AGROBACTERIUM BRONZING AND WILT: CULTIVAR REACTIONS AND EFFECTS OF TEMPERATURE

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Abstract

Sixteen cultivars of cotton were inoculated with a mixture of three *Agrobacterium* biovar 1 strains and grown with complete nutrition in controlled environment chambers at constant temperatures of 24, 27, 30, 33, and 36 °C. After six weeks, leaf, stem, shoot, root, and whole-plant weights and *Agrobacterium* concentrations in roots were determined. Bacterial concentrations per gram of whole plant tissue increased progressively as temperatures were increased, with a major increase occurring between 30 and 33 °C. Concentrations of *Agrobacterium* at 33 and 36 °C were two- to ten-fold higher than at 27 and 30 °C in each of the sixteen cultivars. Maximum cotton growth occurred at 30 °C, and a major decrease in growth occurred between 33 and 36 °C. Certain cultivars developed bronze wilt symptoms at 36 °C and symptom severity was correlated with reduction of growth. The coefficient of variability for root or shoot weight among cultivars was much greater at 36 °C than at 33 °C or lower temperatures. These observations indicated that root, shoot, or plant weight of *Agrobacterium*-inoculated plants after six weeks of growth at 36 °C can be used as a quantitative measure of bronze wilt susceptibility in cultivars. This screen was applied to 120 cultivars and breeding lines, and the results are presented.

Introduction

In 1995, 1996, and 1998, several short-season cultivars grown in short-season production systems were severely affected by a disease referred to variously as "sudden wilt," "copper top," "red top," "bronzing," "early fade out," or "pseudomonas wilt" depending on locality. The name "bronze wilt" has now been adopted by most scientists, producers, and farm consultants for this disease. The symptoms and epidemiology of the disease have been reported in detail (Bell 1998a, 1999).

The only microorganism that can be found consistently in roots of symptomatic plants is *Agrobacterium* biovar 1 (Bell et al. 1997; Bell 1997). Even though all isolates from cotton have very similar chromosome characteristics, they would be variously named *Agrobacterium radiobacter, A. tumefaciens,* and *A. rhizogenes* according to current rules of nomenclature, because they vary considerably in plasmid content (Cui et al. 1997). *Agrobacterium* biovar 1 apparently is an endophyte in cotton, because it can be isolated from nearly all seed of all cultivars and is distributed throughout the plant. In aerial parts, it generally occurs in much lower numbers (less than 1/1000 of the concentrations in roots) and often is latent. For these reasons, Koch's postulates can not be used to prove its causal relationship in bronze wilt. Even if the bacteria were purged from cotton plants, the plants would not necessarily grow better since endophytes often have beneficial as well as detrimental effects.

Correlations between bacterial concentration and bronze wilt symptom severity or yield loss offer alternative approaches to determining the involvement of *Agrobacterium* in bronze wilt. In previous studies, *Agrobacterium* concentrations in roots correlated with symptom severity and yield decline when bronzing and wilt symptoms were increased by increasing clay content of soils, increasing nitrogen content of fertilizers, or causing variable phosphorus deficiencies during boll development (Bell 1998b; Bell et al. 1998; Bell 1999). In the present study, relationships between temperature stress, bronze wilt symptoms, and *Agrobacterium* concentrations were determined.

Materials and Methods

Plants were grown in 16 oz white Solo cups containing 450 g of a soil prepared by mixing a fine sand mined from the Brazos River Valley with a clay soil from the Texas A&M Plantation (3:1). The soil was amended with 10 and 20 g of gypsum and dolomitic limestone, respectively, per 1 kg soil to insure adequate Ca, Mg, and S nutrition. Both soil components were passed through a 5-mm screen before blending. This mix contained about 15% clay (pH 8.0 – 8.5) and has consistently given *Agrobacterium* populations of 5-10 million per gram of root at 24-30 °C. Plants were fertilized weekly with 50 ml of a solution of 3 g of Peter's 15-16-17 soluble fertilizer containing chelated minor elements in 1 liter of water purified by reverse osmosis (RO). The Solo cups were drilled to provide three 6-mm drainage holes, which were covered with a vinyl-coated fiberglass screen cloth before the soil was added. The soil in cups was pasteurized with aerated steam (160 °F) for 6-8 hours immediately before planting.

