

Stability Analysis of Incidence of Tomato Spotted Wilt in Virginia-Type Peanut Cultivars and Breeding Lines

T.G. Isleib^{1*}, S.R. Milla-Lewis¹, W.B. Dong¹, S.C. Copeland¹, B.B. Shew², and C. Arellano³

ABSTRACT

Tomato spotted wilt (TSW) caused by *Tomato spotted wilt tospovirus* (TSWV) has become a serious constraint to peanut (*Arachis hypogaea* L.) production in the Virginia-Carolina production area. Regression stability analysis was applied to TSW incidence data collected in 64 trials conducted over 17 years to determine if an array of 31 virginia-type cultivars and breeding lines exhibited variation in their reactions to increasing levels of general TSW intensity compared with the standard field-resistant cultivar Georgia Green and hirsuta-type line PI 576636. Eight cultivars (NC 7, NC 9, NC 10C, NC-V 11, NC 12C, Perry, Phillips, and Brantley) had mean effects greater than zero ($P < 0.01$) while Bailey, four Bailey siblings, and N96076L, Bailey's resistant parent, all had mean effects less than zero ($P < 0.01$). The deviations of the slope of regression on environmental index ($\hat{\beta}_k$) for four of the eight susceptible cultivars were greater than zero, indicating greater than average reaction to increased levels of TSW. The $\hat{\beta}_k$ for Bailey indicated that its response to increasing levels of TSW was flat. PI 576636 was confirmed as a highly field-resistant line. The slopes of Georgia Green, the standard TSWV-resistant runner-type cultivar, the Bailey siblings and N96076L did not differ from the average of all lines. The correlation between mean effect and $\hat{\beta}_k$ was $r = 0.693$, indicating that approximately half the variation in $\hat{\beta}_k$ could be explained by mean effects. However, the regression analysis provided information useful in describing the TSW reactions of the lines and cultivars.

Key Words: *Arachis hypogaea* L., TSW, TSWV.

Since the mid-1990s, tomato spotted wilt (TSW) caused by *Tomato spotted wilt tospovirus* (TSWV) has become a serious constraint to peanut (*Arachis hypogaea* L.) production in the Virginia-Carolina

(VC) production area (Shew, 2005). Field resistance to TSW is considered to be an important component of programs designed to manage the disease and is one of the primary objectives of the N.C. State University peanut breeding program. The program has monitored the reaction of cultivars and breeding lines to TSW in field plots planted for that purpose since 1996. In these studies, increased seed spacing (25–50 cm) within rows and withholding of in-furrow and other insecticide use was utilized to encourage feeding by thrips (*Frankliniella fusca* Hinds) which leads to increased disease development. Incidence of TSW was also recorded in trials planted for other purposes when symptoms of TSW were obvious.

Prior to its release in 2000, the cultivar Perry (Isleib *et al.*, 2003) was tested for reaction to TSW in eight tests, and it was found to have incidence of TSW comparable to that of Gregory (Isleib *et al.*, 1999) (9.2 vs. 6.5% of emerged plants showing TSW symptoms, NS). However, once Perry was grown commercially it was found to be highly susceptible to TSW. The growing seasons of 2000, 2001, and 2002 were notable for levels of TSW incidence that had not been encountered before or since in the VC production area. It is not known what the cause of this increase in disease severity was whether increased or more efficient transmission of the disease, shifts in thrips species leading to variation in transmission, or the occurrence of different more virulent strains of the virus. Because of the evidently erroneous conclusion made about Perry's reaction to TSW on the basis of data collected prior to 2000, it was clear that some methodology other than simple comparison of means across tests should be employed to identify advanced breeding lines that might exhibit high susceptibility to TSW under high general levels of disease.

