Disease Detection and Losses

Reduction in Plant Development, Yield, and Grain Quality Associated with Wheat Spindle Streak Mosaic Virus

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ABSTRACT

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Wheat spindle streak mosaic virus (WSSMV) caused severe reductions in yield and grain quality of wheat cultivars Florida 301, Florida 302, and Coker 797. Coker 797 is the most susceptible cultivar, on the basis of the various yield and quality criteria. The resistant cultivars Stacy and Coker 916 sustained no significant reduction in any component of yield or grain quality from infection by WSSMV. Most damage began during the winter, 30–60 days after planting, when a rapid increase in WSSMV concentration, documented by enzyme-linked immunosorbent assay (ELISA), was associated with significant reduction in tillering and plant biomass of susceptible cultivars. During one season, record low temperatures in late January further contributed to yield reduction, due to the death of WSSMV-weakened plants. Anthesis was delayed 7–10 days in WSSMV-infected plants, and maturity was delayed 5–7 days. Reduced growth and development of surviving tillers of susceptible cultivars resulted in significant reduction in biomass, 1,000-kernel weight, and test weight. The milling and baking qualities of grain from plants affected with wheat spindle streak mosaic were reduced to unacceptable levels during one season, when 1,000-kernel weight and test weight were severely reduced. Milling and baking qualities were affected less during a second season. A delay in planting beyond recommended dates did not reduce disease incidence or severity, because soil temperatures and moisture conditions were favorable for infection throughout the winter. Resistant cultivars harbor WSSMV in roots, as documented by ELISA. The ELISA data indicate that resistance is related to reduced virus concentration in resistant cultivars. *Polymyxa graminis* cysts were also observed in roots of all cultivars.

Wheat spindle streak mosaic virus (WSSMV) was identified for the first time in the southeastern United States in 1984 (1). The virus is soilborne and vectored by the fungus *Polymyxa graminis* Ledingham. A survey of wheat fields revealed that wheat spindle streak mosaic (WSSM) was widespread in Georgia and was always associated with the planting of cultivars Florida 301 (CI 17769) and Coker 797. Significant yield losses with Florida 301 were documented in two fields. These two cultivars comprised about half of the area (200,000 ha) planted in Georgia in 1984. At least as many hectares were planted in neighboring states. Studies were designed to investigate further the susceptibility of these and other cultivars and yield loss associated with WSSM. The initial phases of the disease were studied as well as the subsequent effects on plant development, components of yield, and milling and baking qualities of grain.

MATERIALS AND METHODS

Experiments were conducted during two seasons in a field naturally infested with WSSMV at Plains, Georgia. The virus and vector were confirmed to be in this field, as reported previously (1). A portion of this land was fumigated with methyl bromide to kill the vector, *P. graminis*, and therefore drastically reduce WSSMV inoculum (7). Experiments were a factorial in a randomized complete block design. Fumigated and unfumigated treatments constituted the main blocks. Three and five wheat cultivars varying in susceptibility to WSSM were compared during two consecutive seasons.

1984–1985 season. Florida 301, Coker 797, and Stacy (CI 17861) were planted on 15 November, near the optimum planting time for the coastal plain region of the state. There were six replications of each cultivar in the unfumigated plots and three replications in the fumigated plots. The cultivars were planted in seven-row plots, 1.3 × 3.8 m. Samples were taken from each plot in early March to test for the presence of the virus with enzyme-linked immunosorbent assay (ELISA) and for microscopic examination of roots for cysts of *P. graminis*. The number of tillers per meter of row was counted twice in early spring. Plant height was measured at decimal growth stage (GS) 71 (10). Yield components determined were grain yield, straw weight, total biomass (weight of grain plus straw), harvest index (grain yield divided by total weight of grain and straw), 1,000-kernel weight, and test weight. Grain yield data were adjusted to 13% moisture. To test seed viability, 100 seeds per replicate from all treatments were germinated at 20 C.

Grain from all replicates of each treatment were bulked following determination of yield components. Samples were sent to the Soft Wheat Quality Laboratory of the U.S. Department of Agriculture at Wooster, Ohio, for analysis of milling and baking characteristics.

