Late Leaf Spot Effects on Growth, Photosynthesis, and Yield in Peanut Cultivars of Differing Resistance

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ABSTRACT

Cercosporidium personatum **(Berk. & Curt.) Deighton causes late leaf spot (LLS) in peanut (*Arachis hypogaea* L.), which leads to necrotic lesions, early leaf senescence and yield losses. Detailed physiological analyses can contribute to an improved understanding of peanut-disease interactions and cultivar improvement. A study was conducted evaluating two peanut cultivars with more (York) and less (Carver) quantitative resistance to *C. personatum* grown under fungicide-sprayed and nonsprayed conditions in the field at Citra, FL over 2 yr. Data were collected on disease severity using the Florida 1 to 10 visual rating scale and by direct measurement of percent canopy lesion area. Leaf lifespan, total canopy photosynthesis (TCP), plant growth, and pod yield were also measured. Disease severity based on canopy lesion area was reduced by 30% in York compared to Carver. No additive effects of combining the resistant cultivar with fungicide were seen, as fungicide use increased yield by 364 kg ha^{-1} for both cultivars. Yield was more strongly related to disease severity based on canopy lesion area than to the Florida scale. Yield improvement with York was not as closely related to disease severity with only a 6% gain in pod yield in York compared to Carver. In addition, reduction in TCP was greater in York compared to Carver given their respective disease severity. These results indicated that combining resistance with the maintenance of physiological function during LLS infection could result in improved peanut yields under diseased conditions.**

Peanut is one of the major sources of protein and oil in the world. It is cultivated on 25 million ha in more than 100 countries, generating an annual production of nearly 38 Tg (FAO, 2008). Nevertheless, worldwide peanut production is severely hampered by the incidence of numerous diseases. Early leaf spot (caused by *Cercospora arachidicola* S. Hori), and late leaf spot [caused by *Cercosporidium personatum* (Berk. & Curt.) Deighton] are among the most widespread and damaging foliar diseases of peanut in the southeastern United States (Nutter, Jr. and Shokes, 1995). Pod yield losses can be >50% when fungicides are not applied (Shokes and Culbreath, 1997). In Florida, LLS is the predominant disease (Jackson, 1982), causing yield losses of up to 50% (Pixley et al., 1990a). Consequently, regular and costly fungicide applications are currently used to minimize yield losses from peanut diseases (Woodward et al., 2008; Monfort et al., 2004). Improved cultivars with moderate resistance to late leaf spot, along with other integrated disease management practices, have also been successfully used to reduce inputs and production costs (Woodward et al., 2010; Woodward et al., 2008; Monfort et al., 2004). However, the effects of LLS on the physiological responses in cultivars of differing leaf spot resistance is not well understood and could contribute to improved cultivar development for disease resistance.

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Cercosporidium personatum is a hemibiotropic soilborne fungal pathogen that infects peanut leaves and stems (Mims et al., 1988). The initial source of inoculum is primarily conidia from crop residues in the soil. Conidia are rain splashed or wind blown onto leaf surfaces where they initiate infection. Symptoms are first recognizable as small necrotic flecks that enlarge to dark brown lesions from 1 to 10 mm in size (Smith et al., 1992). Lesions generally develop within 10 to 14 d of initial infection. Symptoms are influenced by host genotype and environmental conditions, such as high temperature, rainfall, and relative humidity (Shew et al., 1988).

Peanut economic yield is a function of cumulative biomass and harvest index, which is determined by partitioning of assimilates to pod and effective duration of pod fill (Phakamas et al., 2008; Duncan et al., 1978). Premature loss of green leaf area (by necrotic tissue and defoliation) and reduction of leaf photosynthetic capacity due to disease contribute to a loss of canopy carbon assimilation, and thus a loss of yield. Many older peanut cultivars such as Florunner and Georgia Green are poor in resistance to LLS. Loss of leaf area due to accelerated senescence was reported to be the predominant mechanism of yield losses in these cultivars (Bourgeois and Boote, 1992; Boote et al., 1980). However, for cultivars with improved resistance to LLS that experience less defoliation, yield reduction may also be related to leaf physiological response to disease instead of to loss of leaf area alone.

The breeding and selection of cultivars with partial resistance to LLS has been an important part of integrated disease management programs for reducing yield losses in peanut. Several new releases have shown good resistance associated with delayed disease progress and decreased defoliation. Components of resistance identified include extended latent period of the fungus, reduced sporulation, and smaller lesion diameters (Chiteka et al., 1988; Dwivedi et al., 2002; Cantonwine et al., 2008). Selection

Abbreviations: DAP, days after planting; LLS, late leaf spot; stAUDPC, standardized area under disease progress curve; TCP, total canopy photosynthesis; TSMK, total sound mature kernels.

Table 1. Fungicide spray schedule for the field experiments at Citra, FL.

