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Watermelon Germplasm with Resistance to Whitefly-transmitted Viruses

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Abstract. **The current management of whiteflies is largely dependent on insecticides. However, pesticides are costly and do not provide effective control of whitefly-transmitted viruses (WTVs). However, breeding for resistant cultivars can provide a more effective and sustainable solution. Twenty-one *Citrullus* genotypes, including 10 *C. lanatus*, four *C. mucosospermus*, six *C. amarus*, and one *C. ecirrhosus*, were evaluated to determine their resistance to three WTVs common in Georgia in field trials for 2 years. Phenotypic data were collected weekly to determine viral disease severity, and the cumulative season data were calculated as the area under the disease progress curve. Leaves were collected 5 weeks after transplanting (WAT) in 2022 and at 7 WAT in 2023 to determine the viral loads of Cucurbit leaf crumple virus (CuLCrV), Cucurbit yellow stunting disorder virus (CYSDV), and Cucurbit chlorotic yellows virus (CCYV) via a quantitative polymerase chain reaction. The CuLCrV and CYSDV viral loads were higher in 2022 than those in 2023, whereas the CCYV load was higher in 2023. Three accessions (PI 494528, PI 595203, and Grif 16444) outperformed the cultivars for viral disease resistance and CuLCrV load (2022). In 2022, there was a significant difference among cultivars regarding the CYSDV load, with 'AU-Producer', 'Crimson Sweet', and 'Estrella' having lower loads than those of 'Charleston Gray' and 'Sugar Baby'. There were no statistical differences in CCYV loads between the best-performing accessions and 'Charleston Gray'. Grif 16444 is a *C. ecirrhosus* accession, and this species has resistance to whiteflies. The two *C. mucosospermus* accessions (PI 494528 and PI 595203) provide a valuable resource for breeders to develop CuLCrV resistance in watermelon (*C. lanatus*) because there is no reproductive barrier between the two species.**

Watermelon (*Citrullus lanatus*) is economically important in many parts of the world, especially in warm climates. The United States produces 1.53 million tonnes of the world's 102 million tonnes, placing it as the seventh largest producer of watermelon (FAOSTAT 2023). The largest watermelon-producing states in the United States are the southeastern states of Florida and Georgia. In 2023, Georgia ranked second after Florida in both production (333,619 t to 466,162 t) and production area (19,900 acres to 24,800 acres) (US Department of Agriculture 2023). Viral diseases transmitted by the sweetpotato whitefly, *Bemisia tabaci* (Gennadius), are important and emerging threats to watermelon production in the region (Adkins et al. 2009). Whiteflies and whitefly-transmitted viruses (WTVs) can severely impact cucurbit production and are estimated to have reduced Georgia squash production by as much as 35% in 2017 (Little et al. 2018). In 2019 and 2020, 76%, 60%, and 43% of cucurbit samples (n = 820) tested in Georgia were infected with Cucurbit leaf crumple virus (CuLCrV), Cucurbit chlorotic yellows virus (CCYV), and Cucurbit yellow stunting disorder virus (CYSDV), respectively (Kavalappara et al. 2021a). Most plants were infected with more than one virus.

The *Begomovirus*, CuLCrV, is a single-stranded bipartite DNA virus within the family *Geminiviridae* (Hagen et al. 2008) and was first observed in the United States in watermelon fields in California in 1998 (Guzman et al. 2000) and Florida in 2009 (Adkins et al. 2009). In 2019, 81% of watermelon samples collected in Colquitt, GA, USA, were infected with CuLCrV (Adeleke et al. 2022). The CuLCrV symptoms on watermelon include crumpling, downward curling, yellowing, stunting, distortion, and mottling, primarily on new leaves (Hagen et al. 2008). CYSDV is an RNA virus that belongs to the genus *Crinivirus* in the family *Closteroviridae* (Aguilar et al. 2003). This virus spread to the United States in 1999, when it was detected in melon in Texas (Kao et al. 2000), followed by the spread to Arizona and California (Kuo et al. 2007). In 2008, CYSDV was detected in Florida (Polston et al. 2008); in 2016, it was detected in cucurbit crops in Georgia (Gadhave et al. 2018). Additionally, CCYV is a *Crinivirus* in the family *Closteroviridae* and is thought to have been introduced into the Imperial Valley of California in 2014 (Wintermantel et al. 2019). In 2020, CCYV was found in squash in Georgia (Kavalappara et al. 2021b) and, soon thereafter, on watermelon in Florida (Jailani et al. 2022). In Fall 2019, 79% of symptomatic watermelon samples collected in Colquitt, GA, USA, were infected with CCYV (Adeleke et al. 2022). Both CCYV and CYSDV have a similar symptom of chlorotic spots; these spots become mottled and interveinal chlorosis on older leaves near the crown of the plant (Celix et al. 1996; Kavalappara et al. 2021b).

Currently, the control of these viruses in cucurbits relies on controlling the whitefly vector. Management practices include combining cultural, chemical, and biological approaches (Horowitz et al. 2011). Controlling the WTVs in this manner is challenging because it only takes one whitefly to spread a WTV (Hurakadli et al. 2016). The most effective control for the viruses is host plant resistance; however, no commercial watermelon cultivars with high levels of resistance to these viruses have been described.

In melon (*Cucumis melo* L.), resistance to both CuLCrV and CYSDV has been identified in PI 313970 (McCreight and Wintermantel 2011; McCreight et al. 2008). A large screen of *Cucurbita* germplasm identified resistance to WTVs in *C. moschata*, *C. ecuadorensis*, and *C. okeechobeensis* (Luckew et al. 2022). Resistance to adult whiteflies has been identified in the perennial watermelon wild relative *C. ecirrhosus* (PI 673135). This resistance was attributable to nonpreference by adult whiteflies, with reduced oviposition and adult emergence and development compared with those of 'Sugar Baby' (Simmons et al. 2019). Two *C. colocynthis* PIs (PI 346082 and PI 537277) also showed resistance to whiteflies during greenhouse experiments (Coffey et al. 2015). Moderate resistance to squash vein yellowing virus (SqVYV), an *Ipomovirus* also transmitted by *B. tabaci*, was found in two *C. colocynthis* PIs (PI 386015 and PI 386024) (Kousik et al. 2009). However, to date, no resistance to the three predominant WTVs in Georgia has been described in cultivated watermelon.