1985–1986 season. The experiment was expanded in 1985–1986 to include the susceptible cultivar Florida 302 and the resistant cultivar Coker 916. The plots were established in the same field near the site of the previous year's test. The experimental design was the same except that there were four replicates of each cultivar in both the fumigated and the unfumigated treatments. Planting was delayed until 18 December because of wet weather and the time needed for soil fumigation. This is about 1 mo later than the recommended planting date for the area. Winter temperatures were mild, and uniform growth occurred, so that plants were well tillered by mid-February.

A spring infestation of Hessian fly had some effect on the susceptible cultivar Coker 916 in the spring of 1986. Yield was reduced slightly, but the number of tillers affected was proportionally the same in both the fumigated and the unfumigated treatments. During both seasons the spring was dry, and there was no interference by foliar pathogens.

Plants were dug from 1-m sections of an outside row of each replicate, 35, 63, and 97 days after planting, for biomass determination. Samples were placed in an ice chest in the field and then stored at 5 C overnight. The roots were washed free of soil, divided into root and shoot portions, and then dried and weighed.

Plant height and growth stage were recorded four times between GS 37 and GS 76. Yield components and milling and baking quality data were determined as in the previous season.

Enzyme-linked immunosorbent assay. The double-antibody sandwich ELISA procedure employed was similar to that described by Lister (4), with the exception that antigen buffer contained a high molarity (0.4 M) of phosphate (2) and 0.1 M sodium ethylenediaminetetraacetate. Immunoglobulins (polyclonal) against the Georgia WSSMV isolate and WSSMV antiserum from K. Haufler, at Michigan State University, prepared by $(NH_4)_2SO_4$ precipitation, were used at 10 μg/ml. The enzyme conjugates were used at a 1:500 dilution. Antiserum to wheat soilborne mosaic virus, produced by M. Brakke, was obtained from S. Tolin, at Virginia Polytechnic Institute and State University.

Seven to eight samples each of root and shoot tissue were selected randomly from the plants harvested, immediately after washing, for dry-weight determinations. The tissues were stored at 2 C for 2–3 hr until they were triturated with mortar and pestle. ELISA plates were the 96-well Dynatech Immulon II (Dynatech Laboratories, Inc., Alexandria, VA). Three virus controls, three healthy controls, and three blank wells were randomly distributed in each plate. Test sample triturate (200 μl) was added to each of two wells. All ELISA reactions were assessed by reading absorbance at 410 nm in a Dynatech ELISA reader. Absorbance values for blank wells were subtracted from absorbance values from plate wells containing healthy controls, to give absorbance values of healthy controls. These values varied with the cultivar and age of the tissue. Samples judged positive for WSSMV had absorbance values at least twice as large as those of the healthy controls.

Milling and baking qualities of grain. Milling and baking quality scores were determined by a series of tests for flour yield and factors affecting baking quality. The weighted composite scores for milling quality and for baking quality were calculated relative to a standard for the test.

RESULTS

Plant development. Temperatures were above normal through most of December 1984, resulting in rank foliar growth. This was followed by record low temperatures of −17 C on 20–21 January. Leaves of all plants were killed, but recovery varied according to treatment. The plots were examined for WSSM symptoms on 25 February, when substantial regrowth of surviving plants had occurred. Florida 301 and Coker 797 were severely affected in unfumigated plots. All plants exhibited symptoms typical of WSSM and were stunted, with significantly fewer tillers than the controls (Table 1). In fumigated plots, the number of tillers of Florida 301 and Coker 797 was reduced somewhat because of cold injury alone. Stacy recovered with little damage, and the number of tillers was uniformly high in both the fumigated and the unfumigated plots; therefore the tillers were not counted. A second tiller count was made on 13 March. The number of tillers increased in all treatments except Coker 797 planted in unfumigated soil (Table 1). The number of Coker 797 tillers declined because some small young tillers of these severely diseased plants were not able to survive.

Plant height of the susceptible cultivars Florida 301 and Coker 797 was reduced significantly, and maturity was delayed 5 to 7 days by WSSM. The height of Stacy was not reduced significantly in the unfumigated plots, and there was no difference in maturity between the two treatments (Table 1).