Spray	Fungicide
1	Chorothalonil (1.26)†
2	Chorothalonil (1.26)
3	Pyraclostrobin (0.18)
4	Azoxystrobin (0.33)
5	Chorothalonil (0.63) + Tebuconazole (0.23)
6	Chorothalonil (0.63) + Tebuconazole (0.23)
7	Chorothalonil (1.26)
8	Chorothalonil (1.26)

† Numbers in the parentheses denote the rate of fungicide application (kg a.i. ha^{-1}).

of these resistant cultivars is typically based on visual disease ratings (e.g., Florida 1–10 scale) that combine both visual lesion disease severity and defoliation (Gorbet and Tillman, 2008). Direct measures of canopy lesion severity using image analysis may improve estimates of disease severity, especially in resistant cultivars that exhibit decreased defoliation. While these measures of disease severity work well for monitoring disease dynamics, they do not always correlate well with yield reductions (Bergamin Filho et al., 1997; Jesus Jr. et al., 2001), due to a disconnect between the ratings and actual functional impairment (Bastiaans, 1991). In addition, host functional response to pathogens can be variable depending on environment, genotype, and physiological status (Zhang et al., 2009; Erickson et al., 2003).

Better understanding of the physiological responses to LLS related to yield in cultivars differing in resistance is needed to contribute to improved cultivar selection and modeling growth and yield responses of peanut to leaf spot. The objective of this study was to characterize LLS severity and its effects on growth and partitioning, leaf lifespan, canopy photosynthesis, and pod yield of York, a relatively resistant cultivar, compared to Carver, a cultivar with relatively poor resistance to LLS in a field environment.

MATERIALS AND METHODS

Experimental Site and Design

Field experiments were conducted during the 2008 and 2009 growing seasons at the Plant Science Research and Education Unit in Citra, FL (29°23'60" N, 82°12'0" W) on a Gainesville loamy sand (hyperthermic, coated Typic Quartzipsamments) soil. The experiment was a multifactorial design with the main factors being cultivar, fungicide application, and year. Cultivar and fungicide application were arranged in a randomized complete block (RCB) with four replications of each treatment. Two cultivars were selected for differences in resistance to LLS: Carver (Gorbet, 2006) has poor resistance to LLS; while York (D.W. Gorbet and B.L. Tillman, personal communication, 2006) has moderate resistance to LLS (Tillman et al., 2008). Fungicide application included: (i) no fungicide application and (ii) an industry standard fungicide schedule (Table 1) applied on a 14-d interval commencing from approximately 40 DAP. Fungicides were applied using a CO_2 backpack sprayer calibrated to deliver 328 and 374 L ha^{-1} during 2008 and 2009, respectively. A hand-held boom with five flat fan nozzles, spaced 45.7 cm apart was used to spray two rows at a time (spray coverage of 182 cm wide).

Plots were previously sown with bahiagrass (*Paspalum notatum* Fluegge) and rye (*Secale cereale* L.) in a 4-yr rotation with rye (nurse crop to establish bahiagrass) followed by 2 yr of bahiagrass and then peanut. Sowing occurred during the latter part of the recommended planting window for North Central Florida on 20 May in 2008 and 27 May in 2009 to maximize LLS pressure (Wright et al., 2006). Each plot consisted of six rows spaced 0.91 m apart and 4.6 m long. Each block was separated by 3.7-m fallow alleys and the entire study was surrounded by two border rows. Seeds were sown at a rate of 17 to 20 seeds per meter row using a conventional planter. In-furrow application of azoxystrobin was conducted at a rate of 0.16 kg a.i. ha^{-1} while planting to control soilborne diseases. Irrigation was applied as needed with a linear move system. Standard management practices for irrigated peanuts were employed during both years (Wright et al., 2006), including a 3-9-18 blended granular fertilizer that was broadcast before planting at a rate of 560 kg fertilizer ha^{-1} during both growing seasons. To satisfy the calcium requirement for pod and kernel formation, gypsum was broadcast at a rate of 2240 kg ha^{-1} split equally in two applications around 35 to 40 DAP followed by another application 10 to 14 d later. Disodium octaborate tetrahydrate was applied with the first two fungicide sprays at a rate of 5.6 kg ha^{-1} per application to supply B.

Measures of Disease Severity and Growth

Late leaf spot intensity was assessed with the widely used Florida 1 to 10 scale (Woodward et al., 2010; Gorbet and Tillman, 2008; Cantonwine et al., 2008; Chiteka et al., 1988). Values of 1 to 4 indicate increasing leaf spot incidence on leaflets within the lower or upper canopy, but no defoliation. Ratings from 4 to 10 are associated with increasing levels of defoliation (Chiteka et al., 1988). Ratings began when visual symptoms first appeared (87 and 77 DAP in 2008 and 2009, respectively) and continued every 7 to 10 d until harvest. Area under disease progress curve (AUDPC) values were calculated for each plot from these disease ratings (Shanner and Finney, 1977) and were standardized by dividing AUDPC values by the number of days from the first observed symptoms to harvest to account for differences in the duration of LLS epidemics (Woodward et al., 2008, 2010). Microscopic examination of lesions on leaflets indicated that *C. personatum* was the dominant pathogen in both years. We did not observe spotted wilt (caused by tomato spotted wilt virus) and while mold (caused by *Sclerotium rolfsii* Sacc.) in the field plots during both growing seasons.

