N	N	N	N	Y	Y	Y	Y	Y
A06	N	N	N	N	Y	Y	N	N	Y	Y	N
A07	Y	N	Y	Y	Y	Y	N	Y	N	Y	Y
A08	Y	Y	N	Y	Y	Y	Y	Y	Y	N	Y
A09	Y	N	Y	N	Y	N	Y	Y	Y	Y	Y
A10	Y	Y	Y	N	Y	N	Y	Y	Y	Y	Y
A11	Y	Y	Y	Y	Y	Y	Y	Y	N	Y	Y
A12	Y	N	N	N	N	Y	N	Y	Y	Y	Y
A13	Y	Y	N	Y	N	N	N	Y	Y	N	N
D01	Y	Y	N	Y	Y	Y	Y	Y	N	N	N
D02	N	N	N	Y	Y	Y	N	Y	N	Y	N
D03	N	N	N	N	Y	Y	Y	Y	Y	Y	N
D04	N	N	N	Y	N	Y	N	Y	N	Y	Y
D05	Y	N	N	N	N	Y	Y	Y	Y	Y	Y
D06	Y	N	N	Y	Y	Y	N	Y	N	N	N
D07	N	N	N	Y	Y	N	Y	Y	Y	Y	Y
D08	Y	Y	N	N	Y	Y	Y	Y	Y	Y	Y
D09	N	N	N	Y	Y	Y	Y	N	N	Y	Y
D10	N	N	N	Y	Y	Y	Y	Y	Y	Y	Y
D11	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	N
D12	Y	N	N	N	Y	N	Y	N	Y	Y	Y
D13	N	Y	N	Y	N	N	N	Y	Y	Y	Y

[z]Y indicates Pima chromatin detected by polymorphic SNPs

[y]N indicates Upland cotton chromatin

Table 3. Chromosomes showing introgressed regions from Pima cotton transferred to Upland cotton in 21 Fiber Max 966 derived BC2F2 introgressed lines.

Chromosome	NC21-682-1	NC21-686-1	NC21-690-1	NC21-694-1	NC21-700-1	NC21-724-1	NC21-726-2	NC21-727-3	NC21-727-5	NC21-727-7	NC21-727-8	NC21-733-1	NC21-738-1	NC21-750-2	NC21-758-1	NC21-772-1	NC21-798-1	NC21-804-1	NC21-826-1	NC21-828-1	NC21-834-1
A01	N[z]	N	N	Y[y]	N	Y	Y	N	N	Y	N	N	N	N	Y	N	N	N	N	Y	N
A02	N	Y	N	N	N	N	N	Y	N	Y	N	N	N	N	Y	Y	N	N	Y	Y	N
A03	N	N	Y	N	Y	Y	Y	N	N	N	N	N	N	N	N	N	Y	N	N	N	Y
A04	N	N	N	N	N	N	N	N	Y	N	N	N	N	Y	Y	Y	Y	Y	N	N	N
A05	N	Y	N	N	N	Y	N	N	N	Y	N	N	N	Y	Y	Y	N	Y	N	N	N
A06	N	N	N	N	N	N	N	Y	N	N	Y	N	N	Y	N	N	N	N	N	Y	Y

Continued

Table 3. Continued

Chromosome	NC21-682-1	NC21-686-1	NC21-690-1	NC21-694-1	NC21-700-1	NC21-724-1	NC21-726-2	NC21-727-3	NC21-727-5	NC21-727-7	NC21-727-8	NC21-733-1	NC21-738-1	NC21-750-2	NC21-758-1	NC21-772-1	NC21-798-1	NC21-804-1	NC21-826-1	NC21-828-1	NC21-834-1
A07	Y	N	N	Y	N	N	N	N	N	N	N	N	N	N	N	Y	N	N	Y	N	N
A08	N	N	Y	Y	N	Y	N	Y	Y	N	N	Y	N	N	N	Y	N	Y	Y	N	N
A09	Y	N	Y	N	N	N	N	Y	N	Y	Y	Y	N	Y	Y	N	N	Y	Y	Y	Y
A10	Y	Y	N	Y	N	Y	N	N	N	N	Y	Y	Y	Y	N	Y	N	N	Y	N	N
A11	Y	Y	N	Y	N	Y	Y	Y	N	Y	Y	Y	N	N	N	N	Y	N	Y	N	N
A12	N	N	N	Y	Y	Y	N	Y	Y	Y	N	N	N	N	N	N	N	N	N	N	Y
A13	N	Y	N	Y	N	N	N	Y	N	N	Y	N	Y	Y	Y	Y	N	N	N	N	N
D01	N	N	Y	N	N	Y	N	N	N	N	N	N	N	N	N	N	N	N	Y	N	N
D02	N	N	N	N	N	N	N	Y	N	N	Y	Y	N	N	N	N	Y	N	N	N	N
D03	N	N	Y	N	Y	N	N	N	Y	N	Y	Y	N	Y	N	N	N	Y	N	Y	Y
D04	Y	N	N	N	N	N	N	Y	N	N	N	N	N	N	Y	Y	Y	N	N	N	Y
D05	N	Y	N	N	N	Y	Y	N	N	N	N	N	N	Y	N	Y	N	Y	N	N	N
D06	N	Y	N	Y	N	Y	Y	N	N	N	Y	N	Y	N	N	N	N	N	N	N	N
D07	Y	N	N	Y	N	Y	N	N	N	N	N	N	N	N	N	N	Y	N	Y	N	N
D08	N	N	Y	Y	N	N	Y	N	N	Y	N	N	Y	N	Y	N	N	N	Y	N	N
D09	N	N	N	Y	N	Y	N	Y	N	N	N	N	Y	N	Y	N	N	N	N	N	N
D10	Y	N	N	N	N	N	Y	N	Y	Y	N	N	Y	N	N	N	N	N	N	N	N
D11	Y	Y	Y	N	N	N	Y	N	N	N	Y	Y	Y	Y	N	N	N	N	N	N	N
D12	Y	Y	Y	N	N	Y	Y	N	N	N	N	N	N	Y	Y	Y	N	N	Y	N	Y
D13	N	Y	N	N	Y	N	Y	N	Y	N	Y	N	Y	Y	Y	N	Y	N	Y	N	Y