The winter of 1985–1986 was mild, and plants became uniformly established within the plots. Tillers were counted when the plants were at GS 65–71. Fewer tillers were produced in that season than in the previous season, as a result of the later planting date, but the response to WSSM was similar (Table 2). The number of tillers of the three susceptible cultivars was significantly reduced; the greatest reduction was in Coker 797 in the unfumigated soil. Stacy and Coker 916 did not have a significant reduction in number of tillers.

TABLE 1. Effect of wheat spindle streak mosaic virus on yield components of three wheat cultivars, 1984–1985

Cultivar	Soil treatment[w]	Tillers per meter		Plant height (mm)	Total biomass[x] (g)	Straw weight[x] (g)	Grain yield (kg/ha)	Harvest index	1,000-kernel weight (g)	Test weight (kg/hl)
		25 Feb.	13 Mar.							
Stacy	Fumigated	—	—	698 a[y,z]	4,983 a	3,001 a	3,943 a	0.40 a	34.76 a	75.1 a
	Unfumigated	—	—	650 a	4,880 a	2,852 a	4,080 a	0.42 a	34.50 a	75.3 a
Florida 301	Fumigated	143 a	164 a	917 a	3,960 a	1,939 a	4,192 a	0.51 a[z]	38.85 a	76.1 a
	Unfumigated	77 b	94 b	487 b	1,878 b	998 b	1,831 b	0.47 a	31.86 b	66.5 b
Coker 797	Fumigated	107 a	139 a	648 a	2,763 a	1,320 a	2,949 a	0.52 a	32.59 a	75.9 a
	Unfumigated	36 b	31 b	383 b	458 b	273 b	397 b	0.41 b	20.37 b	56.0 b

[w] All plants in fumigated plots were symptomless; Florida 301 and Coker 797 in unfumigated plots were 100% infected with wheat spindle streak mosaic virus.
[x] Mean weight from 4.84-m^2 plots.
[y] In each pair, means followed by the same letter are not statistically different according to the unpaired *t* test using PROC TTEST (SAS Institute) at $P = 0.05$.
[z] Significant at $P = 0.10$.

Plant height and growth stage were determined four times during April, between GS 37 and GS 76. Data are presented for the first and last dates measurements were made (Table 2). Plant height of all susceptible cultivars was greater ($P = 0.05$) in fumigated plots (Table 2). WSSM-stunted Florida 301, Florida 302, and Coker 797 were only about half as tall as their counterparts in the fumigated area on 1 April. Their height was only 75–80% of that of the healthy plants by the time stem elongation ceased, in late April. Development of the WSSM-stunted plants was about 10 days behind that of the healthy plants on 1 April and 5 to 7 days behind on 30 April. This delay continued until crop maturity. The height of the two resistant cultivars also was significantly less in the unfumigated area on 1 April, but the differences were considerably less by GS 72, on 30 April (Table 2).

The wheat was at the two- to three-leaf stage, 35 days after planting, when the first plants were dug for biomass determinations. All plants in fumigated and unfumigated plots had uniform growth and appearance, and there was no difference in biomass between the soil treatments for any cultivar (Fig. 1).

There were perceptible differences in plant growth and color in mid-February (63 days after planting). The susceptible cultivars Florida 301, Florida 302, and Coker 797 were uniformly chlorotic and exhibited mosaic symptoms in the unfumigated plots. Coker 916 and Stacy were uniformly green and had considerably more foliage than Florida 302 and Coker 797 in unfumigated plots. Florida 301 grows considerably more than the other two cultivars during the winter. Although its growth was reduced by WSSM in the unfumigated plots, its shoot dry weight was comparable to that of Stacy and Coker 916 on this sampling date. The plots of all cultivars planted in the fumigated area were green and uniform, with the exception of two plots of Florida 301. Plants along the edge of both plots were partly stunted and the plants exhibited WSSM symptoms. This apparently was due to incomplete soil fumigation. Growth of the susceptible cultivars in the fumigated area was considerably better than that of their counterparts in the unfumigated area.