Stability analysis has been used in many plant breeding programs to dissect genotype-by-environment (GxE) interaction for yield. There are several methodologies that can be used, including variance components (Cockerham, 1963; Comstock and Moll, 1963; Plaisted and Peterson, 1959; Shukla, 1972), regression (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966), and descriptive multivariate approaches (Lin *et al.*, 1986). Each methodology has variation in its details, each has adherents, and each has critics. The regression approach,

¹T.G. Isleib, S.R. Milla-Lewis, W.B. Dong, and S.C. Copeland, Dep. of Crop Sci., Box 7629, N.C. State Univ., Raleigh, NC 27695-7629.

²B.B. Shew, Dep. of Plant Pathology, Box 7903, N.C. State Univ., Raleigh, NC 27695-7903.

³C. Arellano, Dep. of Statistics, Box 8203, N.C. State Univ., Raleigh, NC 27695-8203.

*Corresponding author. E-mail: tom_isleib@ncsu.edu.

partitioning variation due to genotype-by-environment interaction into parts due to response to an environmental index and others due to deviation of the line's value in a particular environment from that predicted by regression, is particularly applicable to disease data. In the case of yield, there are many reasons why an environmental index, usually calculated as the average performance of the lines tested in a particular environment, could be low. Any of numerous yield constraints, *e.g.*, low or toxic levels of plant nutrients, any of the diseases that affect the crop, excessively low or high temperatures during the growing season, poor weed management, too early or too late planting, etc., can reduce the average yield at a given location in a given year. However, in the case of a specific disease, the average disease incidence or severity at a location should provide a reasonably good index for the environment. This sort of approach was used by Wells *et al.* (2002) to examine the reactions of runner-type cultivars C-99R (Gorbet and Shokes, 2002), Georgia Green (Branch, 1996), and Georgia Runner (Branch, 1991) across 13 tests with varying degrees of overall TSW severity. Stability analysis also was used to evaluate host genotype-by-isolate interactions, wherein isolates of *Cercosporidium personatum* constituted the "environment" (Shew *et al.*, 1996). Presumably, interactions indicate specificity of an isolate or isolates on resistant hosts and therefore lack of durability of resistance (Jenns *et al.*, 1982). While not addressed herein, it is possible stability analysis could be used to track changes in virus populations. Over time, increasing deviations from regression could indicate emergence of races, whereas increasing slope could indicate selection for aggressive isolates. However, it is not clear how one would separate environment in the aggregate from the virus "environment."

The objective of this study was to apply a regression stability analysis to TSW incidence data collected over several years to determine if an array of virginia-type cultivars exhibited variation in their reactions to increasing levels of general TSW intensity.

Materials and Methods

Although data were available for a large number of experimental breeding lines, data were retained for use in this analysis for only 31 genotypes tested in at least 8 of the 17 years from 1996 through 2012. These included 11 virginia-type cultivars released by N.C. State Univ.: NC 7 (Wynne *et al.*, 1979), NC 9 (Wynne *et al.*, 1986), NC 10C (Wynne *et al.*, 1991a), NC-V 11 (Wynne *et al.*, 1991b), NC

12C (Isleib *et al.*, 1997), Gregory, Perry, Brantley (Isleib *et al.*, 2006a), Phillips (Isleib *et al.*, 2006b), Bailey (Isleib *et al.*, 2011), and Sugg. Thirteen experimental lines and one unregistered cultivar were included (Table 1) as were three cultivars released by Virginia Polytechnic Inst. and State Univ.: VA-C 92R (Mozingo *et al.*, 1994), VA 98R (Mozingo *et al.*, 2000), and Wilson (Mozingo *et al.*, 2004). Four disease-resistant checks were included: the TSW-field-resistant runner-type cultivar Georgia Green, leaf spot-resistant germplasm line GP-NC 343 (Campbell *et al.*, 1971), multiply disease-resistant germplasm line N960976L (Isleib *et al.*, 2006c) and TSW-field-resistant hirsuta-type (*A. hypogaea* subsp. *hypogaea* var. *hirsuta* Köhler) PI 576636, collected in the state of Guanajuato, Mexico.