Strains 1A, 14A and 34B of *Agrobacterium* biovar I were kept in sterile distilled water at 2 °C. Strains 1A and 14A are natural ketolactose-deficient mutants; 34B has a characterized Ti plasmid that induces tumors on cotton roots. Strain 1A also has a unique fatty acid profile. These markers allow the strains to be traced in biological experiments. Bacteria were spread on potato dextrose agar medium containing 0.8 g calcium carbonate (powder) light (Mallinckrodt U.S.P. Food Grade, LOT 4052 KPTY). The bacteria from 24-hr-old cultures were harvested by adding sterile water and agitating with a glass-spreading rod.

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Suspensions were stirred and adjusted to an absorbance of ca. 0.5 at 600 nm with sterile water.

Seed of the cultivars or lines were obtained from the various commercial companies or breeders that have developed them. When possible, they were subsamples from the seed provided for the uniform variety trials. Cottonseed were washed for about 5 min in 70% acetone and then thoroughly with tap water before placing in germination towels. The germination towels were wet with the bacterial suspension. Seeds were then placed on towels which were rolled and incubated for 24 hours at 30 °C in closed containers. The 24-hr-old seedlings were selected for uniformity and then two were transplanted into each cup. Five replications per cultivar per treatment were used.

After 2 weeks, one seedling was removed to determine shoot weight. After six weeks the remaining plants were severed at the cotylendonary node, leaves (including petioles) were removed, and fresh weights of leaves and stems were determined. The root ball was carefully removed and submerged in tap water where most of the soil was washed away. The root was then placed in a tea strainer and washed thoroughly under running tap water. Roots were blotted with absorbent towels and allowed to air-dry for ca. 20 min. before the fresh weights of the root and hypocotyl were determined. The whole root or a 5-g sample was then placed in a dry plastic bag over cracked ice until roots were analyzed for bacterial content (always within four hours).

The bacterial concentrations were determined from roots ground and diluted in sterile water. The root was placed in sterile water (19 ml/gm root) and homogenized with a 20-mm standard saw teeth polytron generator for 30 – 60 seconds until a uniform homogenate was obtained. Three sequential 1/10 dilutions were normally prepared from the homogenate and four drops (1/6 ml) of the final dilution (1/20,000) was spread on modified D-1 medium (15.0 g mannitol; 5.0 g $NaNO_3$; 6.0 g LiCl; 0.002 g $Ca(NO_3)_2 \cdot 4H_20$; 1.7 g K_2HPO_4; 0.3 g KH_2PO_4; 0.36 g $MgSO_4; \cdot 7H_20$; 0.1 g bromothymol blue; 15 g agar; 1 liter water --- sterilized 20 minutes at 15 p.s.i.). The D-1 plates were generally allowed to dry for 3 days before they were used. The inoculated plates were incubated for 72 hours at 28 °C before the colonies were counted. *Agrobacterium* biovar 1 appeared as butyrous, blue-gray, convex colonies and was easily distinguishable from other bacteria.

Results and Discussion

The mean effects of temperature on plant growth and *Agrobacterium* concentration in roots are shown in Table 1. High temperatures (33 and 36 °C) gave highly significant increases in the *Agrobacterium* concentrations in roots in all cultivars. The lowest concentrations of the bacterium occurred at 24 °C, and a small, but significant, increase in concentrations occurred when temperature was raised from 24 to 27 °C. Because *Agrobacterium* occurs predominately in the root (more than 99%) and the root/shoot ratio also increases significantly with elevated temperatures, the influence of the bacteria on the plant is best predicted by calculating the number of bacteria per gram of whole plant. This value increases progressively with increases in temperature and is greatest at 36 °C (Table 1).