The aim of this study was to evaluate *Citrullus* germplasm, including *C. lanatus*, *C. mucosospermus*, *C. amarus*, and *C. ecirrhosus*, to determine resistance to the predominant WTVs (CuLCrV, CYSDV, and CCYV) in southern Georgia.

Material and Methods

Plant material. A total of 21 genotypes were evaluated (Table 1) and included five *C. lanatus* cultivars, five *C. lanatus* accessions, six wild *C. amarus* accessions, one wild *C. ecirrhosus* accession, and four *C. mucosospermus* accessions. The *C. lanatus* cultivar Charleston Gray, released in 1954, was considered a control in this study because it is a key cultivar in the development of many modern cultivars (Wehner 1999). This cultivar is also the only US watermelon cultivar for which an annotated draft genome sequence is available (Wu et al. 2019). 'Crimson Sweet' was developed from 'Charleston Gray' and was released in 1963 (Cucurbit Genetics Cooperative 2016a; Hall 1963). 'AU-Producer' was released in 1985 and was included in this study because it was developed from a cross between 'Crimson Sweet' and a *C. amarus* accession (PI 189225) (Norton et al. 1986). 'Sugar Baby' was released in 1955 (Cucurbit Genetics Cooperative 2016b) and was included in this study because it has been used as a control in a study of resistance to whiteflies in watermelon (Simmons et al. 2019). Estrella (Syngenta) is a seeded cultivar that represents modern F_1 hybrid cultivars.

The following accessions selected for this study have been described as having virus resistance (Table 1): PI 244019 to Papaya ringspot virus watermelon strain (PRSV-W) (Guner 2004; Strange et al. 2002), Watermelon mosaic virus (WMV) (Gillaspie and Wright 1993), and Zucchini yellow mosaic virus (ZYMV) (Guner et al. 2019); PI 482276 to ZYMV (Guner 2004; Guner et al. 2019); PI482379 to PRSV-W (Strange et al. 2002); PI 482318 to PRSV-W (Strange et al. 2002); PI494528 to Cucumber mosaic virus (Provvidenti 1986), WMV (Guner 2004), and ZYMV (Boyhan et al. 1992; Guner et al. 2019; Provvidenti 1986); and PI 595203 to PRSV-W (Strange et al. 2002), WMV (Xu et al. 2004), and ZYMV (Guner et al. 2019).

Sowing, transplanting, and crop management. All genotypes were evaluated in Tifton, GA, USA, at the University of Georgia, Hort Hill, research farm over two consecutive years, 2022 and 2023; the study had a randomized complete block design with three replications. Each plot consisted of four plants across two rows, with two plants on each side and all having their vines turned to keep plots separated. Each row was a 15-cm raised bed spaced 1.82 m apart, center-to-center, covered with white totally impermeable film plastic mulch (Guardian AgroPlastics, Tampa, FL, USA). In-row spacing was 1.22 m for a plant population of 4485 plants/ha. In both years, drip irrigation was used in the center of each row with emitters at a spacing of 30 cm. Seeds were sown and established in the South Milledge Greenhouses in Athens, GA, USA, on Fafard 3B/Metro-Mix 830 potting soil (Sun Gro, Agawam, MA, USA) in 48-cell seedling trays with daily watering under natural lighting at 27 ± 5 °C. Three-week-old seedlings were transplanted on 15 Aug 2022, and 4-week-old seedlings were transplanted on 17 Aug 2023. Preplant granular 10–10–10 fertilizer was used to supply 22.7 kg/ha of nitrogen. Irrigation was performed twice daily, providing 25.4 mm of water per week, and fertilizer was applied through fertigation for 10 weeks with a liquid 7–0–7 fertilizer to supply the remaining 45.3 kg/ha of nitrogen. To avoid plant death caused by whitefly feeding during high population pressure, plants were sprayed when needed with 700 g/ha Flupyradifurone (Sivanto 200 SL; Bayer CropScience, Research Triangle Park, NC, USA), 560 g/ha Pyriproxyfen (Knack; Valent, Walnut Creek, CA, USA), and 1050 g/ha Cyantraniliprole (Exriel; DuPont, Wilmington, DE, USA). Other insects and pathogens were controlled with weekly sprays using the University of Georgia vegetable fungicide spray program (Dutta 2023).

Germplasm evaluation. In 2022, viral disease was evaluated in the field based on the overall viral symptom severity that was visually assessed. The following scale of 0 to 5 was used for virus severity: 0 = no symptoms; 1 = 1% to 20%; 2 = 21% to 40%; 3 = 41% to 60%; 4 = 61% to 80%; and 5 = 81% to 100% (Luckew et al. 2022). In 2023, leaf yellowing, or general leaf chlorosis, was assessed as an observation separate from the CuLCrV-like symptoms, and this was assessed using the same scale of 0 to 5. Plants were evaluated individually at the presence of first symptoms, 15 d after transplanting (DAT) in 2022; evaluations were continued weekly for a total of five times until 27 Sep 2022. In 2023, CuLCrV-like symptoms (leaf distortion and mottling) were delayed compared with those in 2022; data were not collected until 43 DAT, followed by weekly collection for a total of four times until 19 Oct 2023. In 2023, yellowing was first observed at 21 DAT; data were collected weekly for a total of six times until 19 Oct 2023. When individual plants were not identifiable, each plot was divided into four equal quadrants for data collection using the same scale.

Scores of individual plants and quadrants within a plot were averaged to obtain the per-plot virus symptom severity and yellowing severity. Then, the per-plot severity data were used to calculate the area under the disease progress curve (AUDPC) using the midpoint rule (Madden et al. 2007). The AUDPC was calculated as follows:

$$AUDPC = \sum_{i=2}^{n} [(y_i + y_{i-1})/2](t_i - t_{i-1})$$

with y_i representing the severity score at the i^{th} evaluation, t representing the day of the i^{th} evaluation, and n representing the number of severity evaluations.

