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NC-GSB-524W, NC-GSB-527W, NC-GSB-528W, NC-GSB-530W, NC-GSB-531W, and NC-GSB-532W Watermelon Lines with Gummy Stem Blight Resistance and Good Fruit Quality

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Gummy stem blight (GSB) is a major disease of watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] that leads to significant economic losses. This disease is caused by three genetically distinct *Stagonosporopsis* species, *S. cucurbitacearum* (syn. *Didymella bryoniae*), *S. citrulli*, and *S. caricae* (Stewart et al., 2015). The three species are pathogenic to cucurbits, but *S. caricae* also causes leaf spot, stem rot, and fruit rot in papaya (*Carica papaya* L.) (Stewart et al., 2015). GSB was first observed in 1891 by Fautrey and Roumeguere in France on cucumber (*Cucumis sativus* L.) and in Delaware on watermelon (Sherf and MacNab, 1986). In 1917, GSB was reported in the southern United States, affecting watermelon fruit in Florida (Sherbakoff, 1917). GSB remains an important limiting factor for watermelon production in Florida (Keinath, 1995) and South Carolina (Rennberger et al., 2018, 2019). This disease also affects watermelon production in some important watermelon producing countries (Basim et al., 2016; Huang and Lai, 2019). GSB on watermelon plants is evident as crown blight, stem cankers, and extensive defoliation, with symptoms observed on the cotyledons, hypocotyls, leaves, and fruit (Maynard and Hopkins, 1999). *Stagonosporopsis cucurbitacearum* is seed-borne (Lee et al., 1984), airborne (van Steekelenburg, 1983), and soilborne (Bruton, 1998).

There are seven species of *Citrullus: C. lanatus* (Thunb.) Matsum. & Nakai is the dessert watermelon. It is closely related to egusi watermelon [*C. mucosospermus* (Fursa) Fursa]. Slightly less related is citron (*C. amarus* Schrad). Other related species include *C. ecirrhosus* Cogn. (the tendril-less melon), *C. rehmii* De Winter, *C. colocynthis* (L.) Schrad., and *C. naudinianus* (Chomicki and Renner 2015; Levi et al., 2017). All are cross-compatible to varying degrees. Crosses of citron and dessert watermelon may result in progeny having preferential segregation, and reduced pollen fertility (Levi et al., 2003). That makes it difficult, although not impossible, to obtain new (nonparental) combinations in plant breeding programs. In previous studies, plant introduction (PI) 189225 was identified as the most resistant accession in the USDA-ARS watermelon germplasm collection (Sowell and Pointer, 1962). Later, PI 271778, PI 500335, PI 505590, PI 512373, PI 164247 and PI 500334 were also identified as GSB resistant (Boylan et al., 1994). When resistant PI 189225 was crossed with susceptible 'Charleston Gray', a single recessive gene (*db*) was identified controlling the resistance (Norton, 1979). To develop resistant cultivars with yield and quality, PI 189225 and PI 271778 were chosen as resistant parents in crosses with 'Crimson Sweet' and 'Jubilee'. Cultivars having good fruit quality

Generation	Breeding approach	Description
I_0	PI 482342 × PI 482283 PI 482342 × PI 189225 PI 189225 × PI 482342 PI 482374 × PI 189225 PI 526233 × PI 482283 PI 526233 × PI 189225	Crosses of the most resistant plant introductions
I_1 I_2 I_3 I_4	Four cycles of intercrossing	Intercrossing without selection
I_4F_0	I_4 × Charleston Gray Calhoun Gray Mickylee Minilee Allsweet Crimson Sweet Petite Sweet	Crossing with susceptible elite lines of excellent fruit quality
$I_4F_1I_1$ $I_4F_1I_2$ $I_4F_1I_3$ $I_4F_1I_4$	Four cycles of intercrossing	Intercrossing without selection, while maintaining wild and elite types in the population
$I_4F_1I_4S_1$ $I_4F_1I_4S_2$ $I_4F_1I_4S_3$ $I_4F_1I_4S_4$ $I_4F_1I_4S_5$ $I_4F_1I_4S_6$ $I_4F_1I_4S_7$	Seven cycles of self-pollination	Self-pollination of plants at random to develop RILs

Fig. 1. Pedigree for watermelon breeding lines NC-GSB-524W, NC-GSB-527W, NC-GSB-528W, NC-GSB-530W, NC-GSB-531W, and NC-GSB-532W.