The data for this study were collected in 64 experiments conducted from 1996 to 2012 (Table 2). Most of the tests were conducted specifically for the evaluation of TSW symptoms at the N.C. Dept. of Agriculture and Consumer Services' Peanut Belt Res. Stn. at Lewiston (Bertie Co.), NC, but others were conducted on farmers' fields in Gates, Martin, Northampton, and Perquimans Cos. on North Carolina's northeastern coastal plain. Because the tests comprised large numbers of entries, each was conducted in an incomplete block design, either a square or rectangular lattice commensurate with the number of entries and with two, three or four replicates. Each TSW test was conducted using wide seed spacing (25 or 50 cm) and no in-furrow insecticide. These conditions promoted survival and feeding by tobacco thrips [*Frankliniella fusca* (Hinds)], the predominant insect vector of TSWV in North Carolina. Other trials were planted for purposes other than TSW evaluation, but sufficient TSW developed to allow scoring of symptomatic plants. In TSW trials, plant stands were counted approximately four weeks after planting, and plants expressing symptoms of TSW were counted three to six times during the growing season, starting in July. In trials planted for purposes other than TSW evaluation, one or two counts were made in late September or early October. Symptoms included early to mid-season stunting and flecking or ring-spots on leaves, petiole curling, brown flecking on leaflet undersides, and late-season wilting and death of the plants. Above-ground symptoms of *Cylindrocladium* black rot (CBR) caused by *C. parasiticum* Crous, Wingfield & Alfenas are similar to those of late-season TSW, but they are usually accompanied by root or pod rot. Plants dying from CBR typically can be pulled up easily due to extensive root rot. The main stem of each plant in question was tugged to determine if the root system was healthy. If the plant did not uproot, then it was

Table 1. Origins of N.C. State Univ. breeding lines and the unregistered cultivar tested for field resistance to tomato spotted wilt.

Line	Parentage	Pedigree
N93007L	NC 6 ¹ / GP-NC 343 ²	F2-S-S-B-20: F08
N94015L	GP-NC 343 / NC 9 ³	F2-B-06-01-01: F07
N94040C	NC 7 ⁴ / Florigiant ⁵ , (F2-11-B-B-A06: F08) N90004 /3/ NC Ac 03139, NC 2 ⁶ // A48, NC 4 / Improved Spanish 2B	F2-02-S-01: F06
N99027L	Gregory ⁷ // N92080L (F2-S-S-02: F07), PI 270806 / PI 109839	F2-01-04-01-R02: F08
N99103ol	NC 9 // X90047 (F2-S-S-18: F05), NC 9 / F435 (Fla. high-oleic source)	BC1F2-02-02-04: F07
N00098ol	Gregory // Random ol1ol2, NC 9*2 / F435 (Fla. high-oleic source), X95253 (F1-02-04: F02) /3/ Gregory, X96201 (BC1F1-01: F01) /4/ Gregory	BC2F1-01-03: F04
N01012T	PI 371853 (resistant to <i>Cercosporidium personatum</i> & TSW) / 2*N90010E (Gregory sib, F2-14-B-B-A04: F07), NC 7 / NC 9	BC1F1-05-02-01-01: F07
N01013T	PI 371853 (resistant to <i>Cercosporidium personatum</i> & TSW) / 2*N90010E (Gregory sib, F2-14-B-B-A04: F07), NC 7 / NC 9	BC1F1-05-02-01-03: F07
N03074FT	NC 12C*2 / N96076L ⁹	BC1F1-06-01-S-02-S-01: F09
N03080FT	NC 12C*2 / N96076L	BC1F1-06-01-S-03-S-03: F09
N03085FT	NC 12C*2 / N96076L	BC1F1-06-04-S-02-S-03: F09
N03088T	NC 12C*2 / N96076L	BC1F1-06-04-S-02-S-08: F09
N05042F	Perry ¹⁰ / NC 12C, N97135C // N96076L	F2-01-S-02-S-02: F09
Sugg	Gregory // X98006 (F1), NC 7 / NC 9, N90010E // TAMrun 98R ¹¹	

¹Campbell, W.V., J.C. Wynne, D.A. Emery, and R.W. Mozingo. 1977. Registration of NC 6 peanuts (Reg. No. 20). *Crop Sci.* 17: 346.

