Stability of TSWV General Field Resistance
in the ‘Georgia Green’ Peanut Cultivar

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Accepted for publication 11 May 2015. Published 18 May 2015.

ABSTRACT

There are mainly two types of host-plant disease resistance. General or horizontal resistance is usually controlled by several genes each acting with minor additive effects, and specific or vertical resistance is usually controlled by one or two genes with a dominant major effect. In most cases, general resistance may not provide as high a level of control as specific; however, general type of resistance is usually more desirable for long-term stability. Therefore, the objective of this 13-year study was to determine the stability of the general disease resistance to tomato spotted wilt (TSW), caused by Tomato spotted wilt virus (TSWV), found in the peanut (Arachis hypogaea L.) cultivar ‘Georgia Green’, as indicated by comparisons with the highly susceptible ‘Florunner’ cultivar. The general host-plant TSWV resistance of Georgia Green was found to have consistently lower TSW at mid-season and total disease (primarily TSW and any soilborne disease) incidence at late season, respectively, and higher pod yield compared to Florunner across all 13 years without any genotype-by-year (G×Y) interaction for these variables. Consequently, the general TSWV-resistance of Georgia Green was found to be highly stable across many years, and should be utilized for progress in breeding improved TSWV-resistant peanut cultivars.

INTRODUCTION

According to Flor’s gene-for-gene hypothesis (Flor 1942; Flor 1956), for every gene conditioning resistance in the host-plant there is a corresponding gene conditioning virulence in the pathogen. General or horizontal host-plant disease resistance is usually controlled by several such genes, each acting with minor additive effects (Fehr 1987; Vanderplank 1984). The opposite goes for specific or vertical disease resistance. It is usually controlled by one or two gene(s) with dominant major effect, and the results are normally high levels of resistance (Fehr 1987; Vanderplank 1984). Unfortunately, use of specific or vertical-type resistance often results in heavy selection pressure on the pathogen, so that if strains exist or develop that are virulent on cultivars with that resistance, resistance may be overcome, sometimes very rapidly. Consequently, although in many cases general or horizontal-type resistance may not provide as high a level of control as specific resistance, horizontal resistance may be more desirable for long-term stability, since its use is typically less likely to result in development of populations of the pathogen that can overcome the resistance.

Single dominant genes were first used in tomato (Solanum lycopersicum L.) and pepper (Capsicum annum L.) as specific- or vertical-type host-plant resistance to control tomato spotted wilt (TSW) disease, caused by Tomato spotted wilt virus (TSWV) (Moury et al. 1997; Rosello et al. 1998; Stevens et al. 1992). However, field isolates of TSWV overcame the hypersensitive disease resistance and quickly spread to other host plants (Moury et al. 1997; Roggero et al. 2002; Roggero et al. 1999). No similar, major, single TSWV-resistant genes have been identified in peanut (Arachis hypogaea L.), except for experimental transgenic peanut plants containing nucleocapsid-protein (N) genes (Yang et al. 1998). Unfortunately, TSWV has even been shown to adapt to the N-gene derived resistance by genome reassortment (Qiu and Moyer 1999).

TSWV first began appearing in the southeastern U.S. peanut-production area around the mid-1980s. ‘Florunner’ (Norden et al. 1969) was the predominant cultivar during this time, and it was soon found to be extremely susceptible to TSWV. ‘Georgia Green’ (Branch 1996) was developed and released in 1996 as a TSWV-resistant, runner-type peanut cultivar. Georgia Green quickly replaced Florunner in the southeast because of its TSWV resistance and greater yield. Although the mechanisms and genetic control of TSWV resistance in Georgia Green have not been completely characterized, the resistance is partial, and appears to be quantitative in inheritance. These characteristics suggest that the field resistance of Georgia Green should be relatively stable. A summary of the incidence of TSW in Georgia Green compared to susceptible standards from multiple studies through 2008 indicated that to be the case (Culbreath and Srinivasan 2011). However, long-term comparisons of Georgia Green and a single standard susceptible cultivar have not been reported. Therefore, the objective of this long-term study was to evaluate the stability of the TSWV host-plant field resistance found within Georgia Green over time compared to the susceptible cultivar Florunner.