Plants were at GS 31–36 when the third biomass sample was collected, 97 days after planting. Differences in plant height and tiller numbers between WSSMV-infected plants in unfumigated plots and plants in fumigated plots of the three susceptible cultivars were more pronounced than on the previous sampling date. This was also reflected in greater differences in root and shoot dry weight than on the previous sampling date (Fig. 1). Coker 916 plants in the fumigated plots also were taller and appeared to have denser growth. Some Coker 916 plants in the unfumigated area had mild chlorosis and occasional mottling.

Yield components. WSSM significantly reduced grain yield, total biomass, straw weight, 1,000-kernel weight, and test weight of Coker 797 and Florida 301 in 1984–1985 (Table 1). The disease did not reduce any yield component of Stacy. The WSSM-affected plants of Coker 797 yielded 397 kg/ha, which would have represented a total loss if this had been a commercial field, because the value of the grain was less than the cost of harvesting it. The test weight of the grain, 56 kg/hl (43.4 lb/bu), also made it unacceptable for commercial use. Seed germination was not affected by WSSMV. Germination was 97–100% for all cultivars.

During the 1985–1986 season, yields of the WSSM-susceptible Florida 301, Florida 302, and Coker 797 were reduced 33, 59, and 64%, respectively (Table 2) in the unfumigated plots. Yields of the WSSM-resistant Stacy and Coker 916 were reduced 6.5 and 8.5%, respectively, in the unfumigated plots, but these differences were not statistically significant.

Test weight was significantly reduced by WSSM for all three susceptible cultivars (Table 2). The reduction for Florida 302 (8%) was the greatest difference among all cultivars. As in the previous season there were no differences in seed germination.

The 1,000-kernel weight response was variable in 1985–1986. Both resistant cultivars had significantly higher 1,000-kernel weight in the unfumigated treatment (Table 2). Among the susceptible cultivars, only Florida 302 had a reduction due to WSSM. These inconsistencies are related to drought stress. Although the plots were irrigated twice, leaves died prematurely in all treatments. The fumigated plots, which had more tillers, had relatively more water stress and thus produced smaller seed. The result of drought stress was to mask the effects of WSSM on 1,000-kernel weight.

Harvest index. The harvest index was variable in both seasons (Tables 1 and 2). Because WSSM affected plant height, both straw and grain weight were affected. Drought stress also affected the harvest index in 1985–1986. The harvest index of the resistant cultivars Stacy and Coker 916 was greater in the unfumigated treatment (Table 2).

Virus concentration. ELISA was used to follow the onset of root and shoot infection and the subsequent increase in WSSMV concentration in the five wheat cultivars. WSSMV was detected in roots of all cultivars in late January, 35 days after planting, in the unfumigated soil (Fig. 2). The virus concentration (based on ELISA values) in the three susceptible cultivars was higher than in

TABLE 2. Effect of wheat spindle streak mosaic virus on yield components of five wheat cultivars, 1985–1986

Cultivar	Soil treatment[u]	Tillers per meter	Plant height (mm)		Total biomass[x] (g)	Straw weight[x] (g)	Grain yield (kg/ha)	Harvest index	1,000-kernel weight (g)	Test weight (kg/hl)
			1 Apr.[v]	30 Apr.[w]						
Stacy	Fumigated	97 a[y]	610 a	830 a	4,207 a	2,202 a	4,481 a	0.47 b	31.20 b	75.0 a
	Unfumigated	90 a	510 b	810 b	3,630 a	1,759 b	4,188 a	0.51 a	33.06 a	75.7 a
Coker 916	Fumigated	109 a	560 a	780 a	3,459 a[z]	1,419 a	4,608 a	0.59 b	32.66 b	75.4 a
	Unfumigated	88 a	460 b	700 b	3,070 a	1,192 b	4,217 a	0.61 a	34.56 a	75.4 a
Florida 301	Fumigated	103 a	840 a	1,010 a	4,121 a	2,060 a	4,552 a	0.50 b	37.95 a	77.3 a
	Unfumigated	66 b	410 b	740 b	2,397 b	1,056 b	3,033 b	0.56 a	35.24 b	74.5 b
Florida 302	Fumigated	71 a	480 a	730 a	3,345 a	1,714 a	3,668 a	0.49 a	33.85 a	71.9 a
	Unfumigated	43 b	250 b	560 b	1,411 b	760 b	1,484 b	0.47 a	25.34 b	66.3 b
Coker 797	Fumigated	122 a	610 a	810 a	4,280 a	1,998 a	5,060 a	0.53 b	28.2 a	75.2 a
	Unfumigated	39 b	330 b	670 b	1,312 b	505 b	1,814 b	0.61 a	27.2 a	73.4 b