²Campbell W.V., D.A. Emery D.A., and W.C. Gregory. 1971. Registration of GP-NC 343 peanut germplasm (Reg. No. GP 1). *Crop Sci.* 11-605.

³Wynne J.C., R.W. Mozingo, and D.A. Emery. 1986. Registration of 'NC 9' peanut. *Crop Sci.* 26: 197.

⁴Wynne J.C., R.W. Mozingo, and D.A. Emery. 1979. Registration of NC 7 peanut (Reg. No. 22). *Crop Sci.* 19: 563.

⁵Carver, W.A. 1969. Registration of Florigiant peanuts (Reg. No. 1). *Crop Sci.* 9: 849-850.

⁶Gregory, W.C. 1970. Registration of NC 2 peanuts (Reg. No. 5). *Crop Sci.* 10: 459-460.

⁷Isleib, T.G., P.W. Rice, R.W. Mozingo, R.W. Mozingo, II, and H.E. Pattee. 1999. Registration of 'Gregory' peanut. *Crop Sci.* 39: 1526.

⁸Isleib, T.G., P.W. Rice, J.E. Bailey, R.W. Mozingo, and H.E. Pattee. 1997. Registration of 'NC 12C' peanut. *Crop Sci.* 37: 1976.

⁹Isleib, T.G., P.W. Rice, R.W. Mozingo II, S.C. Copeland, J.B. Graeber, B.B. Shew, D.L. Smith, H.A. Melouk, and H.T. Stalker. 2006. Registration of N96076L peanut germplasm. *Crop Sci.* 46: 2329-2330.

¹⁰Isleib, T.G., P.W. Rice, R.W. Mozingo II, R.W. Mozingo, J.E. Bailey, and H.E. Pattee. 2003. Registration of 'Perry' peanut. *Crop Sci.* 43: 739-740.

¹¹Simpson, C.E., O.D. Smith, and H.A. Melouk. 2000. Registration of 'Tamrun 98' peanut. *Crop Sci.* 40: 859.

counted as having symptoms of TSW. The maximum number of dead or diseased plants in a plot was expressed as a proportion of the early-season plant stand and subjected to analysis of variance. Means, adjusted to a common block effect in cases where the effect of blocks within reps was found to be significant ($P < 0.05$), were compiled in a database. The adjusted mean proportions were used for stability analysis in this study.

Statistical Analysis. Data were analyzed using the general linear models procedure (PROC GLM) of the SAS statistical software package (SAS Institute, Cary, NC). Initially, analysis of variance was performed, removing environments (defined for this analysis as combinations of years and locations), tests within environments, genotypes, and GxE interaction as sources of variation, leaving interaction between genotypes and tests within environments as the residual error. Means for environments adjusted to a common genotypic

effect were estimated using the LSMEANS statement of PROC GLM.

The linear model for partitioning of genotype-by-environment interaction was:

$$Y_{ijk} = \mu + E_i + T_{ij} + G_k + \beta_k E_i + \delta_{ik} + \varepsilon_{ijk}$$

where Y_{ijk} was the TSW incidence in k^{th} genotype in the j^{th} test in the i^{th} environment; μ was the mean of all observations; E_i was the effect of the i^{th} environment; T_{ij} was the effect of the j^{th} test in the i^{th} environment; G_k was the effect of the k^{th} genotype, $1 + \beta_k$ was the slope of regression of incidence in the k^{th} genotype on the effect of the i^{th} environment, δ_{ik} was the deviation from regression, and ε_{ijk} was the residual error term. Note that because the slope of regression on the environmental effect was defined as $1 + \beta_k$, the β_k 's represent the deviation of the slope from unity. In a balanced design, this would imply that the sum of the β_k 's

Table 3. Mean squares from analysis of variance of TSW incidence.