Canopy defoliation and disease severity, the components that make up the Florida scale ratings, were also measured objectively throughout the growing season to compare to the more subjective Florida 1 to 10 scale assessment. Approximately biweekly, a randomly selected 61-cm segment of the outer two rows of each plot was harvested, minimizing disturbance or border effects on the inner two final harvest yield rows. A representative subsample excluding the largest and the smallest plants was selected from each harvested sample (Bourgeois et al., 1991; Pixley et al., 1990a). Forty leaflets were randomly selected throughout the canopy from this subsample plant. All leaflets were scanned at 300 dpi using a flatbed scanner (Microtek ScanMaker 5800, Microtek Int. Inc., Industrial Park Hsinchu, Taiwan) and stored as .tiff files. Leaf images were processed using ASSESS ver 2.0 image analysis software (American Phytopathological Society, St. Paul, MN) to give the percent canopy lesion area (Erickson et al., 2003). The AUDPC values for serial measurements of canopy lesion area were calculated and standardized for each plot similarly to the AUDPC values from the Florida 1 to 10 scale disease progression assessment. The remaining harvested sample was immediately

oven dried for 72 h at 60°C and subsequently weighed. Leaflets and pods were separated from all subsamples. Pods were counted and then leaves, stems, and pods were oven dried to a constant mass. Stem, leaf, and pod dry weights (DW) were determined for the entire sample by multiplying their respective fractions of the subsample times the total weight of the harvested sample.

In the central two rows of each six-row plot, five plants were chosen at random and the first fully expanded leaf on each main stem was tagged using colored plastic tags at 49 and 92 DAP in 2008, and at 50, 65, and 79 DAP in 2009. These leaves were examined at weekly intervals until defoliation to calculate the total leaf lifespan in days for all the leaflets.

Measures of Canopy Photosynthesis and Yield

Starting approximately 35 DAP, a 61-cm section of row was selected randomly from the outer two rows to measure canopy photosynthesis. Measurements were taken at 10 to 15 d intervals, using a 91 by 61 cm aluminum-frame mylar chamber and a portable photosynthesis system (LICOR LI-6200, Li-Cor Inc., Lincoln, NE) as explained by Bourgeois and Boote (1992). Carbon exchange rate was measured on two plots from each treatment under full sunlight and total darkness (achieved by covering the large chamber with a black plastic sheet) conditions between 1000 and 1400 h. Measured carbon exchange rates under dark conditions were considered to represent canopy, root, and soil respiration. Total canopy photosynthesis (TCP, Boote et al., 1983) was calculated by adding the absolute dark respiration to the observed carbon exchange rate.

The central two rows of each six-row plot in each genotype were dug at maturity (determined by hull scrape method; Williams and Drexler, 1981) using a conventional two-row digger-shaker inverter. Plants were allowed to sun-dry in the field for 3 to 4 d. Afterward, stationary threshers were used to harvest pods. Peanut yields were determined after drying to uniform moisture content of 9% (wt/wt). Sprayed plots of Carver were inverted at 135 and 127 DAP in 2008 and 2009, respectively. Nonsprayed plots were harvested approximately 7 d earlier in each year due to leaf spot pressure. Both sprayed and nonsprayed York plots were inverted on 149 and 145 DAP, respectively.

In 2009, a subsample of 200 g of pods per plot was subjected to a standard analysis for peanut quality. Pod samples were graded using standard farmer stock grading equipment in accordance with the federal-state inspection service method. Pod grades were defined as percent total sound mature kernels (TSMK) which included sound mature kernels and sound split kernels.

Statistical Analysis

Statistical analyses were performed using analysis of variance procedures in the GLIMMIX procedure of SAS (SAS Institute, 2009). Cultivar, fungicide regime, year, and their interactions were considered fixed effects and block by year as a random effect. Degrees of freedom were determined using the Kenward–Roger method. Where significant ($P < 0.05$) fixed effects were seen, pairwise comparisons were made using the LSMEANS statement with TUKEY method. Relations between yield and disease severity were analyzed using linear regression procedures.