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and moderate resistance to GSB were released as 'AU-Jubilant' and 'AU-Producer' (Norton et al., 1986), 'AU-Golden Producer' (Norton et al., 1993), and 'AU-Sweet Scarlet' (Norton et al., 1995). However, they were less resistant to GSB than the resistant parents, PI 189225 and PI 271778. In cucumber, it was reported that there were about five genes controlling resistance, and that genetic factors were weaker than environmental factors (St. Amand and Wehner, 2001). Watermelon accessions PI 189225, PI 482283, and PI 526233 having GSB resistance were crossed with susceptible cultivars, and segregating progeny generations had a continuous distribution for resistance, with partial failure of the data to fit the hypothesis of single-gene inheritance. Thus, resistance to GSB in PI 189225, PI 482283, and PI 526233 may be controlled by a more complex genetic system (Gusmini et al., 2017).

Variation in fungicide effectiveness to GSB in watermelon has been reported (Li and Brewer, 2016), thus increasing the importance of developing resistant cultivars. Also, an efficient screening method has been developed for identifying resistant germplasm (Song et al., 2004), including a system for mass production of inoculum of *S. cucurbitacearum* for large field screening experiments (Gusmini et al., 2003). The available PI accessions (1274 accessions) from the USDA-ARS watermelon germplasm collection, along with 51 cultivars, were tested to identify new sources of resistance to GSB (Gusmini et al., 2005). A total of 59 accessions were identified that were at least as good as PI 189225 and PI 271778 in field and greenhouse tests. Two of the most resistant were PI 482283 (*Citrullus amarus*) and PI 526233 (*Citrullus lanatus*).

Resistance to pathogens can be qualitative or quantitative. However, quantitative resistance requires more time and resources to use, as inheritance is complex and the levels of resistance often are less distinct. Since our efforts to transfer resistance to an elite background were not successful in previous work, we decided to change our approach. Resistant accessions were intercrossed multiple times, and then progenies were crossed to adapted cultivars. Following that, we intercrossed progeny from resistant × elite crosses four times. In that way, we hoped to improve our chances of transferring resistance genes from *Citrullus amarus* to *C. lanatus*.

Fig. 2. NC-GSB-524W fruit.

We used the rating method for GSB resistance of Gusmini et al. (2002) as follows: 0 = no disease; 1 = yellowing on leaves (a trace of disease only); 2 to 4 = symptoms on leaves only; 5 = some leaves dead, no symptoms on stem; 6 to 8 = symptoms on leaves and stems; and 9 = plant dead. The scale was used for screening accessions from the watermelon germplasm collection for resistance (Gusmini et al., 2005), as well as for genetic analysis of large numbers of plants tested in multiple environments (Gusmini et al., 2017; Rivera-Burgos et al., 2021).

In addition to GSB resistance, we were interested in retaining as much fruit quality (exterior and interior traits) as possible (Haejeen et al., 2010). Some traits are used only for morphological characterization (descriptors) of watermelon (Szamosi et al., 2009). Usually, fewer traits are evaluated in breeding programs. Fruit shape is an important characteristic to meet the various market requirements. Fruit shape can be elongate, round, or oval, controlled by the *o* gene (Wehner, 2008). Similarly, rind pattern and toughness are important characteristics of watermelon fruit. Rind patterns can be gray, striped, or solid, and rind stripes can be narrow, medium, or wide (Gusmini and Wehner, 2006). Rind toughness is important to reduce losses in shipping. Ideally, the rind should be thick and tough for large-fruited cultivars, and thin and tough for small-fruited cultivars. In general, the thickness should be a small percentage of flesh diameter for maximum edible volume. Rind toughness can be measured by driving a spring-loaded punch into the rind, dropping the fruit onto the ground from knee height to see whether it breaks, or by pressing on the rind (Wehner, 2008).

Table 1. Field performance of watermelon breeding RILs and cultivars.