Bronze wilt symptoms occurred only in certain cultivars and only at 36 °C. All of the cultivars that were severely inhibited in growth at 36 °C also showed extensive necrosis of the root system, especially at points where secondary roots emerged. In addition, the plants were stunted and leaves of many cultivars were smaller, bronzed, or yellowed, and often curled with epinasty. In line with the stunting, stem weight was reduced more than leaf weight, root weight, or hypocotyl weight. However, less variability occurred with shoot, root, or whole plant weight than stem weight, indicating that these are the more reliable quantitative measurements of damage caused by *Agrobacterium* and heat stress.

At two weeks after planting, there were no symptoms or significant reduction of shoot weight in the susceptible cultivars compared to the resistant cultivars at 36 °C. There also was no selective reduction of weight at 33 °C at six weeks (Table 3). Thus, heat alone apparently is not the cause of bronze wilt symptoms or the selective plant damage. During the first two weeks, *Agrobacterium* concentrations per gram of total plant are relatively low, which may explain the absence of bronze wilt symptoms and selective damage. Bronze wilt symptoms induced by *Agrobacterium* and high clay content of soil, excess nitrogen, or phosphorus deficiency also, are not expressed until plants are two to three weeks old (Bell 1998b, 1999), probably for the same reasons. Disease resistance reactions involving condensed tannins are also poorly developed in seedlings and could limit consequences of a hypersensitive response (Hunter 1978).

The coefficients of variability among cultivars for plant growth parameters and bacterial concentrations are shown in Table 3. The greatest variability among cultivars occurred in root growth or shoot growth at 36 °C, and occurred in association with differential expression of bronze wilt symptoms. This indicates that root, shoot, or whole plant weight at 36 °C are the best quantitative measures of damage caused by *Agrobacterium* and heat stress. This conclusion is supported by the fact that highly significant increases in growth parameters of several cultivars over those of Stoneville 373 and Paymaster 1220 BG/RR cultivars could be shown at 36 °C (Table 4). In contrast, at 33 °C, none of the cultivars had significant differences in whole plant weight (Table 2). Thus, there is a very sharp break between 33 and 36°C where susceptibility to *Agrobacterium* bronzing and wilt is induced by heat stress. Since all cultivars showed

significant reduction of growth at 36 ¤C, it may be that the bacterium itself undergoes a critical change at these temperatures to cause it to become more toxic to the plant. The dark brown lesions and general discoloration of roots without softening of tissues (root size relative to shoot size actually increased), may indicate that the plants are responding hypersensitively to the bacteria at 36 ¤C but not at lower temperatures. In this case, the cultivars that are most damaged may also be the ones showing the greatest resistance response to the bacteria. If this is the case, genes used for resistance to bacterial blight, Fusarium wilt, or Verticillium wilt might also be causing susceptibility to bronze wilt by causing the plant to express hypersensitive resistance to a normally congenial endophytic bacterium.

A total of 120 cultivars and breeding lines were inoculated with *Agrobacterium* and incubated at 36 ¤C for six weeks before measuring growth characteristics. The results of these tests are shown in Tables 5 and 6. In general, the results agree very well with field observations. Stoneville 132 and 373, Paymaster 1220, Fibermax 989, and *Gossypium barbadense* cultivars, such as Seabrook Sea Island 12B, have consistently been among the most susceptible cultivars to bronze wilt in the field and also had the least plant growth in the *Agrobacterium*–36 ¤C screen. Only five plants were examined in this study. As many as 40 plants need to be examined to determine the extent of variability in cultivars.

Tamcot SP 37 is a common parent in the breeding background of Stoneville 132 and 139, Hartz 1215 and 1220, and Paymaster 1220 BG/RR, and has been suggested as a source of the gene(s) for susceptibility to bronze wilt. In the *Agrobacterium*–36 ¤C screen, however, Tamcot SP 37 was significantly more resistant than Stoneville 373. Other Tamcot cultivars from the early releases of the MAR program were as susceptible as Stoneville 373 but are not in its parental background.