Statistical analyses of total biomass and its partitioning, and TCP were performed using nonlinear regression procedures of the nlme library of R (R Development Core Team, 2008). A 3-parameter logistic function (Eq. [3] in Yin et al., 2003)

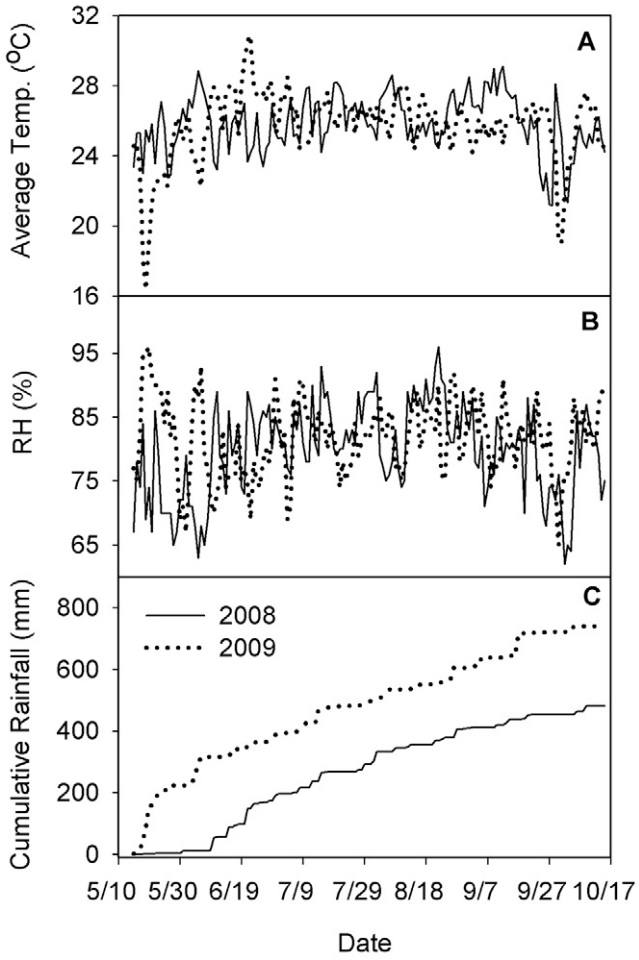

Fig. 1. (A) Average daily temperature, (B) relative humidity, and (C) cumulative rainfall for the field experiment during the study period (Source: Florida Automated Weather Network, Citra, FL).

was employed to fit stem, pod, and total biomass data, which provided a y-asymptote value, shape parameter related to growth rate, and DAP value at inflection point, which represent the DAP at half of the maximum value on the *y* axis. Leaf weight and TCP were fit with a 3-parameter gaussian function (Gauch, Jr. and Chase, 1974), which provided the maximum value on the *y* axis, DAP at which the maximum value was achieved, and a peak width parameter at 1/2 of the maximum value. Analysis of variance was run on these parameters using GLIMMIX of SAS, as explained earlier (except for TCP as data was collected for only two replicates). Results of this analysis were reported only when significant.

RESULTS

Growth Environment

Environmental conditions during the 2008 and 2009 growing seasons were quite favorable for LLS development (Fig. 1). Rainfall from mid-May through harvest in mid-October was 481 and 745 mm in 2008 and 2009, respectively. This precipitation was received in 58 events in 2008 and 74 events in 2009. Irrigation was not applied in either year after onset of disease as rainfall was adequate for crop growth. Average daily temperature during the same period was 25.8 and 25.5°C in 2008 and 2009, respectively. Relative humidity ranged from 62 to 96% in 2008 and 65 to 96% in 2009.

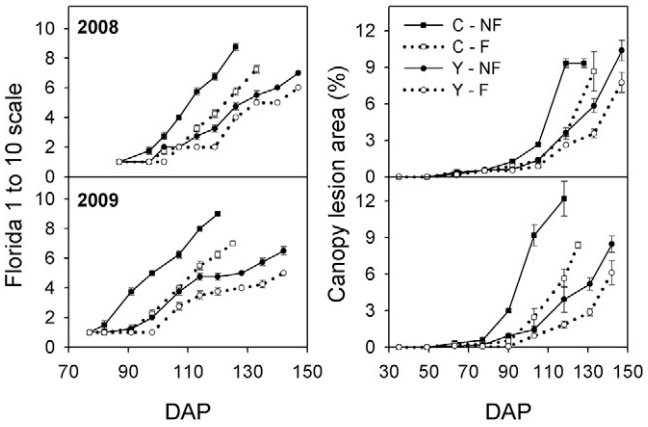

Fig. 2. Progress of late leaf spot as estimated with the Florida 1 to10 scale and percent canopy lesion area during 2008 and 2009 growing seasons for the two peanut cultivars (C-Carver; Y-York) grown under fungicide sprayed (F) and nonsprayed (NF) conditions. Vertical bars greater than symbols represent ± standard error of the mean (*n* = 4).

Disease Assessment

Late leaf spot epidemics occurred in both years of the study, but appeared earlier in 2009 compared to 2008 (Fig. 2) consistent with more frequent and abundant rainfall in 2009 compared to 2008. Late leaf spot symptoms were first observed visually in the field around 95 and 80 DAP during 2008 and 2009 on both cultivars, respectively. Carver, the less resistant cultivar, showed more rapid disease progress than York during both years, especially in nonsprayed plots. Fungicide delayed the initial progress of disease symptoms in both cultivars (Fig. 2).