[u] Nearly all plants in fumigated plots were symptomless; Florida 301, Florida 302, and Coker 797 in unfumigated plots were 100% infected with wheat spindle streak mosaic virus.

[v] Plants were between GS 37 and GS 39, except Florida 301 (fumigated), which was at GS 51.

[w] Plants were between GS 61 and GS 76.

[x] Mean weight from 4.84-m^2 plots.

[y] In each pair, means followed by the same letter are not statistically different according to the unpaired *t* test using PROC TTEST (SAS Institute) at $P = 0.05$.

[z] Significant at $P = 0.10$.

the two resistant cultivars and remained so at the two subsequent assay dates. Concentrations found in roots of Coker 916 and Florida 301 grown in the fumigated plots were only slightly higher than background values. No WSSMV was detected in the shoots of any cultivar 35 days after planting.

By 63 days after planting visible differences in plant growth and vigor were evident. Positive ELISA results were associated with these observations (Fig. 2). WSSMV was detected in the roots but not the shoots of Stacy and Coker 916 in fumigated plots. The WSSMV concentration was almost as high in shoots of susceptible cultivars as that detected in roots of plants growing in unfumigated soil. No WSSMV was found in shoots of Coker 797 and Florida 302 in fumigated soil, but a significant amount was found in shoots of Florida 301, probably because of incomplete fumigation (Fig. 2). The soil of two replicates was not completely fumigated from the edge of the plots from which samples were taken.

WSSMV was detected in shoots of Coker 916 and Stacy 97 days after planting in fumigated soil (Fig. 2). ELISA values for the roots of these resistant cultivars were higher for plants growing in unfumigated soil than for plants growing in fumigated soil, but the level was still less than that of the three susceptible cultivars. Cysts of *P. graminis* were observed in roots of all cultivars. The WSSMV concentration remained high in roots of the susceptible cultivars in unfumigated plots. The virus concentration increased in roots of Florida 302 and Coker 797 in fumigated soil but was still much less than that in roots in the unfumigated treatment.

Pearson correlation coefficients were calculated for relationships between the biomass and ELISA determinations made at each of the three sampling dates and the various yield components recorded at maturity (Table 3). The ELISA values for roots 35 days after planting were highly negatively correlated ($P = 0.01$) with the number of tillers and with grain yield. Root and shoot dry weights at this date were not correlated with ELISA values, reflecting the lack of differences in biomass between the treatments. There were highly significant correlations between root and shoot dry weights of the 63- and 97-day samples and the number of tillers, straw weight, grain yield, and total biomass. Root and shoot dry weights therefore were both affected by WSSM during the course of the season. The ELISA values for roots and shoots were negatively correlated with these same yield components and root and shoot dry weights at both dates; the correlation coefficients were greatest at the 63-day sampling date (19 February) in almost all cases. Root and shoot dry weights at the 35-day sampling date were not correlated with test weight (data not presented). At the two later sampling dates the correlations generally were not as great as with the other yield components. Most correlations were significant at $P = 0.05$, but a few were significant only at $P = 0.10$. The ELISA value for roots was negatively correlated with test weight at all three dates, but the level of correlation also varied from $P = 0.01$ to $P = 0.10$. The number of tillers, grain yield, total biomass, straw weight, and test weight were all highly correlated with each other. Correlation coefficients of the combined values for root plus shoot dry weight, root plus shoot ELISA values, and total biomass (straw plus grain) with the other parameters were similar to the correlation coefficients of the individual components of each pair.