Source	df	Sum of squares	Mean squares	Probability
Corrected total	709	38.8685		
Environment	21	21.2525	1.0120**	<0.0001
Test in environment	42	3.3803	0.0805**	<0.0001
Genotype	30	6.6229	0.2208**	<0.0001
GxE interaction	389	5.1240	0.0132	0.0644
Heterogeneous regression	30	0.9060	0.0302**	<0.0001
Deviation from regression	359	4.2180	0.0117	0.2857
Error	227	2.4888	0.0110	

**Denotes mean squares significant by F-test at $P < 0.01$.

across all genotypes must be zero. A design matrix was developed to partition the variation among genotypes, environments, and regression of TSW incidence on the environmental effect. Genotypic and environmental effects were parameterized so as to sum to zero when unweighted by the frequency of the genotype or environment among the data.

Environmental effects were estimated as the deviation of the environmental mean adjusted to a common genotypic effect from the grand mean. Estimates of genotypic effects and slopes were compared with critical values (zero for effects and unity for slopes) using t tests and also subjected to mean separation using protected t-tests.

Table 4. Mean effect and deviation of regression on environmental index from one ($\hat{\beta}_k$) for 30 peanut cultivars and breeding lines.

Cultivar or line	Mean effect \pm SE	Rank	Deviation of regression	
			slope from 1 \pm SE	Rank
Bailey	-0.155 \pm 0.021 ^{a**}	2	-0.4859 \pm 0.2075 ^{abc*}	3
Brantley	0.152 \pm 0.024 ^{m**}	29	0.1204 \pm 0.1636 ^d	20
Gregory	0.004 \pm 0.015 ^{fgh}	17	-0.0050 \pm 0.0884 ^d	13
NC 7	0.117 \pm 0.022 ^{klm**}	26	0.2279 \pm 0.1120 ^{d*}	27
NC 9	0.219 \pm 0.023 ^{n**}	31	0.1175 \pm 0.1078 ^d	19
NC 10C	0.153 \pm 0.032 ^{lmn**}	30	0.2799 \pm 0.1392 ^{d*}	29
NC-V 11	0.059 \pm 0.016 ^{ijk**}	23	0.1239 \pm 0.0997 ^d	21
NC 12C	0.140 \pm 0.017 ^{lm**}	27	0.2208 \pm 0.0996 ^{d*}	26
Perry	0.146 \pm 0.015 ^{m**}	28	0.2149 \pm 0.0905 ^{d*}	25
Phillips	0.099 \pm 0.020 ^{j-m**}	25	0.2727 \pm 0.1412 ^{d†}	28
Sugg	-0.032 \pm 0.023 ^{d-g}	14	0.0578 \pm 0.2286 ^{acd}	15
VA-C 92R	0.032 \pm 0.026 ^{ghi}	20	-0.0490 \pm 0.1357 ^{acd}	11
VA 98R	0.021 \pm 0.020 ^{ghi}	19	0.1301 \pm 0.1128 ^d	23
Wilson	-0.008 \pm 0.027 ^{fgh}	16	0.3225 \pm 0.1768 ^{d†}	31
N93007L	0.043 \pm 0.030 ^{g-j}	21	0.1157 \pm 0.1422 ^d	18
N94015L	-0.062 \pm 0.030 ^{a-f*}	10	-0.0102 \pm 0.1525 ^{cd}	12
N94040C	-0.046 \pm 0.035 ^{a-g}	11	-0.0627 \pm 0.1465 ^{acd}	10
N99027L	-0.105 \pm 0.032 ^{a-d**}	6	-0.4979 \pm 0.1884 ^{ab**}	2
N99103ol	0.071 \pm 0.031 ^{h-l*}	24	0.3006 \pm 0.1850 ^d	30
N00098ol	0.019 \pm 0.034 ^{f-i}	18	0.1291 \pm 0.1907 ^d	22
N01012T	-0.043 \pm 0.034 ^{a-g}	12	-0.1092 \pm 0.1898 ^{a-d}	9
N01013T	-0.039 \pm 0.028 ^{c-g}	13	-0.1583 \pm 0.1787 ^{a-d}	8
N03074FT	-0.138 \pm 0.039 ^{ab**}	3	-0.2827 \pm 0.4512 ^{a-d}	5
N03080FT	-0.117 \pm 0.033 ^{abc**}	5	0.0362 \pm 0.3346 ^{a-d}	14
N03085FT	-0.094 \pm 0.033 ^{a-e**}	8	0.1997 \pm 0.3348 ^{acd}	24
N03088T	-0.095 \pm 0.032 ^{a-e**}	7	-0.2583 \pm 0.3348 ^{a-d}	6
N05042F	-0.126 \pm 0.034 ^{abc**}	4	0.0880 \pm 0.3527 ^{a-d}	17
Georgia Green	0.054 \pm 0.023 ^{h-k*}	22	0.0723 \pm 0.1304 ^d	16
GP-NC 343	-0.020 \pm 0.021 ^{efg}	15	-0.3676 \pm 0.1570 ^{abc*}	4
N96076L	-0.085 \pm 0.017 ^{a-e**}	9	-0.2122 \pm 0.1114 ^{acd†}	7
PI 576636	-0.164 \pm 0.020 ^{a**}	1	-0.5310 \pm 0.1160 ^{a**}	1