Since Seabrook Sea Island 12B2 (SBSI) also is highly susceptible, it too might be the source of susceptibility, especially if hypersensitivity is involved. This cultivar is in the background of nearly every cotton grown today, since it was first used as a source of genes for resistance to Fusarium wilt and later was used as a source of genes for resistance to Verticillium wilt (Wilhelm 1981). The genes in SBSI cause a hypersensitive response to both Fusarium wilt and Verticillium wilt pathogens, which leads to early intense synthesis of terpenoid antibiotics and condensed tannins (Bell 1995). The tannins when oxidized give rise to the dark brown pigments typically found in cotton tissues in association with disease (Bell et al. 1992). Thus, it might be that genes conserved for resistance to wilt diseases also cause vulnerability to *Agrobacterium* by promoting hypersensitive reactions under certain conditions of stress or unusually high bacterial populations. Hopefully, the screen reported here can be used to describe the genetics of bronze wilt susceptibility as well as evaluate cultivars for potential susceptibility to bronze wilt in the field.

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Table 1. Mean effects of temperature on characters of 16 cotton cultivars.

	Temperature °C				
Character	24	27	30	33	36
Shoot Wt. (gm)	27.0	29.8	37.7*	33.1*	9.9*
Root Wt. (gm)	7.3	6.8	12.5*	11.5	5.5
S/R Ratio	4.0	4.6	3.1*	2.9	1.9*
Bacteria Concn. (M/gm root)	7.7	9.8*	10.7	26.5*	24.1
Bacteria Concn. (M/gm plant)	1.5	1.8	2.6*	6.8*	8.3

*Significantly different from the next lower temperature (t-test, 5% confidence).

Table 2. Whole plant weight (g) at six weeks after inoculation with *Agrobacterium* and incubation at 33 °C or 36 °C.

	Incubation temperature	
Cultivar	33 °C	36 °C
Stoneville 373	41.7 (6.4) [a]	4.5 (0.7)
Paymaster 1220 BG/RR	43.4 (4.1)	5.7 (2.3)
Paymaster 1244 BG/RR	48.4 (4.8)	8.4 (4.9)
Deltapine 20	48.7 (3.7)	11.2 (5.3)
Stoneville 132	40.8 (4.5)	13.2 (6.5)
Paymaster 1215 BG/RR	44.3 (5.6)	13.2 (4.1)*
Acala Maxxa	49.6 (0.8)	13.4 (5.4)*
Deltapine 5409	42.3 (6.7)	14.9 (4.3)*
Paymaster 1560	40.9 (7.4)	14.9 (5.0)*
Stoneville 474	47.3 (2.5)	15.4 (2.4)**
Deltapine 50	44.6 (6.4)	15.9 (3.0)**
PR-80	45.8 (7.2)	20.9 (5.8)**
Tamcot Sphinx	47.1 (6.8)	20.9 (2.1)**
NuCotn 33B	47.7 (3.3)	23.1 (3.2)**
Stoneville LA887	36.2(1.4)	23.2 (6.6)**
Sure-Grow 125	45.2 (2.8)	27.6 (5.1)**

[a] – Standard deviation in parentheses; n=5 for each cultivar

*,** - Greater than either Stoneville 373 and Paymaster 1220 BG/RR at 36 °C at the 5% and 1% level of confidence, respectively. No significant differences occurred at 33 °C.

Table 3. Coefficients of variability among 16 cotton cultivars at different temperatures.

	Temperature °C				
Character	24	27	30	33	36
Shoot Wt. (S)	16	13	5	7	41
Root Wt. (R)	33	27	21	15	47
S/R Ratio	25	23	19	14	21
Bacteria Concn. (M/gm root)	32	27	34	23	26

Table 4. Root and shoot weight at six weeks after inoculation with *Agrobacterium* and incubation at 36 °C.