EFFECT OF DISEASE ON PERFORMANCE OF TWO PEANUT CULTIVARS

Over 13 consecutive years (2002-2014), two runner-type peanut cultivars (Florunner and Georgia Green) were evaluated each year in field tests. These tests were conducted at the University of
Georgia, Coastal Plain Experiment Station, Tifton Campus utilizing early planting dates (mid-April) to maximize TSW disease pressure.

A randomized complete block design was used in each test with five replications. Seeding rates were six seeds per 30.5 cm of row. Plots consisted of two rows 6.10 m long by 1.83 m wide (0.81 m within and 1.02 m between rows on adjacent plots). Georgia Cooperative Extension Service recommended cultural practices of herbicides, fungicides, and insecticides with irrigation were used throughout each growing season. Tobacco thrips [Frankliniella fusca (Hinds)], the primary vector of TSWV in peanut, was controlled by an in-furrow systemic insecticide at planting. These field trials were in a three-year rotation following cotton (Gossypium hirsutum L.) and corn (Zea mays L.). Both cultivars were dug near optimum maturity based upon the hull-scrape method (Williams and Drexler 1981) as determined from adjoining border rows of each test.

**Disease assessment.** A disease hit equaled one or more symptomatic plants within a 30.5-cm section of row (Rodriguez-Kabana et al. 1975). Incidence of TSW was first assessed at approximately 70 days after planting. TSW is likely to be the most predominant foliar disease present at this time during the growing season. Early-season TSW symptoms included chlorotic spots on leaflets and stunted plants, whereas general yellowing and wilting are symptoms of TSW that typically occur late in the season (Culbreath et al. 2003). These symptoms are not always accompanied by other more diagnostic symptoms of the disease, and are often very similar to above-ground symptoms of white mold or stem rot caused by Sclerotium rolfsii Sacc. Therefore, percentages of total disease which were scored prior to digging included primarily TSW and any occasional fungicide-escaped soilborne disease.

**Pod yields.** After digging and threshing, pods were dried with forced warm air to 6% moisture. Pod samples were then hand-cleaned over a screen table before weighing for yield determinations in each crop-year.

**Statistical analysis.** Data from each year of the two cultivars were assessed using analysis of variance. Years were considered as random factors in the combined analyses. Overall, mean data from each test was assessed using analysis of variance, and least significant differences (LSD) were used for cultivar mean separation at $P \leq 0.05$. Kendall’s coefficient of concordance was calculated as an indication of the consistency of ranking of the two cultivars, and thus an indication of genotype × year (G×Y) interaction for the early and final disease ratings across years (Madden et al. 2007). For this calculation, the genotypes were ranked within each replication according to disease incidence ratings, where the higher disease level was ranked as one and the lower disease level was ranked as two for each replication. The average rank of each cultivar was calculated across replications for each year. The sum of squares (S) of the rank totals across the overall mean were calculated as:

$$S = \sum_{i=1}^{K} \left( N \bar{R}_i - \frac{N(K + 1)}{2} \right)^2$$

where $K$ = the number of cultivars; $N$ = the number of years; and $\bar{R}_i$ = the mean rank of cultivar $i$ within a year (Madden et al. 2007). The maximum possible sum of squares ($S_{\text{max}}$) was calculated as:

$$S_{\text{max}} = \frac{N^2K(K^2-1)}{12}$$

Kendall’s coefficient of concordance ($W$) was calculated as the ratio of sum of squares to the maximum sum of squares:

$$W = \frac{S}{S_{\text{max}}}$$

where $W$ has a value of one when $S$ ranks are identical within all years and a value of zero when there is no concordance in the rankings among years (Madden et al. 2007).

**DISEASE AND CULTIVAR EFFECTS**

Thirteen years (2002–2014) were used to evaluate a common set of two peanut cultivars (Florunner and Georgia Green) for disease resistance and yield performance. Significant differences ($P \leq 0.05$) were found among years for TSW incidence, total disease incidence, and pod yield, and between the two runner-type cultivars within each year. Kendall’s coefficient of concordance ($W$) was calculated to be one for TSW incidence and total disease incidence, which indicated that ranks were similar across all years. This strongly supports no G×Y interaction between the two cultivars, Florunner and Georgia Green, for these variables.