^{a,b,c} Effects followed by the same letter are not significantly different by t-test ($P < 0.05$).

†, *, ** Denote effects significantly different from zero at $P < 0.10$, $P < 0.05$ and $P < 0.01$, respectively.

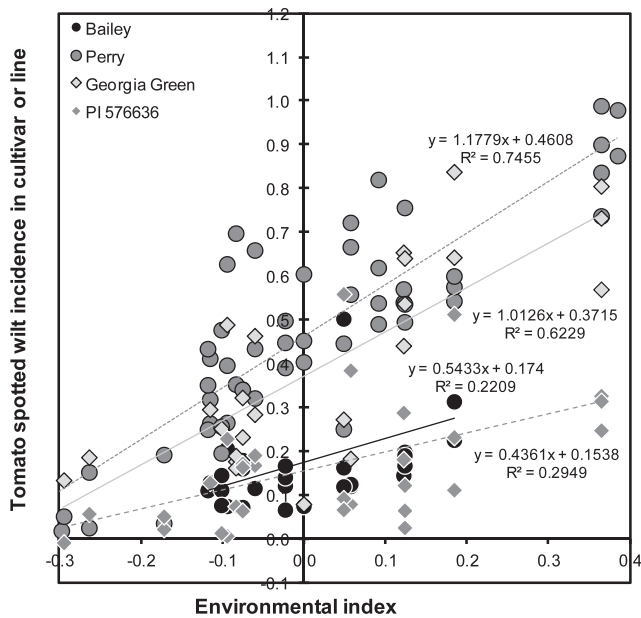


Fig. 1. Tomato spotted wilt (TSW) reactions of Bailey, Perry, Georgia Green, and PI 576636 versus environmental indices across 22 environments in 17 years.

Results and Discussion

The conventional analysis of variance for TSW incidence indicated that there were significant differences among the 22 environments, among tests within environments, and among the 31 genotypes. Overall G \times E interaction was not significant ($P=0.0644$) (Table 3). However, partition of the G \times E sum of squares revealed significant variation among the regression slopes of the 31 genotypes. The aggregate deviation from linear regression was not significant ($P=0.286$).