Virus quantification. To quantify individual virus loads, the fourth leaf and fifth leaf from the shoot apex of all individual plants were collected at 36 DAT in 2022 and 54 DAT in 2023 in 4-mL cryotubes and placed in liquid nitrogen until storage at −80 °C. If plants were grown into each other, then vines were traced to ensure that samples were collected from each individual plant. Each sample was homogenized to create a uniform plant sample before total nucleic acid (TNA) extraction. The TNA extraction was performed using the Mag-Bind® Plant DNA Plus 96 Kit (Omega Bio-Tek, Norcross, GA, USA) using the manufacturer's protocol but omitting the RNAse step. The resulting TNA was aliquoted into two 96-well plates (Axygen Scientific, Glendale, AZ, USA) for DNA and RNA purification. For DNA purification, 1 µL of RNAse A was added per 10 µL of TNA, heated to 37 °C for 1 h, and then returned to −80 °C for storage. Additionally, RNA purification was performed following the Turbo DNA-free kit (Invitrogen, Carlsbad, CA, USA) manufacturer's recommendations. Both DNA and RNA samples were standardized to 25 ng/µL.

For CuLCrV quantification, 25 ng/µL of total DNA was amplified using the 2X GoTaq quantitative polymerase chain reaction (qPCR) Master Mix (Promega, Madison, WI, USA) in a final reaction volume of 10 µL in a 384-well plate in a Lightcycler 480 (Roche, Basel, Switzerland) using primers and conditions described by Gautam et al. (2020). Every sample had a technical replicate, and primer specificity was evaluated by performing a

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Table 1. Twenty-one *Citrullus* genotypes evaluated for the whitefly transmitted viruses Cucurbit leaf crumple virus (CuLCrV), Cucurbit yellow stunting disorder virus (CYSDV), and Cucurbit chlorotic yellows virus (CCYV) in Tifton, GA, USA, during Fall 2022 and 2023.

Cultivar/PI	Species	Seed source	Improvement status	Previously reported virus resistance	Reference
PI 189225	*C. amarus*	US NPGS, Griffin, GA, USA	Wild		
PI 244019	*C. amarus*	US NPGS	Wild	PRSV-W, WMV, ZYMV	Gillaspie and Wright al. (1993); Guner (2004); Guner et al. (2019); Strange et al. (2002)
PI 296341	*C. amarus*	US NPGS	Wild		
PI 379243	*C. amarus*	US NPGS	Wild		
PI 482276	*C. amarus*	US NPGS	Wild	ZYMV	Guner (2004); Guner et al. (2019)
PI 482379	*C. amarus*	US NPGS	Wild	PRSV-W	Strange et al. (2002)
Grif 16444	*C. ecirrhosus*	US NPGS	Wild		
AU-Producer	*C. lanatus*	Hollar Seeds, Rocky Ford, CO, USA	Cultivar		
Charleston Gray	*C. lanatus*	Eden Brothers Arden, NC, USA	Cultivar		
Crimson Sweet	*C. lanatus*	Johnny's Selected Seeds, Winslow, ME, USA	Cultivar		
Estrella	*C. lanatus*	Seedway Hall, NY, USA	Cultivar		
PI 169233	*C. lanatus*	US NPGS	Unknown		
PI 271778	*C. lanatus*	US NPGS	Unknown		
PI 482318	*C. lanatus*	US NPGS	Cultivated	PRSV-W	Strange et al. (2002)
PI 526233	*C. lanatus*	US NPGS	Landrace		
PI 549160	*C. lanatus*	US NPGS	Wild		
Sugar Baby	*C. lanatus*	Reimer Seeds, Saint Leonard, MD, USA	Cultivar		
PI 490377	*C. mucosospermus*	US NPGS	Cultivated		
PI 494528	*C. mucosospermus*	US NPGS	Unknown	CMV, WMV, ZYMV	Boyhan et al. (1992); Guner (2004); Guner et al. (2019); Provvidenti (1986)
PI 560023	*C. mucosospermus*	US NPGS	Wild		
PI 595203	*C. mucosospermus*	US NPGS	Breeding material	PRSV-W, WMV, ZYMV	Guner et al. (2019); Strange et al. (2002); Xu et al. (2004)

CMV = Cucumber mosaic virus; PRSV-W = Papaya ringspot virus watermelon strain; WMV = Watermelon mosaic virus; ZYMV = Zucchini yellow mosaic virus.

melting curve analysis. The CuLCrV viral load in unknown samples was determined by creating a standard curve using a 10 ng/µL CuLCrV plasmid and performing serial dilution to 0.0001 ng/µL.

For CYSDV and CCYV quantification, 25 ng/µL of total RNA was used to create cDNA using the protocol of the manufacturer of the GoScript Reverse-Transcription System (Promega, Madison, WI, USA). The qPCR was performed using a final reaction volume of 10 µL with iTaq Universal Probes Supermix (Bio-Rad, Hercules, CA, USA) on a 384-well plate in a Lightcycler 480 (Roche) following the multiplex reaction protocol previously described by Mondal et al. (2023). As described, the Melon ADP gene was used to determine the relative concentration of CYSDV and CCYV using the ΔCt method. Samples with a cycle threshold less than 35 cycles were considered positive.

Statistical analysis. Initially, viral load data were analyzed for both years; however, because of a significant ($P \leq 0.05$) year effect (data not shown) and the different symptom evaluation methods used during the two years, the final analyses were performed separately for the two years. Analyses were performed using a one-way analysis of variance of the viral symptoms AUDPC (2022 only), CuLCrV-like symptom AUDPC (2023 only), yellowing AUDPC (2023 only), CuLCrV viral load, CYSDV relative concentration, and CCYV relative concentration with genotypes as fixed effects and replications as random effects. Spearman rank correlations using genotypic averages for each evaluation metric were calculated separately for both years. The statistical significance threshold was $P \leq 0.05$. The R version 4.4.1 (R Core Team 2024) statistics program within RStudio (Posit team 2024) was used for all analyses.