The validity of the ELISA tests using the Georgia antiserum was confirmed by obtaining positive reactions to the field samples with WSSMV antiserum from Michigan and negative reactions to wheat soilborne mosaic virus antiserum.

Milling and baking qualities of grain. Florida 301 (fumigated) was chosen as the standard for tests on the quality of grain for milling and baking. The milling and baking qualities of Stacy in 1985 were the same in plants grown in unfumigated soil as in those grown in fumigated soil, indicating no effect of WSSMV on this cultivar (Table 4). The milling and baking qualities of Florida 301 and Coker 797 were affected by WSSM. Flour yield was significantly reduced. The baking quality score, a weighted score of protein content, alkaline water-retention capacity (AWRC), and softness equivalent, reflects the poor quality of grain from plants with WSSM in 1985. The protein content increased in grain from virus-infected plants, reflecting a significant reduction in seed

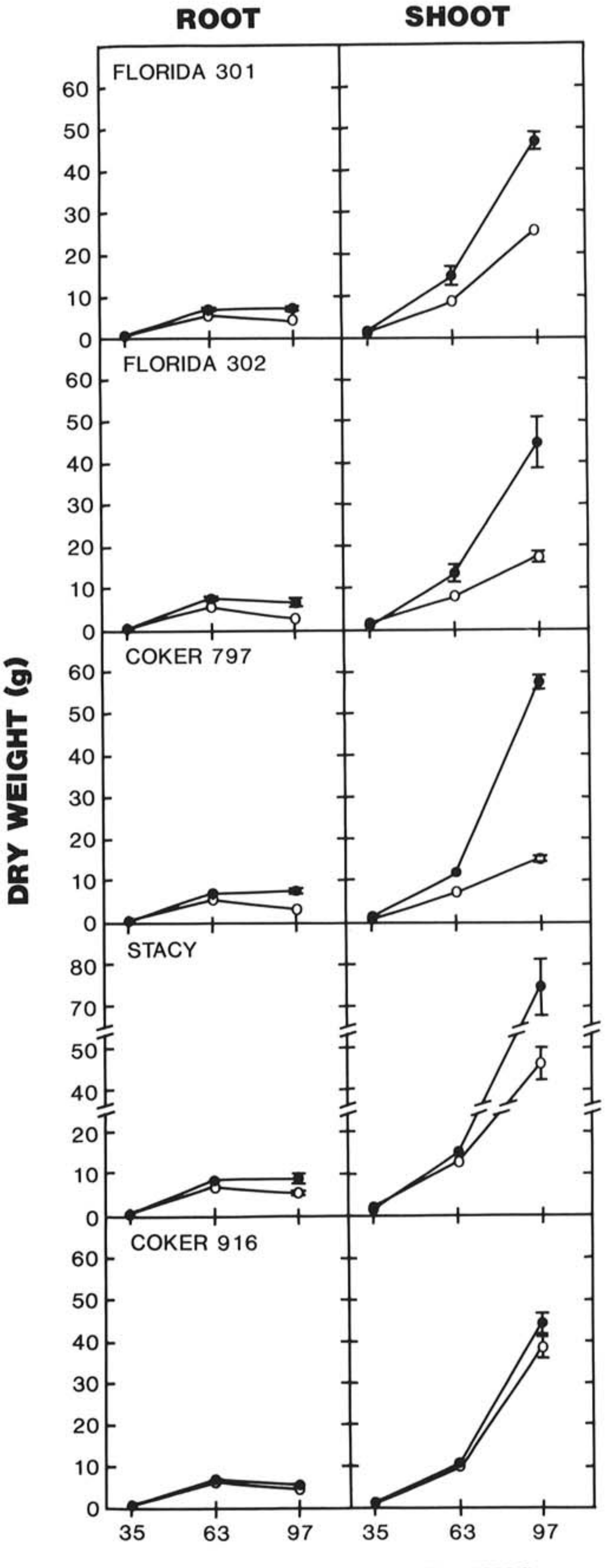

Fig. 1. Mean dry weight of roots and shoots from 1 m of row of each replicate, determined on three dates during winter and early spring of 1986, for five wheat cultivars differing in their reaction to WSSMV and grown in fumigated (●) and unfumigated (○) soils. Points on which standard errors are not noted are ±0.30 for roots and ±1.00 for shoots.