The 13-year percentage of TSW incidence during mid-season when planted early in mid-April varied from year to year (Fig. 1). There were significant year differences with 2004 having the highest TSW incidence. This variation could be related to many uncontrollable environmental factors influencing TSWV levels. However, the relative rank among the two cultivars was consistent across all 13 years with Georgia Green having the lowest mean ($\bar{x}$) TSW incidence at 13.0% and Florunner having the highest mean ($\bar{x}$) TSW incidence at 28.8%. Thus, the general host-plant TSWV-resistance of Georgia Green exhibited long-term stability without G×Y interaction.

The 13-year percentage of total disease (TD) incidence, which included primarily TSW and any other soilborne disease during late season when planted in mid-April each year, also varied from year to year (Fig. 2). There were again significant year differences with 2004 having the highest TD incidence, but it was not significantly different from 2005, 2007, and 2009. Likewise, the relative rank among the two cultivars was again consistent across all 13 years with Georgia Green having the lowest mean ($\bar{x}$) TD incidence at 33.6% and Florunner having the highest mean ($\bar{x}$) TD incidence at 68.6%. Despite variability in TSW and TD incidence across years, this data indicates that Georgia Green exhibited long-term stability of general host-plant TD resistance at late-season (Fig. 2) as well as mid-season (Fig. 1).

The 13-year pod yield among the two runner-type cultivars, Georgia Green and Florunner, when planted early in mid-April each year seems to support the disease data (Fig. 3). There were significant year differences with 2010–2012 having the highest pod yields. Also, the relative rank among the two cultivars was again consistent and significant across all 13 years with Georgia Green having the average approximately 55% yield advantage over Florunner.

This 13-year study agrees with an earlier 3-year (1995–1997) report (Branch and Culbreath 1999) which also found significantly lower TSW intensity and greater yield (47%) advantage for Georgia Green as compared to Florunner. Results of this study are also in agreement with a summary of consistent relative effects of Georgia Green on incidence of TSW disease compared to Florunner from 1993–1996, and compared with other susceptible standards from 1997–2008 reported by Culbreath and Srinivasan (2011).
FIGURE 1
Thirteen-year (2002-2014) percentage of tomato spotted wilt (TSW) incidence during mid-season among two peanut cultivars, Georgia Green and Florunner, when planted early at Tifton, GA. Within years, cultivar means followed by the same letter are not significantly different at $P \leq 0.05$.

FIGURE 2
Thirteen-year (2002-2014) percentage of total disease (TD) incidence during late-season among two peanut cultivars, Georgia Green and Florunner, when planted early at Tifton, GA. Within years, cultivar means followed by the same letter are not significantly different at $P \leq 0.05$. 
Together, the combination of these studies now extends the documented duration of TSWV resistance in Georgia Green to over 20 years without changes to the host-plant resistance. Thus, the stability in TSWV resistance and yield performance of Georgia Green versus Florunner, respectively, is clearly apparent.

**IMPLICATION FOR BREEDING TSWV RESISTANT PEANUT CULTIVARS**

For the past several years, tomato spotted wilt (TSW) has been controlled in peanut by cultivars possessing general resistance coupled with other cultural practices outlined by the TSWV risk index (Brown et al. 2005). This approach has recently proven beneficial in reducing disease incidence and increasing yield with such improved cultivars like ‘Georgia-06G’ (Branch 2007).

Similarly, old virus isolates (collected in 1998) and new (2010) isolates of tomato spotted wilt virus (TS WV) have likewise not shown any evidence for positive selection (Sundaraj et al. 2014). Purifying selection, population expansion, and differentiation seem to have only temporarily influenced the TSWV population rather than positive selection induced by specific or vertical host-plant resistance.

Results from this long-term, 13-year study show that the TSWV-resistant Georgia Green cultivar was found to have consistently lower TSW and total disease incidence and higher pod yield compared to Florunner when planted early in mid-April each year. Consequently, this general or horizontal TSWV resistance appears to be stable across many years, and should continue to be utilized for future progress in breeding TSWV-resistant peanut cultivars.

**LITERATURE CITED**