As mentioned above, the trials conducted in 2000, 2001, and 2002 had the greatest mean levels of TSW incidence (34, 68, and 55%) while mean incidence in 1996–1999 was less than 15% and in 2003–2012 ranged from 20% to 50%. This variation in TSW incidence over years is well documented, but has not been fully explained by weather (Olatinwo *et al.*, 2008) or evolution of the virus (Kaye *et al.*, 2009). As a point of reference, the mean effect of Georgia Green, the standard TSW-resistant runner-type cultivar, was actually slightly greater than zero ($+0.054 \pm 0.023$, $P=0.0180$), and its slope of regression did not differ from one (Table 4, Fig. 1). Georgia Green's performance in these tests was close to the mean of all lines. Eight virginia-type cultivars from N.C. State Univ. (NC 7, NC 9, NC 10C, NC-V 11, NC 12C, Perry, Phillips, and Brantley) had susceptible reactions with mean effects greater than zero ($P<0.01$). Six of the eight had estimates of β_k greater than zero ($P<0.05$). Only one cultivar, Bailey, had a mean

effect and $\hat{\beta}_k$ less than zero ($P<0.05$). Clearly Bailey exhibited resistance both in terms of its mean level of TSW and in its reaction to increasingly severe disease (Table 4, Fig. 1). Among the breeding lines, several had mean effects significantly ($P<0.05$) less than zero, including N94015L, N99027L, and Bailey siblings N03074FT, N03080FT, N03085FT, and N03088T. Bailey and its siblings apparently derive their field resistance to TSW from their non-recurrent parent N96076L rather than from recurrent parent NC 12C which was found to be susceptible.

The heterogeneous slopes of regression on the environmental index resolved into only four statistical groups. For Bailey, $\hat{\beta}_k = -0.49$, indicating that Bailey had a fairly flat response to increasing general level of TSW. None of Bailey's siblings, all of which were tested in the same array of environments as Bailey, had a value of $\hat{\beta}_k$ significantly different from zero, indicating that, unlike Bailey, they would be expected to exhibit greater incidence of TSW in increasingly severe environments.

The Bailey siblings were not the only closely related group to share similar responses to TSW. N99103ol is a high-oleic line derived from the first backcross in a program to transfer the trait from the Univ. of Florida's F435 (Moore and Knauft, 1989) into NC 9, a very TSW-susceptible cultivar. Although N99103ol had a lower mean effect than NC 9 (0.07 vs. 0.22, $P<0.05$), its $\hat{\beta}_k$ was numerically but not statistically greater (0.365 vs. 0.184, NS). Similarly, N00098ol is a backcross-derived high-oleic version of Gregory, a cultivar long considered to manifest partial field resistance to TSW. Because it was selected from the second backcross to its recurrent parent, N00098ol should be even more similar to Gregory than N99103ol is to NC 9. Neither the mean effect (0.019 vs. 0.004, NS) nor the $\hat{\beta}_k$ (0.129 vs. -0.005, NS) of N00098ol was different from that of Gregory.

PI 576636 was introduced from central Mexico in 1993 as part of a group of hirsuta-type collections that included PI 576638, the TSW-resistant hirsuta-type parent of Univ. of Florida breeding line NC94022 (Culbreath *et al.*, 2006). PI 576636 was found to combine superior field resistance to TSW with adequate adaptation to the growing conditions of North Carolina (data not shown). It has been used as a TSW-resistant check in the N.C. State Univ. breeding program for a number of years, including all but two of those represented in the current study. In this study, the field resistance of PI 576636 to TSW is confirmed, especially in light of its having been tested in the period of greatest average incidence of TSW, the period 2000–2002 (Table 4, Fig. 1).

The results of the stability analysis suggest that Bailey may be as field resistant as PI 576636, but it is clear that trials of Bailey in more severe TSW environments would be desirable. Across the 31 cultivars and breeding lines used in this study, the correlation of mean effect with $\hat{\beta}_k$ was $r = 0.693$ ($P < 0.01$) while the rank correlation was $r_{\text{rank}} = 0.722$ ($P < 0.01$). With the mean effect accounting for approximately 50% of the variability in $\hat{\beta}_k$, one might conclude that calculation of the mean effect is sufficient. However, with the false-positive example of Perry in mind, it is clear that the remaining half of the variation in $\hat{\beta}_k$ is unpredictable and that application of the stability analysis does contribute to better understanding of the reaction of lines to increasing general levels of TSW.

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