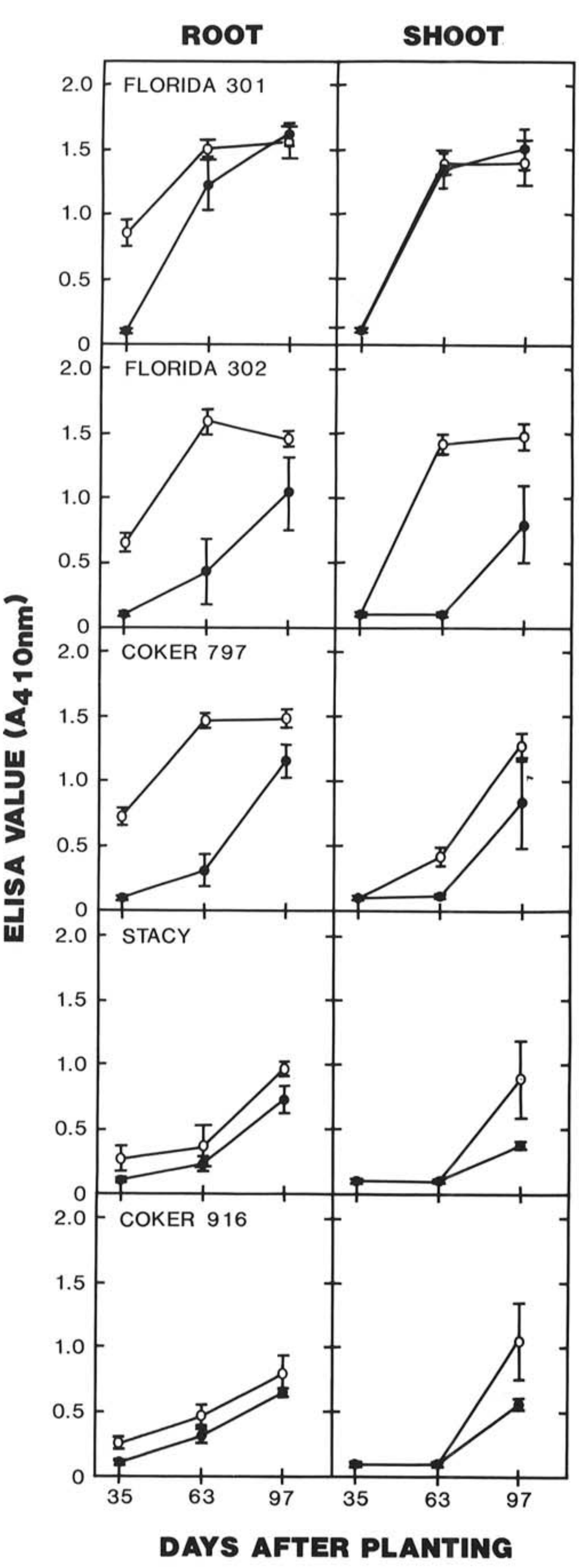

Fig. 2. ELISA values, determined on three dates during winter and early spring of 1986, for roots and shoots of five wheat cultivars differing in resistance to WSSMV and grown in fumigated (•) and unfumigated (o) soils. Values for the healthy controls were 0.11 in the 35- and 63-day samples and varied up to 0.38 in the 97-day sample.

endosperm. Elevated values for AWRC, indicating excessive binding of water by the flour, lowered baking quality. The elevated softness equivalent of WSSM-affected samples improved baking quality, but it was not sufficient to improve the baking quality score.

Differences in milling and baking qualities between grain produced in fumigated plots and that produced in unfumigated plots were considerably less in 1986 (Table 5). Florida 301 and Florida 302 from fumigated plots had better milling quality than the grain from unfumigated plots. There were no differences between treatments for Coker 916 and Coker 797. The milling quality of Stacy from fumigated plots was lower than that of its counterpart from unfumigated plots. The milling quality score is related to test weight and flour yield.