[Z]N indicates Upland cotton chromatin

[Y]Y indicates Pima chromatin detected by polymorphic SNPs

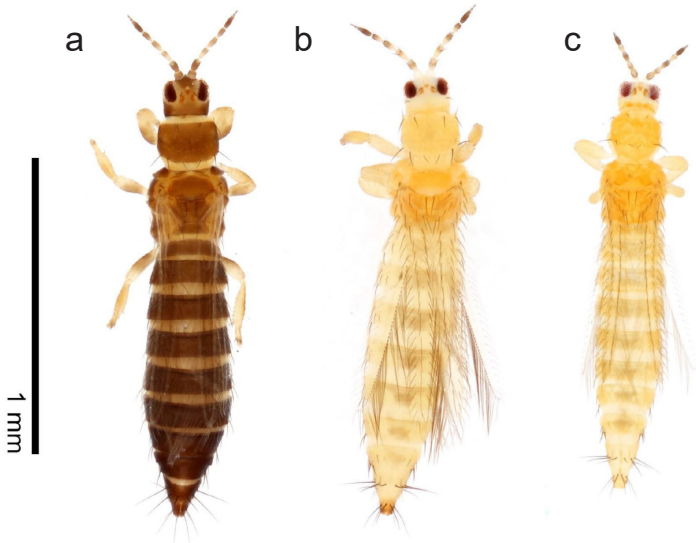

Figure 5. Identification of thrips species in a cotton thrips screening nursery in Rocky Mount, NC in summer 2022. The most predominant thrips species were tobacco thrips (*Frankliniella fusca*) (Figure 5a) followed by western flower thrips (*F. occidentalis*) (Figure 5b), and flower thrips (*F. tritici*) (Figure 5c).

DISCUSSION

Pesticides, specifically, neonicotinoid seed treatments, in-furrow granular or liquid sprays, and foliar sprays (Greene et al., 2020; Studebaker et al., 2010; Wang et al., 2018) are generally used to control thrips in cotton. Heavy reliance on chemical pesticides strategies impose environmental threats and the buildup of resistance to these chemicals in the target insects. Host plant resistance to thrips is the most feasible option of reducing the crop losses due to these pests, as it is an economically viable and ecologically sustainable method of crop management (Stout, 2014; Conzemius et al., 2023). Genetically modified cotton, MON 88702 which is (developed by Bayer Crop Science) commercially trademarked as ThryvOn consisting of *Bacillus thuringiensis* (Bt) toxin Cry51Aa2.834_16 displayed resistance to thrips (Akbar et al., 2019; D'Ambrosio et al., 2020, Graham et al.,2023). Even though ThryvOn cotton demonstrates substantial resistance to thrips, the transference of thrips resistance genes from Pima cotton is crucial for conventional cotton cultivars and serves as a valuable alternative in the event of ThryvOn resistance to thrips breaks down. Therefore, identifying and deploying host plant resistance to thrips would help develop long-term integrated pest management strategies for reducing the losses due to thrips in cotton. Our current research (Figure 4) and other studies found that *F. fusca* was the dominant early season thrips species in cotton fields (Stewart et al., 2013; Reay-Jones et al., 2017; Wang et al., 2018; Conzemius et al., 2023). Studies indicate that *F. fusca* is becoming resistant to neonicotinoid pesticides, the most commonly used insecticide to treat cotton seeds for thrips control (Huseth et al., 2016). Therefore, there is a critical need to develop cotton cultivars with thrips resistance/tolerance to prevent the yield losses to thrips infestation while ensuring economic viability and sustainability of cotton production. This current study is the first report of the introgression of thrips resistance from Pima cotton into Upland cotton.