Results

Symptom severity evaluation. During field trials conducted during two years in Tifton, GA, USA, the typical symptoms of CuLCrV, including crumpling and downward curling, rolling of leaves, mottling, distortion, mosaic, and stunting were observed, as well as symptoms of CYSDV and CCYV, including chlorotic spots developing into interveinal chlorosis beginning on the leaves closest to the crown of the plant.

Differences among genotypes for disease severity were observed and measured as overall virus symptoms (2022), CuLCrV-like (2023), and yellowing (2023). In 2022, there was no difference in disease severity between Charleston Gray and the other cultivars, but that of Crimson Sweet and Sugar Baby was significantly lower ($P < 0.05$) than that of AU-Producer and Estrella (Fig. 1A). In 2023, when CuLCrV-like symptoms and yellowing were scored separately, 'AU-Producer', 'Crimson Sweet', and 'Sugar Baby' displayed significantly fewer ($P < 0.05$) CuLCrV-like symptoms compared with those of 'Charleston Gray' (Fig. 1B). For yellowing (2023), only 'Estrella' performed similar to 'Charleston Gray', with 'Sugar Baby', 'AU-Producer', and 'Crimson Sweet' performing worse ($P < 0.05$) than "Charleston Gray' (Fig. 1C). Two C. *mucosospermus* accessions (PI 494528 and PI 595203) and the *C. ecirrhosus* accession (Grif 16444) had significantly lower ($P < 0.05$) disease symptoms during all three visual observations compared to those of all the watermelon cultivars (Fig. 1A–C). PI 494528 particularly stood out because of its visual qualities, with lush green leaves that did not show any virus symptoms, even at the end of the growing season (Fig. 2).

Virus quantification. There was a statistically significant ($P < 0.05$) year effect (data not shown) for the CuLCrV load, with higher viral loads identified in 2022 (Fig. 3A) compared with those in 2023 (Fig. 3B). In 2022 (Fig. 3A), the five *C. lanatus* cultivars had CuLCrV loads that allowed them to be ranked in the middle of the 21 genotypes tested, with no statistical differences ($P > 0.05$) from those of 'Charleston Gray'. Significant differences were detected in 2023; the CuLCrV load was low and no genotypes performed better than 'Charleston Gray' (Fig. 3B). In 2022, the three *C. mucosospermus* accessions (PI 494528, PI 560023, and PI 595203) and the *C. ecirrhosus* accession (Grif 16444) had the lowest CuLCrV loads.

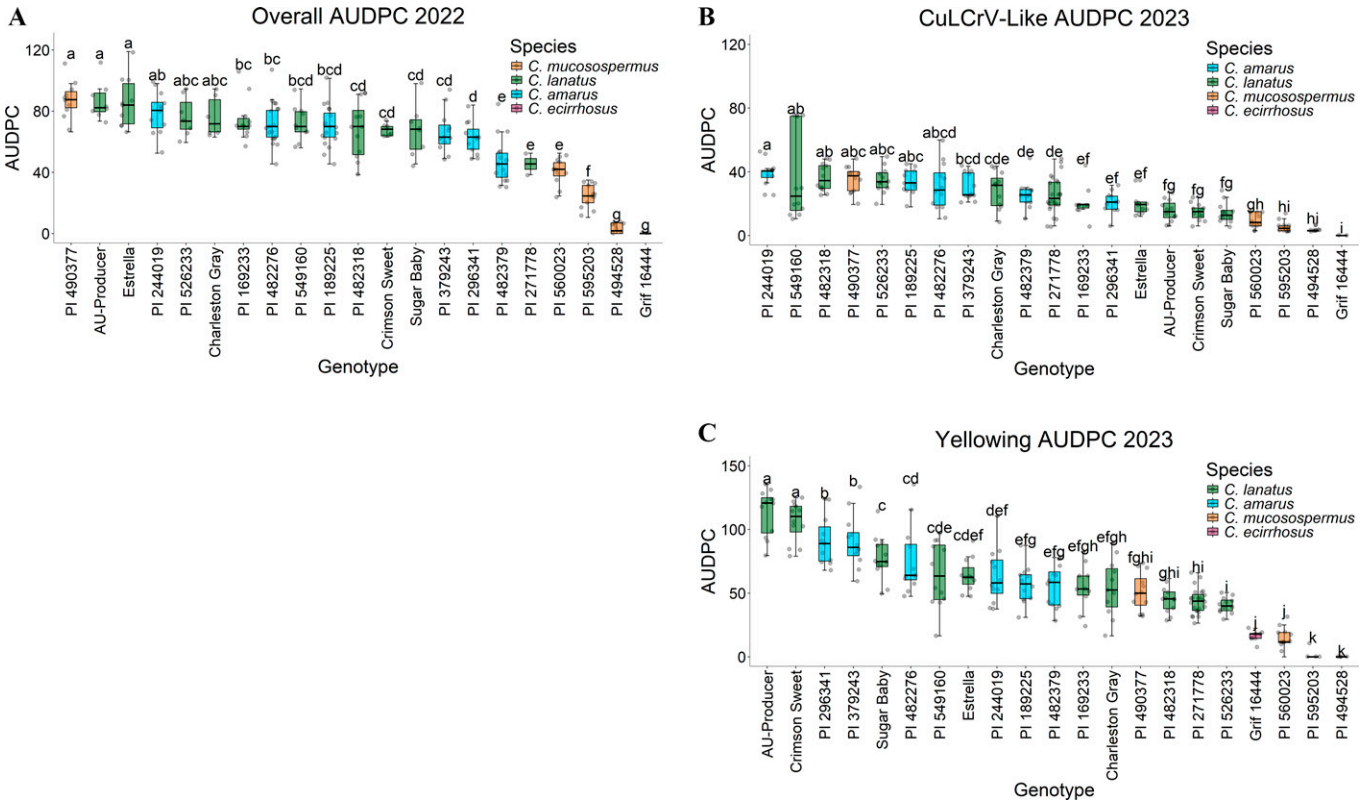

Fig. 1. Area under the disease progress curve (AUDPC) values calculated for 21 *Citrullus* genotypes from (**A**) five weekly observations of overall viral symptoms in 2022, (**B**) four weekly observations of CuLCrV-like symptoms in 2023, and (**C**) six weekly observations of leaf yellowing in 2023.