Standardized values for the area under disease progress curves for both Florida 1 to 10 scale ratings (st$AUDPC_{FL}$) and percent canopy necrotic lesion area (st$AUDPC_{Les}$) were generally in good agreement and showed significantly reduced disease intensity associated with fungicide inputs and with the moderately resistant cultivar York compared to the poorly resistant cultivar Carver (Table 2). For example, st$AUDPC_{Les}$ and st$AUDPC_{FL}$ were 30 and 19% lower in York compared to Carver, respectively. Similarly, fungicide-sprayed plots showed a 43% reduction in st$AUDPC_{Les}$ and a 26% reduction in st$AUDPC_{FL}$ compared to nonsprayed plots. A significant year × cultivar × fungicide effect on st$AUDPC_{Les}$ resulted from higher values in York in 2008 compared to 2009, whereas higher values in Carver were seen in 2009 compared to 2008 (Table 2). This pattern was not seen in st$AUDPC_{FL}$, as 2009 values were significantly higher in both cultivars, resulting in a significant year effect.

Plant Growth and Development

Although the cultivars did not differ ($P > 0.05$) in their maximum stem or leaf DW (or leaf area index, data not shown), Carver achieved maximum leaf DW 10 d earlier ($P = 0.03$, Fig. 3) and the DAP value at inflection was 10 d earlier ($P < 0.001$) for stem DW. Maximum leaf DW was attained at 79 and 89 DAP in Carver and York, respectively, across both growing seasons. In both years, following attainment of maximum leaf DW, we observed defoliation in all treatments, but defoliation in nonsprayed plots generally exceeded that of fungicide-sprayed plots, as indicated by narrower peak widths for leaf DW ($P < 0.01$). This effect was greater in Carver compared to York as leaf lifespan data of tagged leaf cohorts showed greater differences in leaf lifespan in sprayed plots compared to nonsprayed plots for Carver (Table 3). In addition, defoliation occurred more quickly and to a greater extent in Carver compared to York, as indicated by narrower peak widths ($P = 0.03$) in Carver (Fig. 3). Notably, partitioning to leaf and stem weight largely occurred before appreciable disease was found,

Table 2. Treatment means (*n* = 4) and analysis of variance results for standardized area under the disease progress curve for Florida 1 to 10 scale (st$AUDPC_{FL}$) and percent canopy lesion area (st$AUDPC_{Les}$), pod yield, pod number, average pod weight, and total sound mature kernels (TSMK). Fungicide treatments were no fungicide application (NF) and standard 14-d calendar based application (F). Cultivars were Carver (C) and York (Y).

Year	Cultivar	Fungicide treatment	st$AUDPC_{FL}$	st$AUDPC_{Les}$	Pod yield	Pod no.	Pod weight	TSMK
					kg ha^{-1}	m^{-2}	g	%
2008	C	NF	4.13	3.36	3098	406	0.95	–†
		F	3.11	2.23	3290	395	0.95	–
	Y	NF	3.45	2.97	2925	284	1.03	–
		F	2.71	2.06	3122	354	1.08	–
2009	C	NF	5.17	4.93	2498	509	0.90	72.7
		F	3.51	2.25	3144	533	0.92	75.2
	Y	NF	3.78	2.53	3136	511	0.87	74.9
		F	2.91	1.39	3556	550	0.90	74.7
Significance								
Cultivar (Cult)			***	***	*	ns‡	ns	ns
Fungicide (Fung)			***	***	***	ns	ns	ns
Cult × Fung			***	**	ns	ns	ns	ns
Year (Yr)			*	ns	ns	*	*	–
Cult × Yr			**	***	***	*	*	–
Fung × Yr			*	**	*	ns	ns	–
Cult × Fung × Yr			ns	*	ns	ns	ns	–

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

† Data not recorded.

‡ ns = $P > 0.05$.

whereas much of the partitioning to pod weight occurred after disease (Fig. 3). For example, DAP at inflection for stem weight in Carver was at 53, while DAP for pod weight was 82. In addition, DAP value at inflection for pod weight occurred sooner ($P < 0.001$) in Carver (82 DAP) compared to York (101 DAP).

Canopy photosynthesis was in agreement with seasonal patterns of leaf and stem accumulation, as maximum TCP occurred at 70 DAP in Carver and 80 DAP in York, but maximum TCP was similar between cultivars (Fig. 4). In addition, similar peak width values indicated similar declines in TCP between cultivars, despite disease progress that was comparatively slower in York than Carver (Fig. 2). However, fungicide application resulted in a slower decline in TCP, as indicated by a peak width of 34 d in fungicide-sprayed plots compared to 28 d in their nonsprayed counterparts (Fig. 4).