Cultigen name	Fruit yield (kg/ha)	Cull (%)	Fruit size (kg/fruit)	Soluble solids (°Brix)	Flesh color (1–9)	Overall quality (1–9)	Rind tough (1–9)	GSB damage (0–9)
GSB resistant RILs								
NC-GSB-524W	158.8	0	6.8	11.5	6.5	6.5	8.0	4
NC-GSB-527W	172.8	0	5.2	11.2	7.0	7.0	7.0	4
NC-GSB-528W	65.8	0	6.5	9.2	4.0	6.0	5.5	4
NC-GSB-530W	102.1	0	4.3	11.3	6.5	6.0	8.0	4
NC-GSB-531W	181.9	5	7.2	10.7	5.0	4.5	8.0	4
NC-GSB-532W	134.3	0	5.9	12.0	5.5	5.0	4.0	4
Check cultivars								
Sugar Baby	127.0	0	3.5	10.7	8.0	8.0	8.0	7
Tendersweet OF	110.2	0	8.5	11.0	4.0	4.0	7.0	8
Allsweet	109.3	8	8.9	10.3	5.0	6.0	8.0	7
Royal Flush F1	174.6	10	6.9	10.5	7.0	6.5	7.5	8
LSD (5%)	92	4	0.7	1.8	1.7	1.8	1.9	1

Data are means of 2 years (2017 and 2018), two locations (Clinton and Goldsboro), two replications, and two harvests.
Soluble solids measured in °Brix; color, overall, toughness rated 1 to 9 (1–3 = poor, 4–6 = medium, 7–9 = excellent); GSB resistance rated 0 to 9 (0 = no damage, 1–3 = slight, 4–6 = medium, 7–9 = severe).

Flesh color can be scarlet red ($Y^{Scr}Y^{Scr}$), coral red ($Y^{Crl}Y^{Crl}$), orange (y^oy^o), salmon yellow (*yy*) or other colors such as canary yellow (*CC*) or white (Zhang et al., 2017). Canary yellow (*CC*) is epistatic to the *y* locus. Coral red is hypostatic to the white flesh color that is common in citron. Additionally, seed color and seed are important traits for the market. Seed color can be white, tan, brown, black, red, or green (and the pattern can be rimmed, tipped, clump, or dotted). Seed size can be tomato, short (small), medium size, or long (large). In many programs, black seed color is thought to be most attractive when associated with red flesh color (Wehner, 2008).

Material and Methods

Plant material. NC-GSB-524W, NC-GSB-527W, NC-GSB-528W, NC-GSB-530W, NC-GSB-531W, and NC-GSB-532W are inbred lines of watermelon that are resistant to GSB, and have good fruit quality. The elite lines were developed as follows: three *Citrullus amarus* accessions, PI 189225 (Democratic Republic of the Congo), PI 482283 (Zimbabwe) and PI 482342 (Zimbabwe), and two *Citrullus lantus* accessions PI 482374 (Zimbabwe) and PI 526233 (Zimbabwe) were chosen for high resistance to GSB. Six crosses were made among these resistant accessions and their progeny intercrossed for 4 generations. The cycle 4 progeny (I_4) were then crossed with seven *Citrullus lanatus* subsp. *lanatus* cultivars that were chosen for high fruit yield, quality and earliness: 'Allsweet', 'Calhoun Gray', 'Charleston Gray', 'Crimson Sweet', 'Mickylee', 'Minilee', and 'Petite Sweet'. Finally, the progeny (I_4F_1) were intercrossed four generations ($I_4F_1I_4$) and then self-pollinated for seven generations ($I_4F_1I_4S_7$) (Fig. 1).

Planting and management. Yield trials were conducted in the field at the Horticultural Crops Research Station at Clinton and Goldsboro, NC, during the summer of 2017 and 2018. Seeds were sown on raised, shaped beds on 3.1 m centers in single hills, 1.2 m apart covered with black plastic mulch. Irrigation, along with fertilizer were provided using drip irrigation. The fields were culturally managed in accordance with North Carolina recommendations (Kemble et al., 2020).

Inoculum preparation. The isolate of *S. cucurbitacearum* was originally obtained from diseased cucumber tissues harvested from naturally infected plants in the field in 1998. In the fall of 2001, we reisolated *S. cucurbitacearum* from watermelon plants that were artificially inoculated with the isolate and developed a new stock of inoculum from single spores. Pycnidia were identified with a dissecting microscope (20×) and transferred to petri plates containing potato dextrose agar (PDA; 25 mL/petri plate). Isolates were selected from the first subculture on PDA based on macroscopic observations: colonies dark in color and showing concentric circles of growth were kept and transferred to fresh PDA. Uncontaminated cultures were transferred to a medium containing 25% PDA to stimulate abundant sporulation. We observed pycnidia/pseudothecia and spores to verify that their shape and size matched those of *S. cucurbitacearum* as published (Zitter and Thomas, 1996). Additionally, we isolated genomic DNA of the GSB isolates, and a polymerase chain reaction-based marker test was run to genetically identify *S. cucurbitacearum* that causes GSB in cucurbit crops (Brewer et al., 2015; Rivera-Burgos et al., 2021).