Similar to CuLCrV, a significant year effect ($P < 0.05$) was found for CYSDV loads, with higher viral loads in 2022 (Fig. 4A) than those in 2023 (Fig. 4B). Significant differences ($P < 0.05$) among the 21 genotypes for the CYSDV load were detected in 2022 (Fig. 4A), but not in 2023 (Fig. 4B). Three cultivars, AU-Producer, Estrella, and Crimson Sweet, had a significantly ($P < 0.05$) lower viral load compared with that of Charleston Gray (Fig. 4A). Although the genotypes with the lowest CYSDV load detected were Grif 16444 (*C. ecirrhosus*) and PI 244019 (*C. amarus*), they were not significantly different ($P > 0.05$) from the best-performing cultivars.

The CCYV loads also had a year-to-year effect, with lower viral loads ($P < 0.05$) in 2022 (Fig. 5A) compared with those in 2023 (Fig. 5B). There were no significant differences among the cultivars and the best-performing accessions for CCYV loads in 2022 (Fig. 5A). In 2023, 'Crimson Sweet' and 'Estrella' were not significantly different ($P < 0.05$) from 'Charleston Gray', whereas 'Sugar Baby' and 'AU-Producer' had significantly higher ($P < 0.05$) CCYV loads (Fig. 5B). Although the lowest average CCYV loads were detected in Grif 16444 (*C. ecirrhosus*), PI 494528 (*C. mucosospermus*), and PI 482276 (*C. amarus*), they were not significantly different ($P > 0.05$) from the cultivar control in 2022. In 2023, PI 482276 had the lowest CCYV load, but the differences among the best-performing accessions and 'Charleston Gray' were not statistically significant.

Correlations. Correlations between the AUDPCs and viral loads for 2022 and 2023 were analyzed separately. In 2022, the overall viral disease AUDPC was not correlated with the viral loads of CuLCrV, CCYV, or CYSDV (Table 2). The CCYV load in 2022 was significantly ($P < 0.05$) correlated with that of CuLCrV ($R = 0.4935$) and CYSDV ($R = 0.6610$) (Table 2). In 2023, the CuLCrV-like symptom AUDPC showed a significant

Fig. 2. Lush green leaves of (**A**) PI 494528 and (**B**) the leaves of cultivar Charleston Gray (*C. lanatus*) containing CuLCrV-like symptoms, distortion, and mottling of the leaf and yellowing symptoms in Tifton, GA, USA, in 2022.