Pod Yield and Quality

Mean pod yields across all treatments ranged from 2500 to 3500 kg ha^{-1} (Table 2). Fungicide application resulted in a significant increase in pod yield (12.5%) over nonsprayed plots. However, there was a significant year × fungicide interaction whereby differences were significant in 2009, but not in 2008. Averaged across all treatments, pod yields were not different among growing seasons ($P = 0.71$). This was due to a significant cultivar × year interaction, whereby the poorly resistant cultivar (Carver) outyielded the moderately resistant cultivar (York) in 2008, whereas the opposite was true in 2009. Notably, there was no cultivar × fungicide interaction seen in either year of the study, indicating no diminished response of fungicide on absolute yield gain with improved cultivar. Averaged across all treatments, number of pods per unit area was greater ($P = 0.03$) while average pod size was smaller ($P < 0.01$) in 2009 compared to 2008. Pod yield was negatively related to stAUDPC$_{FL}$ and stAUDPC$_{Les}$ and the slopes of these relationships were not affected by cultivar or fungicide schedule (Fig. 5). Overall, the relationship between pod yield and stAUDPC$_{Les}$ was better than that between pod yield and stAUDPC$_{FL}$, which was especially evident at relatively low disease severities. Finally, neither cultivar nor fungicide affected peanut TSMK during 2009 (Table 2).

DISCUSSION

The overall objective of the present study was to gain an improved understanding of peanut response to disease by looking at effects of LLS on peanut physiology, growth, and yield of two cultivars differing in resistance, which will be important for continued cultivar improvement and lower fungicide input in peanut production. We found that the more resistant cultivar contributed to delayed disease progress, which resulted in slower development of canopy lesion area and less defoliation. Improved yield in the more resistant cultivar was seen in 1 yr of the study when the LLS disease severity was high. We also found no additive effects of combining improved cultivar resistance and application of fungicide on pod yield, as the absolute gains in yield associated with fungicide treatment were the same between both cultivars across both years of the study. Pod yield was better related to stAUDPC$_{Les}$ compared to stAUDPC$_{FL}$. Finally, we found that TCP declined similarly in both cultivars despite the slower progress of disease noted in the more resistant cultivar.

Delayed disease progress in more resistant cultivars like that seen in the present study has been demonstrated in other studies using the Florida 1 to 10 scale ratings (Woodward et al., 2010; Monfort et al., 2004) and canopy disease severity (Pixley et al., 1990b). Visual disease presence in the improved cultivar appeared to start at the same time as in the less resistant cultivar during both years; however, the progress of the disease was slower in the improved cultivar. This differing pattern of disease progress could be explained by several factors including a reduced number of

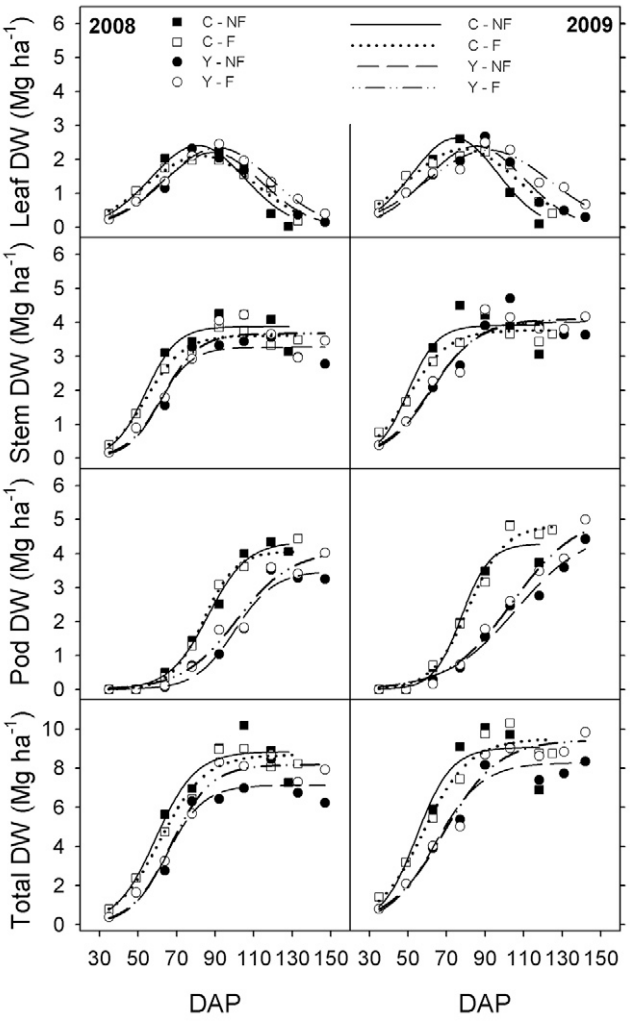

Fig. 3. Leaf, stem, pod, and total dry weight (DW) vs. days after planting (DAP) for two peanut cultivars Carver (C) and York (Y) grown under fungicide sprayed (F) and nonsprayed (NF) conditions at Citra, FL during 2008 and 2009. Symbols represent treatment means ($n = 4$) while regression lines represents gaussian (for leaf biomass) and logistic (for stem, pod, and total biomass) model fits.