In this study, we attempted to transfer the thrips resistance from Pima cotton (*G. barbadense*) into Upland cotton (*G. hirsutum*), two species that are cross compatible. However, hybrid breakdown (Stephens, 1949; Stephens, 1950) has been a hindrance to introgress beneficial alleles from Pima cotton into Upland cotton. Selective elimination of alleles, predominantly the *G. barbadense* alleles in the F_2 and later generations, results in segregation distortion (Reinisch et al., 1994: Jiang et al., 2000; Gore et al., 2014), and loss of fitness, hybrid vigor, and fertility (Stephens, 1950: Gore et al., 2014). In spite of these barriers, studies have shown that it is possible to successfully introgress beneficial traits from Pima into Upland cotton. For example, dominant glandless gene (*Gl2e*) responsible for gossypol-free cotton seed (Yuan et al., 2000), verticillium wilt resistance (Wilhelm et al., 1974; Zhang et al., 2011), spider mite resistance (S1) (Zhang et al., 1992), and the bacterial blight resistance gene B_5 (Percy & Kohel, 1999) were introgressed into Upland cotton from Pima cotton. Transfer of pest resistance traits also have been transferred from diploid *Gossypium* species into Upland cotton. For example, the reniform nematode (*Retylenchus reniformis Linford & Oliveira*) resistance locus (Ren^{ari}) was transferred from *G. aridum* (D genome diploid) (Romano et al., 2009), and tolerance to leafhopper from *G. arboreum* (Jindal et al., 2022) into *G. hirsutum*. The above studies involved transfer of major genes, but interspecific introgression of traits controlled by multiple genes or quantitative trait loci (QTLs) are less frequent.

In the current study, we introgressed thrips resistance from Pima cotton to Upland cotton and characterized the ILs with SNP markers. Characterization of ILs with SNP markers showed that introgressed regions were detected on all the chromosomes. The size of introgressed regions varied from one chromosome to another and there was no effect of background cultivar on the Pima cotton introgression size. Although we did not study the inheritance of the thrips resistance in the introgressions, the presence of introgressions on multiple chromosomes suggests that thrips resistance could be due to multiple major genes or minor genes with quantitative inheritance. This was also evident from the previous works that showed thrips resistance in cotton displaying both qualitative (Wann et al., 2017; Zhang et al., 2011) and quantitative inheritance (Abdelraheem et al., 2021).

Marker-defined genomic segments equivalent to more than 100 Kb and 300 Kb in the telomeric and interstitial regions, respectively, were considered as CL320 introgressions in the selected BC_2F_2 ILs. A total of 201 introgressed regions were identified in 11 AM derived BC_2F_2 ILs and 198 in 21 FM966 derived BC_2F_2 ILs. Both interstitial and terminal Pima introgressions occurred in the thrips resistant introgression lines (unpublished results). AM derived BC_2F_2 IL 21-551-1 possessed the highest number (28) of introgressions followed by the IL NC21-641-1 with 27 introgressions and IL NC21-652-2 with 22 introgressions. ILs NC21-581-1 and NC21-661-1 had 20 introgressions each

and NC-630-1 had 19 (unpublished results). Similarly, among the 21 FM966 derived BC_2F_2 ILs, two ILs, NC21-724-1 and NC21-758-1 possessed the highest number (13) of introgressions followed by three ILs NC21-727-8, NC21-772-1 and NC21-826-1 with 12 introgressions and five ILs NC21-6582-1, NC21-686-1, NC21-694-1, NC21-726-2, and NC21-750-2 with 11 introgressions. Two ILs NC21-690-1 and NC21-727-3 had 10 introgressions (unpublished results). Interestingly, from the genotyped introgression lines, the introgressed regions identified on FM966 derived ILs NC21-733-1 and NC21-750-2 on chromosome A09 overlaps with the thrips resistance QTL reported by Abdelraheem et al. (2021). Further, the four ILs NC21-652-2, NC21-661-1, NC21-727-5, and NC21-758-1 carried the identical introgressed regions on chromosome D13 (unpublished results). These BC_2F_2 ILs have also been further backcrossed to the recurrent parents to develop near isogenic lines (NILs) with thrips resistance and to enable their evaluation in multi-location trials for thrips response and agronomic performance. The lines with thrips resistance serve as source of genetic variability for developing germplasm lines and cultivars with pest resistance in cotton.

DISCLAIMER

Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the North Carolina State University and does not imply its approval to the exclusion of other products that may also be suitable.

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