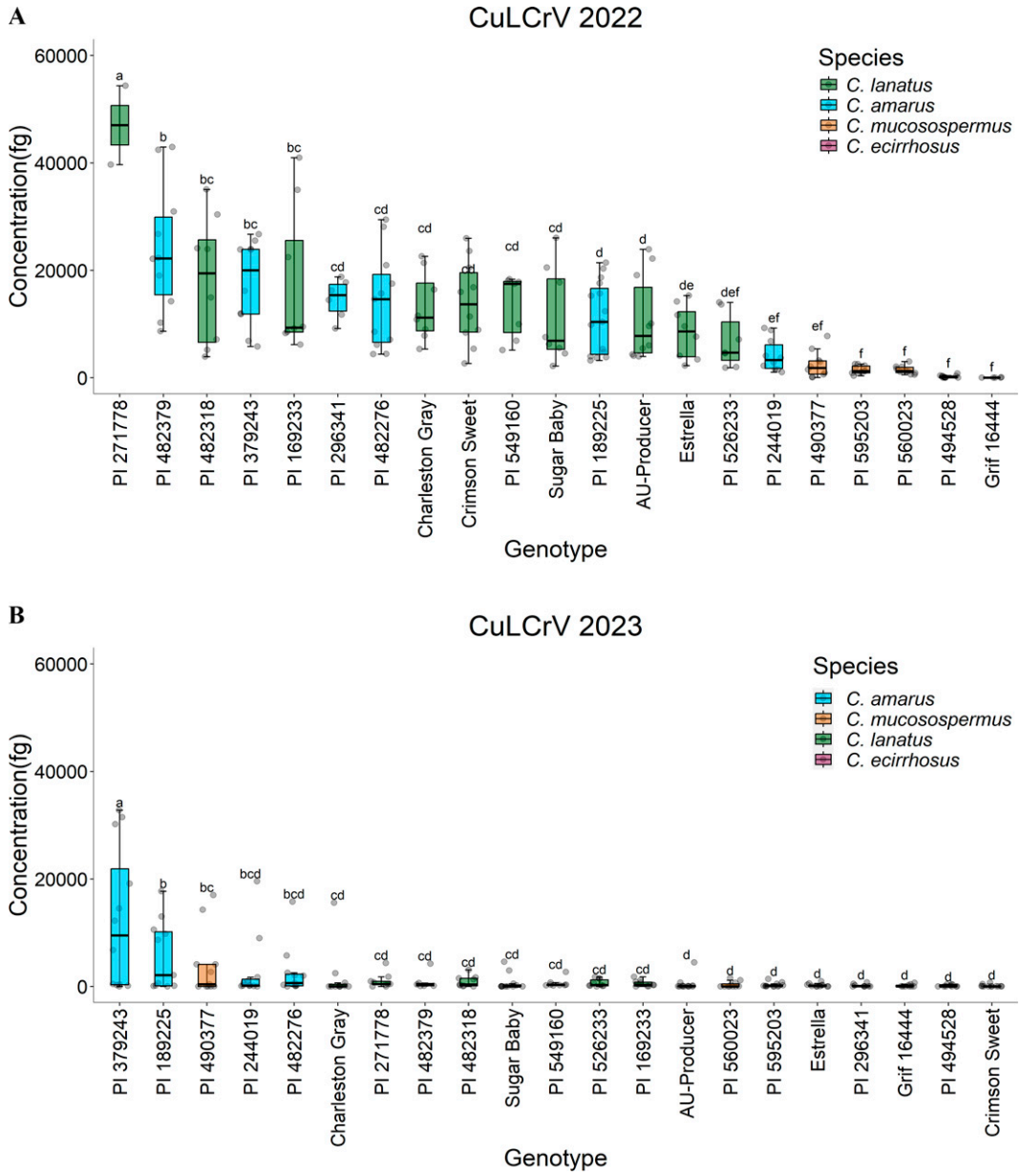

Fig. 3. Cucurbit leaf crumple virus (CuLCrV) load determined using a plasmid of known DNA concentrations in 21 *Citrullus* genotypes evaluated in Tifton, GA, USA, measured in the fourth leaf and fifth leaf from the shoot apex (**A**) 36 d after transplanting (DAT) in 2022 and (**B**) 54 DAT in 2023.

($P < 0.05$) correlation with CuLCrV load ($R = 0.6481$) and a significant negative correlation with CCYV ($R = -0.4571$) (Table 3). In 2023, the yellowing AUDPC was not significantly correlated with viral load (Table 3).

Discussion

Important WTVs that infect cucurbit crops, causing yield and quality losses, are CuLCrV, CYSDV, and CCYV (Keinath et al. 2018; López-Sesé and Gómez-Guillamón 2000; Peng and Huang 2011). Currently, control efforts are focused on reducing whitefly pressure using chemicals and cultural strategies such as row covers, host-free periods, removing infected plants, and reflective mulches (Rojas et al. 2018). Genetic host resistance is one of the most effective strategies for controlling plant viruses (Anikina et al. 2023).

Differences were observed among 21 *Citrullus* genotypes that belong to *C. lanatus*, *C. mucosospermus*, *C. amarus*, and *C. ecirrhosus* because of their phenotypic response to CuLCrV, CYSDV, and CCYV under field conditions in Tifton, GA, USA, during Fall 2022 and Fall 2023. Two *C. mucosospermus* accessions, PI 494528 and PI 595203, and one *C. ecirrhosus* accession, Grif 16444, had the lowest overall virus severity symptoms in 2022, CuLCrV-like symptoms in 2023, and CuLCrV load in 2022. These three genotypes also had the lowest leaf yellowing symptoms in 2023. However, they did not differ from the cultivar controls in terms of the CYSDV or CCYV load in either year.

Visual phenotyping was modified in 2023 after observing a lack of correlation between the AUDPC and viral loads in 2022. Scoring CuLCrV-like and yellowing as two distinct scores resulted in improved correlations between CuLCrV-like visual scores and CuLCrV loads determined by the qPCR. However, there was no significant correlation between yellowing symptoms and the CYSDV or CCYV load. Yellowing of older leaves can have many different biotic and abiotic causes, including senescence. Our data suggest that visual scoring of yellowing symptoms is not a reliable measure of viral loads for these two yellowing viruses and possibly indicate that testing at different times and leaves would be better. Our results underscore the usefulness of virus load quantification when assessing host resistance.

Economic losses caused by the whitefly comprise hundreds of millions of dollars in the United States (Li et al. 2021). For watermelon, yields were reduced by as much as 56% in Brazil, and the cost of controlling the whitefly pest was calculated at $157.74/ha