Table 3. Treatment means ($n = 4$) for leaf lifespan of leaf cohorts tagged at different times (DAP) throughout the growing season. Fungicide treatments were no fungicide application (NF) and standard 14-d calendar based application (F). Cultivars were Carver (C) and York (Y).

		Tagging date (DAP)				
		2008		2009		
Cultivar	Fungicide treatment	49	92	50	65	79
		d	d	d	d	d
C	NF	66ab†	29c	53b	41c	31c
	F	69a	38b	62a	50a	42a
Y	NF	63bc	44a	52b	43bc	35b
	F	60c	47a	47c	44b	42a

† Numbers followed by the same letter within a column do not differ ($P > 0.05$).

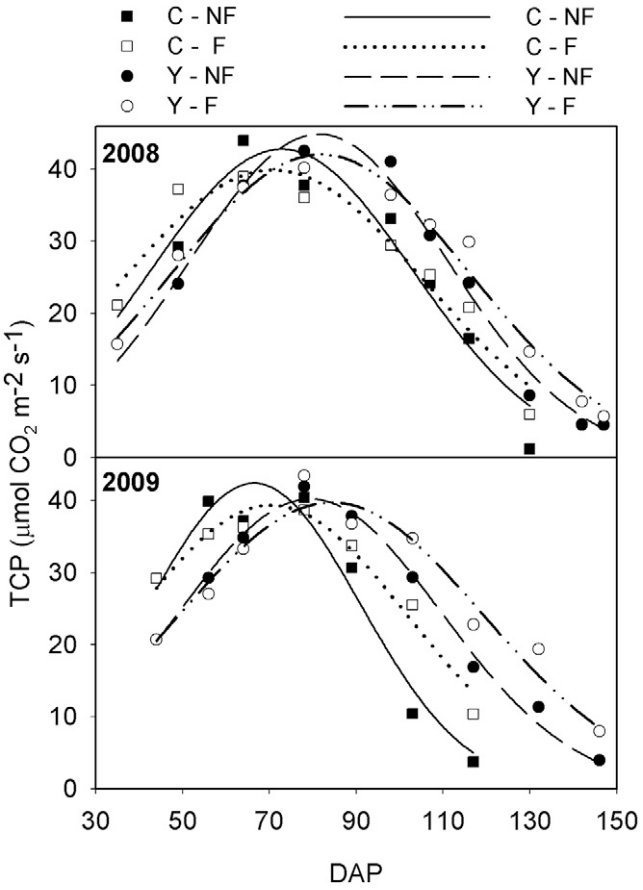

Fig. 4. Mid-day total canopy photosynthesis (TCP) for two peanut cultivars (C-Carver; Y-York) grown under fungicide sprayed (F) and nonsprayed (NF) conditions at Citra, FL during 2008 and 2009. Symbols represent treatment means (*n* = 2) while regression lines represents gaussian model fits.

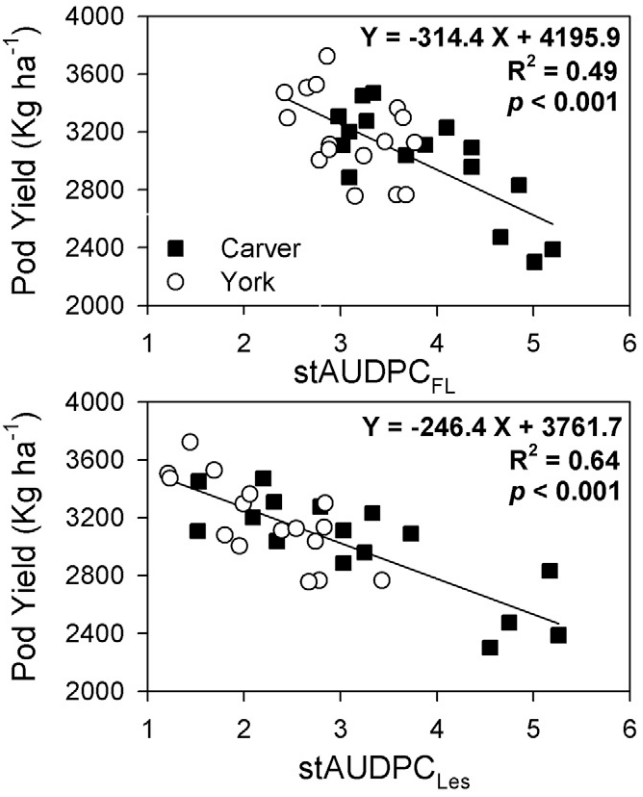

Fig. 5. The relationship between pod yield and the standardized area under the disease progress curve based on the Florida 1 to 10 scale (st$AUDPC_{FL}$) and percent canopy lesion area (st$AUDPC_{Les}$) for the two peanut cultivars, Carver (C) and York (Y).

initial infection points (foci) and/or differences in the latent period of the fungus. Prior studies have found little difference in the incubation period among a wide range of peanut genotypes, while the latent period tended to be longer in more resistant genotypes, which resulted in slower temporal progression of the disease (Cantonwine et al., 2008; Dwivedi et al., 2002; Chiteka et al., 1988).