Cultivar	Root Wt. (g)	Shoot Wt. (g)
Stoneville 373	1.4 (0.3)[a]	3.1 (0.5)
Paymaster 1220 BG/RR	1.6 (0.7)	4.1 (1.7)
Paymaster 1244 BG/RR	2.7 (1.9)	5.7 (3.0)
Deltapine 20	3.7 (2.0)	7.5 (3.5)
Acala Maxxa	4.2 (1.5)*	9.2 (4.1)
Stoneville 132	5.3 (1.5)*	7.9 (3.9)
Deltapine 5409	5.4 (1.7)*	9.5 (2.6)*
Deltapine 50	5.5 (1.5)*	10.5 (2.2)**
Paymaster 1215 BG/RR	5.8 (2.3)*	7.5 (1.8)
Stoneville 474	6.0 (1.2)**	9.4 (1.3)**
Tamcot Sphinx	6.1 (1.0)**	14.8 (1.3)**
Paymaster 1560	6.2 (2.2)*	8.7 (3.0)
PR – 80	6.4 (3.5)*	14.5 (3.2)**
NuCotn 33 B	8.1 (1.6)**	15.0 (2.1)**
Stoneville LA887	8.6 (2.6)**	14.6 (4.4)**
Sure-Grow 125	11.6 (3.3)**	16.0 (2.1)**

[a] – standard deviation in parenthesis; n=5 for each cultivar.

*,** - Greater than Stoneville 373 and Paymaster 1220 at the 5% and 1% level of confidence, respectively.

Table 5. Whole plant weight at six weeks after inoculation with *Agrobacterium* and incubation at 36 °C.

Cultivar	Plant Weight (g)
FiberMax 989	10.49 (2.30)[a]
Paymaster 1218 BG/RR	11.55 (2.78)
Seabrook Sea Island 12B2	11.79 (1.82)
PSC – 636	12.82 (2.66)
Stoneville 373	13.42 (4.39)
Paymaster 1220 RR	13.86 (1.39)
PSC – 569	15.58 (6.39)
Paymaster 2145 RR	15.76 (1.35)*
SeedCo 5400	15.79 (6.61)
Paymaster Tejas	16.68 (4.37)
Paymaster 280	16.86 (5.71)
Paymaster 2200 RR	17.28 (1.19)**
PSC – 952	17.54 (1.11)**
Paymaster 1220 BG/RR	17.62 (5.08)
Paymaster 2326 BG	17.65 (4.03)*
DPX – 8C27	17.82 (5.31)
Paymaster – Ute	17.88 (2.34)**
Sure - Grow 501	17.91 (5.37)
Paymaster 1244 RR	17.95 (3.56)*
Deltapine 5415 RR	18.21 (2.93)**
Paymaster 1333 BG/RR	18.31 (1.47)**
Sure - Grow 248	18.33 (2.31)**
Paymaster 1266	18.36 (4.05)*
PMX – 2106	18.41 (3.20)**
FiberMax 963	18.48 (3.34)**
Paymaster 1325 BG/RR	19.00 (3.57)**
Agri Pro 7115	19.16 (3.71)*
Stoneville H338	19.67 (3.49)**
Paymaster 1244 BG	19.70 (2.38)**
Agri Pro HS44	19.77 (4.28)**
Stoneville 474	19.78 (4.54)*
FiberMax 819	20.03 (2.18)**
PSC – 262	20.07 (2.69)**
FiberMax 832	20.17 (1.14)**
Stoneville 239	20.23 (4.95)*
Paymaster 1560 BG/RR	20.25 (3.13)**
Stoneville BG 4740	20.61 (6.15)*
Paymaster 9307 – 0755	20.79 (4.05)**
Paymaster 2280 BG/RR	20.96 (4.71)**
Stoneville BXN 47	21.12 (1.75)**
Agri Pro 6102	21.14 (6.46)*
Paymaster 1440	21.38 (5.09)**
Paymaster 330	21.44 (3.99)**
Sure - Grow 821	21.54 (4.50)**
Sure - Grow 125	21.57 (2.76)**
Paymaster 1225 BG/RR	21.69 (1.38)**
Sure - Grow 747	21.70 (2.21)**
Stoneville LA887	22.06 (2.64)**
Rowden	22.12 (2.10)**
PSC – 355	22.33 (4.30)**
Deltapine 20 B	22.78 (2.81)**
Deltapine 2379	23.06 (3.04)**
TAM 88 – G – 104	23.09 (4.61)**
Holland 186	23.32 (3.52)**
TAM 90 – O – 24L	23.36 (2.59)**
Agri Pro 4103	23.48 (3.64)**
Agri Pro 6101	23.48 (5.79)**
Paymaster 1560	23.48 (2.89)**
Deltapine 51	23.50 (5.22)**
Paymaster 2326 BG/RR	23.53 (1.61)**
PSC – 556	24.07 (2.33)**
DPX – 9758	24.31 (1.19)**
All Tex Atlas	24.47 (4.46)**
Deltapine 5409	24.51 (1.32)**
Deltapine 5557	24.86 (4.22)**
Acala Maxxa	25.09 (1.88)**
Paymaster 1230 BG/RR	25.27 (2.98)**
Paymaster 1330 BG	25.30 (4.05)**
Deltapine 458 B/RR	25.51 (2.60)**
Paymaster 1560 BG/RR	25.52 (3.72)**
Paymaster 2326 RR	25.84 (2.42)**
Deltapine 2156	26.44 (3.94)**
Deltapine 50 B	27.17 (2.52)**