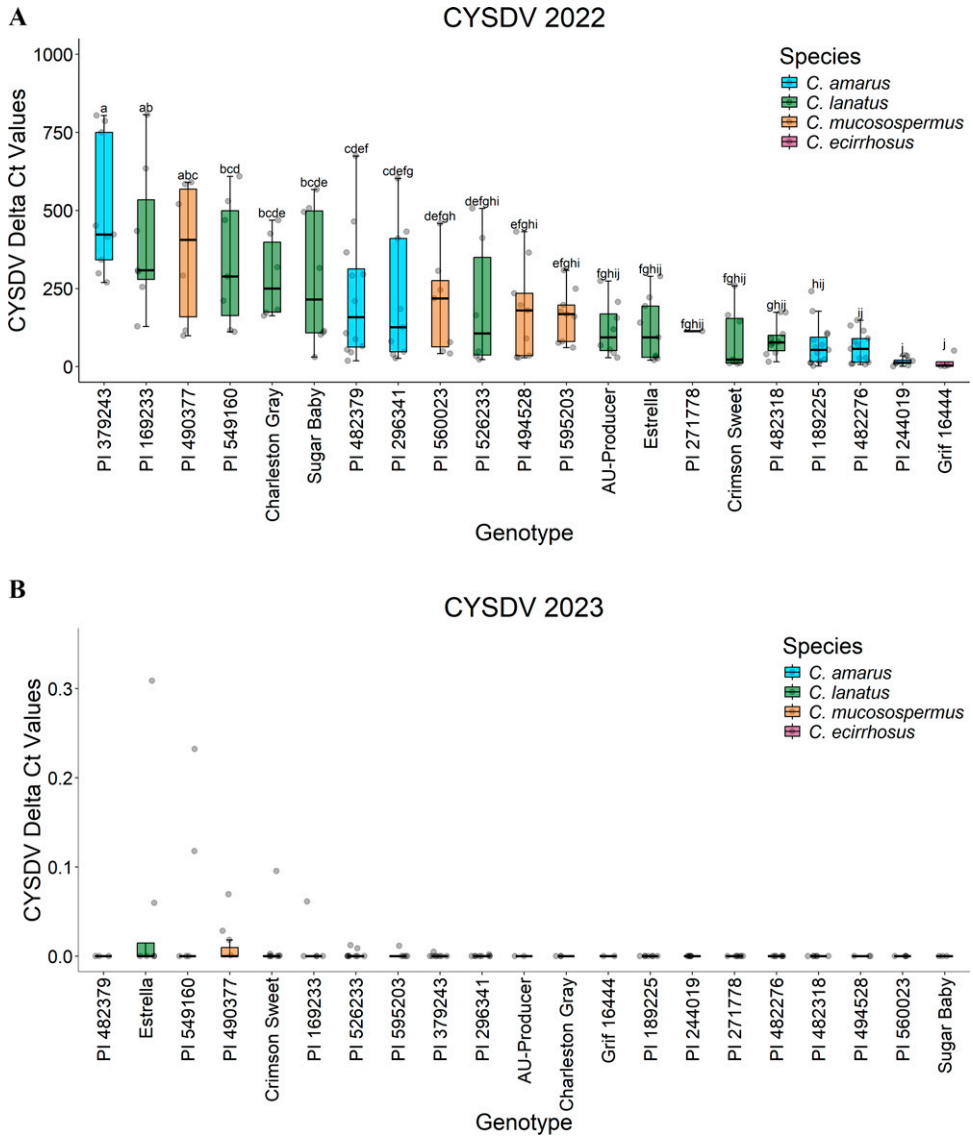

Fig. 4. Cucurbit yellow stunting disorder virus (CYSDV) relative concentrations of 21 *Citrullus* genotypes evaluated in Tifton, GA, USA, measured in the fourth leaf and fifth leaf from the shoot apex (**A**) 36 d after transplanting (DAT) in 2022 and (**B**) 54 DAT in 2023.

(de O Lima et al. 2019). The reduced virus symptoms and viral loads of the *C. ecirrhosus* genotype, Grif 16444, was likely associated with the previously reported nonpreference of this species by whiteflies (Simmons et al. 2019). The latter study was performed using *C. ecirrhosus* accession PI 673135, but it is likely that the same mechanism may exist for Grif 16444. Further studies are required to determine whether Grif 16444 has any virus resistance in addition to the nonpreference of *C. ecirrhosus.* The nonpreference of *C. ecirrhosus* would allow farmers to reduce these control costs. However, *C. ecirrhosus* is a perennial species, which might result in some challenges to introgressing resistance quickly into *C. lanatus*.

Noticeably, *C. mucosospermus* PI 494528 exhibited very few visible virus symptoms during this study. In 2022, it also had some of the lowest CuLCrV loads. It is interesting to note that all four *C. mucosospermus* genotypes had high levels of resistance to CuLCrV. Several of the genotypes used in this study have documented resistance to potyviruses (Table 1). It is possible that potyvirus symptoms contributed to the visual symptom scores because PRSV-W was detected using a PCR for a subset of samples in both years (data not shown). Notably, PI 494528 and PI 595203, which both have resistance to multiple potyviruses, had few visual symptoms. However, PI 244019 also has resistance to several potyviruses, but it had high disease severity symptoms. Therefore, it seems unlikely that potyvirus resistance alone was responsible for the differences in visual symptoms. Nevertheless, it further highlights the need for virus diagnostics and quantification when performing field evaluations in areas where multiple viruses are likely present. This resistance identified in *C. mucosospermus* provides a potentially more efficient pathway than that of *C. ecirrhosus* for introgressing resistance into *C. lanatus*. *C. mucosospermus* is an annual species that is closely related to *C. lanatus*, with no reproductive barrier between the species and very little segregation distortion (Sandlin et al. 2012).

Because PI 494528, PI 595203, and PI 244019 have potyvirus resistance and some of the lowest viral loads, it is possible that either the same gene or genes are involved in resistance, or there is some type of virus–virus interaction that leads to lower loads of some viruses. During a large screen of *Cucurbita*, the *Potyvirus*-resistant *C. moschata* 'Nigerian local' (Brown et al. 2003) was also identified as one of the most resistant lines against these same WTVs (Luckew et al. 2022). *Potyvirus* resistance in PI 595203 and PI 244019 is associated with the eukaryotic translation initiation factor 4E (elF4E) (Branham et al. 2020; Ling et al. 2009). PI 595203 and PI 244019 have different alleles for the elF4E gene, with mutations changing the 71st amino acid from aspartic acid to glycine and the 81st amino acid from threonine to proline in the gene region associated with binding the virus cap protein (Zhou et al. 2024). Additionally, elF4E can provide resistance to