Although the 14-d calendar-based fungicide program did not achieve 100% disease control, fungicide application delayed the progress of disease symptoms (Pixley et al., 1990b; Bourgeois et al., 1991). Substantial necrosis and defoliation due to LLS was observed in the control plots (Fig. 2, 3, and 4; Table 3) during both growing seasons which is typical for nonsprayed peanut. This was also observed by other studies conducted under different growing seasons and locations (Woodward et al., 2010; Monfort et al., 2004). Our study also showed that yield benefits associated with applying fungicide did not differ significantly between cultivars varying in their resistance to LLS. Therefore, based on our results, growers might be reluctant to reduce fungicide applications even on more resistant cultivars. However, other studies have shown nonsignificant yield losses in more resistant cultivars with reduced fungicide application compared to a 14-d calendar-based schedule (Woodward et al., 2010; Monfort et al., 2004). This discrepancy might be due to differences in peanut cultivars, LLS severity, environment, and/or fungicide schedule.

Resistance to LLS in southeastern United States runner-type peanut cultivars has generally been associated with later maturing varieties that possess a later onset of pod fill and a reduced pod growth rate, but possess longer effective pod-fill duration (Pixley et al., 1990a). In the present study, York showed later initiation of pod fill, slower pod growth rate, and longer duration of pod fill compared to Carver (Fig. 3). Implications of these growth patterns for LLS effects on yield depended on onset of the disease epidemic in our study. In 2008, when LLS was relatively late in arrival, partitioning to pod yield was nearly complete in Carver, and thus relatively high yields were attained with Carver with little effect of fungicide on yield. In contrast, in 2009 when LLS arrived about 2 wk earlier compared to 2008, LLS effects on pod yield were greater and effect of fungicide was greater. Thus, where later planting dates are desired (e.g., to minimize incidence of tomato spotted wilt virus), cultivars with improved LLS resistance are beneficial. Finally, since LLS had no effect on TSMK or average pod size in our study (Table 2), the determinant of yield impacted by LLS was pod number, which is consistent with the Phakamas et al. (2008) study that showed that peanut yield was primarily determined by pod number and not pod size across genotypes.

Relations between yield and disease severity measurements are often weak (Jesus, Jr. et al., 2001); however in our study we found significant regression relationships (Fig. 5). This finding may be due to the wide ranges of disease severity and yield observed in our study. In addition, yield was more strongly related to st$AUDPC_{Les}$ compared to st$AUDPC_{FL}$. This suggests that pod yield response to disease epidemics is better explained by measured canopy lesion area rather than the visually determined Florida 1 to 10 scale, which is likely due to

the fact that $stAUDPC_{Les}$ was determined using an objective digital image analysis instead of subjective visual ratings.

While pod yield reductions were generally related to disease ratings (Fig. 5), yield reductions in York due to LLS were greater than the ratings indicated. Reduction in disease severity under nonsprayed conditions in York compared to Carver were 22 and 34% based on $stAUDPC_{FL}$ and $stAUDPC_{Les}$, respectively. Moreover, the leaf lifespan in nonsprayed York was longer than Carver (Table 3). However, this relatively lower disease severity resulted in only 8% yield improvement in York compared to Carver. Thus, the yield improvement in York was not proportional to the reduction in disease severity in this study. One potential explanation for this disconnect between disease reduction and yield improvement is the existence of at least two separate mechanisms: (i) the ability to sustain leaf photosynthesis during disease progression and (ii) resistance to the progression of disease symptoms. In our study, the more resistant cultivar, York, may lack the ability to sustain photosynthesis at a given disease severity. This idea is supported by similar reductions in TCP in both York and Carver despite reduced disease severity in York (Fig. 2). Thus, a combination of LLS resistance (i.e., delayed disease progress) combined with host physiological tolerance (i.e., maintenance of physiological function in the presence of disease) may offer the most promising approach for peanut cultivar improvement and reduced fungicide input production systems.

In conclusion, this study demonstrates that cultivar resistance is an important component for integrated disease management of LLS in peanut, particularly during years with high disease pressure. Nevertheless, we observed no diminished effect of fungicide with improved cultivar on absolute yield gain. So, foliar application of fungicide still seems to play an important role in minimizing damage caused by LLS epidemics. Despite substantial reduction in disease severity and defoliation in the resistant cultivar York, yield improvement over the less resistant cultivar, Carver, was marginal and most beneficial under heavy LLS pressure. We attributed these findings in part to a lack of improved physiological tolerance to LLS in York. These results indicate that combining resistance to disease progression with enhanced ability to sustain canopy photosynthetic capacity in the cultivar selection procedure could provide significant improvement in our efforts to improve peanut yields under diseased conditions.

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