For long-term storage (Sinclair and Dhingra, 1995), we transferred the fungus onto sterile filter paper (Whatman #2, 70 mm diameter), subcultured the fungus for 2 to 4 weeks, dehydrated the filter paper disk and the mycelium for 12 to 16 h at room temperature (24 ± 3 °C) in a sterile laminar-flow hood, cut the filter paper into squares (5 × 5 mm), and stored them in sterile test tubes in a refrigerator (3 ± 1 °C) in the dark. Liquid cultures were grown in 1 L flasks containing 500 mL of 25% potato dextrose broth (PDB) and two to three plugs of PDA cultures of *S. cucurbitacearum*. The flasks containing liquid culture were incubated in a shaker at 180 RPM for 8 to 10 d at 24 ± 2 °C under alternating periods of 12 h of fluorescent light (40–90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD) and 12 h of darkness. For all inoculations, we filtered the liquid from each flask through four layers of sterile cheesecloth to remove dislodged agar and some mycelia. Spore concentration was measured with a hemacytometer and adjusted to a concentration of 5 × 105 spores/mL by adding deionized water. Tween 20 (0.06 $g \cdot L^{-1}$) was added to the inoculum to keep the spores well dispersed in the inoculum solution (Song et al., 2004).

Inoculation. We inoculated plants when they reached the fourth-true-leaf stage (4 weeks after sowing), after overhead irrigation of about 12 mm of water during the two previous days to promote guttation on the day of inoculation, and damaging the trichomes on the leaf surface before inoculum application by brushing the plants with a wooden stake (20 × 200 mm) mounted on an aluminum handle 600 mm long (Lou et al., 2013; Song et al., 2004). Plants were inoculated at least two times at 2-week intervals by spraying the inoculum onto all upper leaf surfaces. We delivered the inoculum as a fine mist using a backpack-sprayer operated at a pressure of 200 to 275 kPa (30–40 psi). In the late afternoon of the day of inoculation, we irrigated with ≈12 mm of water to promote disease development with high relative humidity at night.

Data collection. Plants were rated 1 week after inoculation in the greenhouse, and when the symptoms appeared on the leaves and stems of the susceptible checks in the field (1 week after the second inoculation). Plants were rated for disease severity at 7 (R-1), 14 (R-2), 21 (R-3), and 28 (R-4) days after inoculation (DAI). From these four ratings, average GSB damage was estimated in both years and locations. An ordinal disease assessment scale was used (Gusmini et al., 2002), with 0 = no disease; 1 = yellowing on leaves (a trace of disease only); 2 to 4 = symptoms on leaves only; 5 = some leaves dead, no symptoms on stem; 6 to 8 = symptoms on leaves and stems; and 9 = plant dead. Plants with a disease rating of 6 or greater had lesions on the stem, thus being prone to death from subsequent development of the disease. Plants with a disease rating of 5 or less had lesions only on the leaves. Leaf ratings are important because plant survival and yield are affected by leaf area, which is reduced in susceptible plants. Stem ratings are important because large, localized lesions can kill the plant, especially if they are near the shoot apex.

Fig. 3. NC-GSB-527W fruit.

Data collected were fruit shape, rind pattern, rind toughness, seed size, seed color, flesh color, flesh color intensity, overall fruit quality, and hollow heart damage, as described by Wehner (2008). Fruit shape was classified as elongate, oval, and round. Rind pattern was gray, narrow striped, medium-wide striped, wide striped, or solid dark. Rind toughness was tender = 1, intermediate = 5, or tough = 9. Seed size was classified as tomato = 2, small = 4, medium = 6, or large = 8. Seed color was classified as white = 2, tan = 4, brown = 6 or black = 8. Flesh color was classified as red, orange, salmon, canary, or white. Color intensity was classified as faded and irregular = 1 to dark and uniform = 9. The overall quality was classified as poor = 1 to excellent = 9. Finally, the hollow heart was classified as 0 = none to 9 = severe (Wehner, 2008).