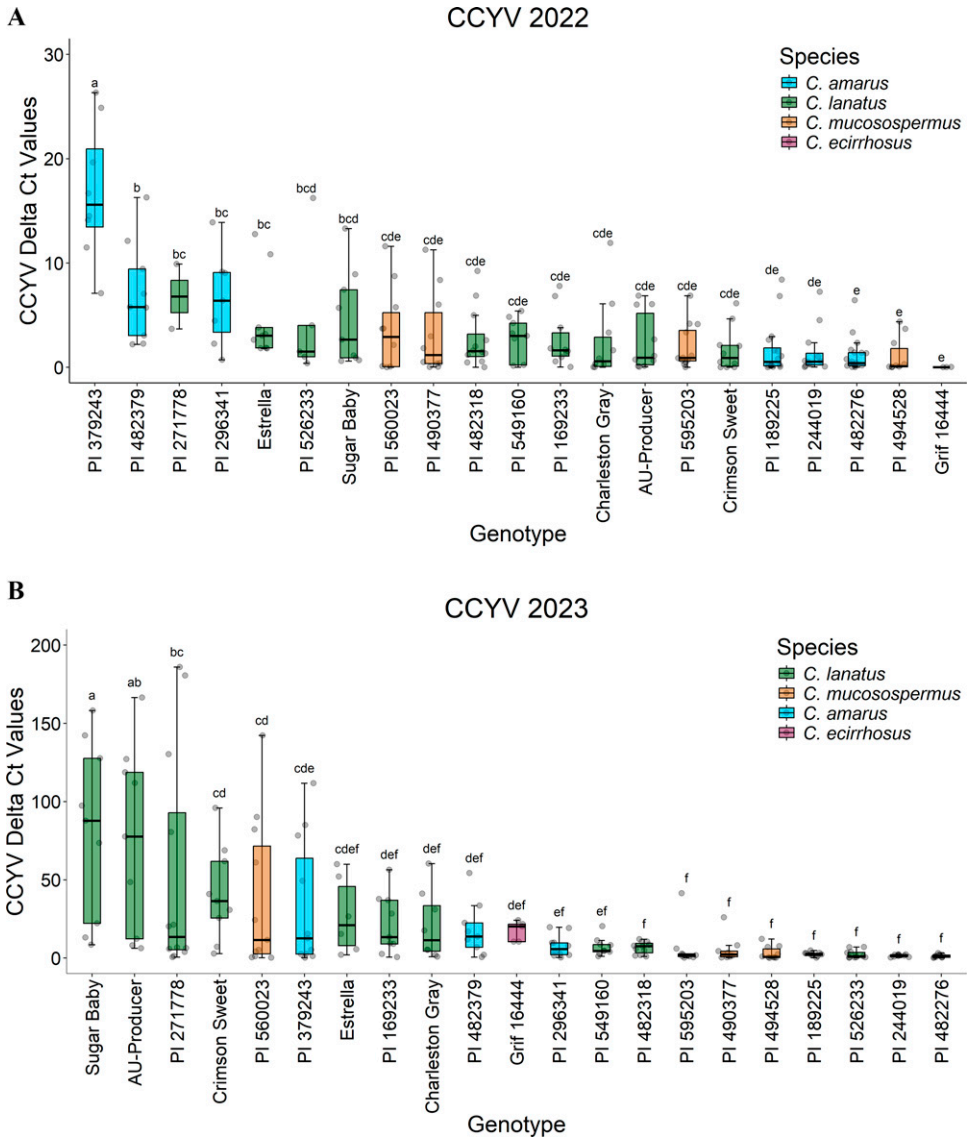

Fig. 5. Cucurbit chlorotic yellows virus (CCYV) relative concentrations of 21 *Citrullus* genotypes evaluated in Tifton, GA, USA, measured in the fourth leaf and fifth leaf from the shoot apex (**A**) 36 d after transplanting (DAT) in 2022 and (**B**) 54 DAT in 2023.

other (+) sense RNA viruses (Sanfaçon 2015), and both CYSDV and CCYV are (+) sense RNA *Crinivirus* (Aguilar et al. 2003). Further research should be conducted to identify whether eIF4e is associated with resistance of any of the WTVs in these accessions.

This experiment was conducted during the fall over the course of two years, when whitefly populations are highest in southern Georgia. It has previously been shown in the southeastern United States that cucurbit plants are infected with multiple viruses during the growing season (Adeleke et al. 2022; Kavalappara et al. 2021a; Luckew et al. 2022). In *Cucurbita pepo* infected with *Potyviruses*, a movement-impaired Cucumber mosaic virus regained movement function when ZYMV coinfected the same plant, allowing for a more severe Cucumber mosaic virus infection (Choi et al. 2002). In melon, a WMV and CYSDV mixed infection resulted in higher CYSDV loads than those associated with single infection, but no change in the WMV load (Domingo-Calap et al. 2020). With a mixed infection of CuLCrV and CYSDV in squash, the viral load of CYSDV was reduced compared to that with a single infection, but no effect on CuLCrV loads was observed (Gautam et al. 2020). In cucumber, a CCYV and CYSDV mixed infection led to lower viral loads of each when compared with those of single infections; however, transmission efficiency by whiteflies increased with both viruses when acquired from plants with mixed infections (Orfanidou et al. 2021). Lower viral loads may have been attributable to the mixed infection. Therefore, controlled single-virus greenhouse studies are necessary to confirm the resistance identified in this study.

Table 2. Spearman rank correlation rho by genotype (n = 21) for each disease evaluation metric in Tifton, GA, USA, during Fall 2022.

	Spearman correlation			
Evaluation metric	AUDPC	CuLCrV load	CYSDV load	CCYV load
AUDPC	1			
CuLCrV load	0.0364	1		
CYSDV load	0.1675	0.2506	1	
CCYV load	−0.0545	0.4935*	0.6610**	1

Significant at ***$P \leq 0.001$, **$P \leq 0.01$, and *$P \leq 0.05$.

Conclusion

In the southeastern United States, WTVs are a growing problem. This problem is expected to become worse in the coming years because whitefly pressure is likely to increase with a shift to warmer climates in the region

Table 3. Spearman rank correlation rho by *Citrullus* genotype (n = 21) for each disease evaluation metric in Tifton, GA, USA, during Fall 2023.

	Spearman correlation				
Evaluation metric	CuLCrV-like AUDPC	Yellowing AUDPC	CuLCrV load	CYSDV load	CCYV load
CuLCrV-like AUDPC	1				
Yellowing AUDPC	0.1914	1			
CuLCrV load	0.6481**	−0.0429	1		
CYSDV load	0.0332	−0.1104	0.1979	1	
CCYV load	−0.4571*	0.3013	−0.3766	−0.1546	1

Significant at ***$P \leq 0.001$, **$P \leq 0.01$, and *$P \leq 0.05$.

(Devendran et al. 2023). Current whitefly control focuses on expensive insecticide sprays that cost farmers $157/ha or approximately 4% of the production value of watermelon (de O Lima et al. 2019), and they do not guarantee the prevention of WTVs because it only takes a single whitefly to enable transmission (Hurakadli et al. 2018). Host resistance has been proven to be the most effective at controlling plant viruses (Anikina et al. 2023); however, no commercial watermelon cultivars that are resistant to or tolerant of the WTVs, CuLCrV, CYSDV and CCYV have been reported (Devendran et al. 2023).

This study performed in an area where the whitefly population was relatively high identified three cultivars, AU-Producer, Estrella, and Crimson Sweet, with a lower CYSDV load than that of Charleston Gray. Three accessions were identified as sources of resistance to CuLCrV. The *C. ecirrhosus* accession, Griff 16444, is resistant to whiteflies. The *C. mucosospermus* accessions, PI 494528 and PI 595203, provide breeders with a manageable pathway for introgressing this resistance into elite cultivars because of their lack of reproductive barriers.

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