Table 5. Cont.

Cultivar	Plant Weight (g)
NuCotn 33 B	27.50 (3.84)**
Deltapine 32 B	27.53 (3.25)**
Paymaster HS26	29.50 (6.72)**
Paymaster 183	30.36 (8.58)**
Paymaster 1215 BG/RR	30.44 (2.23)**
Deltapine 50	31.43 (4.88)**
Paymaster 1215 BG	33.35 (3.23)**

[a] - Standard deviation in parentheses; n =30 for Stoneville 373 and n=5 for each of the othercultivars.
*,** - Greater than Stoneville 373 at the 5% and 1% confidence levels.

Table 6. Whole plant weight at six weeks after inoculation with *Agrobacterium* and incubation at 35 °C.

Cultivar or Line	Plant Weight (g)
Tamcot SP21S	15.64 (1.40)[a]
Tamcot CAMD – E	16.79 (2.00)
Paymaster 2183 BG	16.87 (4.34)
Deltapine 5690	17.25 (2.37)
Tamcot SP21	17.60 (5.03)
Stoneville 373	17.61 (3.12)
Hartz 1215	17.78 (3.04)
Hartz 1220	18.01 (2.34)
UAP 206 – 4	18.64 (5.53)
Tamcot CAB – CS	18.92 (3.18)
Tamcot SP37H	19.15 (4.48)
Tamcot HQ 95	19.15 (4.36)
Deltapine 5415	19.74 (2.30)
Tamcot CD3H	19.81 (3.52)
Deltapine 5690 RR	20.01 (4.18)
Tamcot SP37	20.35 (1.30)*
Tamcot Pyramid	20.64 (3.30)
Tamcot CDPS – 1 - 77	20.71 (1.76)*
TAM 93 – WA - 122	20.85 (3.72)
Tamcot SP23	21.09 (3.25)
Tamcot Luxor	21.22 (3.00)*
Tamcot Lotus	21.41 (5.64)
Deltapine 436 RR	21.43 (1.15)**
Tamcot Sphinx (S – 1)	21.44 (2.53)*
Deltapine 90 RR	21.47 (3.69)
UAP 205	22.11 (2.92)*
Deltapine 655 B/RR	22.38 (1.51)**
UAP 201	22.83 (2.81)**
Deltapine 90	22.89 (2.86)**
TAM 94 – L – 25	22.91 (2.75)**
TAM 96 – WA – 126	23.02 (3.18)**
Texas 300	23.04 (2.43)**
Deltapine 20	23.69 (2.33)**
Texas 121	23.76 (3.50)**
Deltapine 90 B	23.99 (0.65)**
Deltapine 425 RR	25.53 (1.95)**
Tamcot Sphinx (S – 2)	26.07 (3.29)**
TAM 93 – WB – 575	26.13 (3.74)**
Texas 141	26.69 (2.66)**
Tamcot 8104	28.14 (3.92)**
Texas 242	29.22 (3.43)**

[a] - Standard deviation in parentheses; n=15 for Stoneville 373 and n=5 for each of the other cultivars and lines.
*,** - Larger than Stoneville 373 at the 5% and 1% confidence levels.