Statistical analysis. A randomized complete block design with 2 years, 2 locations, and 2 replications. The watermelon lines were considered fixed, and years and locations were considered random effects in the model. Analysis of variance (ANOVA) was performed using the PROC MIXED procedure from the SAS 9.3 statistical package. Restricted maximum likelihood (REML) with and without the GROUP statement and the TYPE III test of fixed effect methods were used for a preliminary analysis of the disease severity assessment. The best method was selected based on Bayesian and Akaike's information criterion (BIC and AIC), which measure the goodness of fit for each. Therefore, the methodology that showed the lowest BIC and AIC was chosen as the best, because it gives the correct balance between the fit to the data and model complexity. In our study, the TYPE III test of fixed effect was the best method to determine differences in means of RILs. Adjusted means for GSB damage and yield were obtained using LSMeans from SAS.

Fig. 4. NC-GSB-528W fruit.

Results

NC-GSB-524W, NC-GSB-527W, NC-GSB-528W, NC-GSB-530W, NC-GSB-531W, and NC-GSB-532W are inbred lines of watermelon that are resistant to GSB, and have good fruit quality from the North Carolina State University cucurbit breeding program in Raleigh, NC. The lines were selected from the GSB watermelon breeding population for their fruit quality and GSB resistance across years (Rivera-Burgos et al., 2021).

NC-GSB-524W (NC-524), previous number 18GH-031 (RIL-039), is a monoecious watermelon with GSB resistance (4 on a 0–9 scale), elongate fruit shape, wide-stripe pattern, tough rind, coral red flesh, sweetness of 11°Brix, medium-size black seeds, high quality (8 on a 1–9 scale), hollow heart resistance, with fruit similar to 'Allsweet' and adaptation to the southern United States (Fig. 2; Table 1).

NC-GSB-527W (NC-527), previous number 18GH-221 (RIL-267), is a monoecious watermelon with GSB resistance (4 on a 0–9 scale), round fruit shape, solid light-green rind pattern, tough rind, coral red flesh, sweetness of 10°Brix, medium-size black seeds, high quality (8 on a 1–9 scale), hollow heart resistance, fruit similar to 'King & Queen' and adaptation to the southern United States (Fig. 3; Table 1).

NC-GSB-528W (NC-528), previous number 18GH-222 (RIL-268), is a monoecious watermelon with GSB resistance (4 on a 0–9 scale), round fruit shape, solid light-green rind pattern, tough rind, coral red flesh, sweetness of 11°Brix, medium-size black seeds, high quality (8 on a 1–9 scale), hollow heart resistance, fruit similar to 'King & Queen' and adaptation to the southern United States (Fig. 4; Table 1).

NC-GSB-530W (NC-530), previous number 18GH-049 (RIL-066), is a monoecious watermelon with GSB resistance (4 on a 0–9 scale), round fruit shape, solid light-green rind pattern, tough rind, coral red flesh, sweetness of 9°Brix, small black seeds, high quality (8 on a 1–9 scale), hollow heart resistance, fruit similar to 'King & Queen' and adaptation to the southern United States (Fig. 5; Table 1).

NC-GSB-531W (NC-531), previous number 18GH-099 (RIL-125), is a monoecious

Fig. 5. NC-GSB-530W fruit.

Fig. 6. NC-GSB-531W fruit.

watermelon with GSB resistance (4 on a 0–9 scale), oval fruit shape, medium-wide stripe pattern, tough rind, scarlet red flesh, sweetness of 11°Brix, large black seeds, high quality (8 on a 1–9 scale), hollow heart resistance, fruit similar to 'Crimson Sweet' and adaptation to the southern United States (Fig. 6; Table 1).

NC-GSB-532W (NC-532), previous number 17GH-154 (RIL-131), is a monoecious watermelon with GSB resistance (4 on a 0–9 scale), round fruit shape, solid light-green rind pattern, tough rind, coral red flesh, sweetness of 12°Brix, large black seeds, high quality (8 on a 1–9 scale), hollow heart resistance, fruit similar to 'King & Queen' and adaptation to the southern United States (Table 1).

Availability

Small amounts of seeds of NC-GSB-524W, NC-GSB-527W, NC-GSB-528W, NC-GSB-530W, NC-GSB-531W, and NC-GSB-532W are available for distribution to interested researchers and plant breeders who make writen request to Dr. Todd Wehner at the Department of Horticultural Science at North Carolina State University, Raleigh, NC 27695-7609 (tcwehner@gmail.com). It is requested that appropriate recognition of the source be given when this germplasm contributes to research or development of a new breeding line or cultivar.

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