There were no differences in softness equivalent and AWRC between the healthy and the WSSM treatments for any cultivar, and only Stacy had a significant difference in protein content between treatments. There were no differences in baking quality score between the healthy and the WSSM treatments for Florida 301, Florida 302, and Coker 797 (Table 5). Differences in the baking quality score for Stacy and Coker 916 were due mainly to higher protein values in the healthy treatment. Overall, WSSM had little effect on milling and baking qualities in 1986.

DISCUSSION

Our diagnosis of WSSM in Georgia in 1984 was the first record of the disease in the southeastern United States (1). We speculated that the occurrence of the disease was due primarily to continuous cropping of wheat in the severely affected fields and the very wet fall and winter of the 1983–1984 season. The fall and winter of the 1984–1985 season were considerably drier. The late fall of 1985, just before planting, was very wet, but record drought occurred during the winter months and early spring of 1986. Therefore, planting of highly susceptible cultivars in successive seasons appears to be the major factor in the development of WSSM. High soil moisture is needed primarily for the release of infective zoospores of *P. graminis*.

Stunting and mosaic symptoms were evident by late February of both seasons, well before jointing began. This is in contrast to the results of Nguyen and Pfeifer (5), who observed few leaf symptoms, although tillering and yield components were reduced in susceptible cultivars. WSSM reduced both root and shoot growth significantly within 63 days after planting. Wheat soilborne mosaic virus, also vectored by *P. graminis*, caused great reductions in root growth, but shoot growth was not affected in greenhouse tests on seedlings (3).

The increase in WSSM in the Southeast is related to the widespread planting of Florida 301 and Coker 797 (1). Florida 302 is a new cultivar, which is being grown widely. The results show that Coker 797 is the most susceptible cultivar of the three, sustaining about two or more times as much yield loss as Florida 301 in both years. Florida 302 is nearly as susceptible as Coker 797. Test weight, 1,000-kernel weight, and milling quality were also more adversely affected, especially in 1984–1985. During both years Stacy exhibited no visible effects of severe WSSM pressure. A few plants of Coker 916 exhibited very mild mosaic in the unfumigated plots.

Slykhuis (7) reported that late planting in Ontario reduced WSSM incidence to as low as 5%, because soil temperatures were well below optimum for virus infection during the critical tillering stage. Nguyen and Pfeifer (5), in Pennsylvania, likewise reported reduction in WSSM with late planting. Although comparison of planting dates was not an objective of the current study, we did have an opportunity to observe the effect of a locally recommended planting date (12 November) and a late planting (18 December) the next season in the same field. WSSM incidence was 100% both years. Air temperature data were available from the University of Georgia Southwest Branch Experiment Station, located 3 km from the test site. Temperature data were computed for the two years of this study and the 1983–1984 season, when WSSM was first observed in this field (1). Temperatures ranged from 5 to 14 C in each season, based on averages computed from the daily maxima and minima between the date of planting and 1 March, when symptoms were well expressed. During 1985–1986 temperatures averaged 7 C between planting, on 18 December, and 22 January, when the first biomass sample was collected. During the next 28-day period, when symptoms developed, temperatures averaged 9 C. Slykhuis (7) determined that about 60 days with air or soil temperatures between 5 and 13 C is needed for symptom development. This favorable period exists continuously from shortly after fall planting until spring each year throughout much of the Southeast. In all three years temperatures were near optimum for infection and subsequent disease development (7–9). Therefore, unless inoculum levels are low, it is unlikely that late planting reduces the incidence of WSSM in the Southeast.

Delayed maturity caused by WSSM can have several secondary effects. Although foliar diseases were not a problem in either season of the study, a 5–7 day delay in maturity can allow sufficient time for damage from diseases such as Septoria nodorum blotch and leaf rust. Most wheat grown in the Southeast where WSSM is a problem is grown in a double-cropping system, usually with soybeans as the summer crop. Growers plant the summer crop with no or minimum tillage immediately after the wheat harvest, because delays in planting can adversely affect yield. Therefore, WSSM may affect the yield of the subsequent crop as well as that of wheat.

ELISA was used to document the relative concentration of WSSMV in both resistant and susceptible wheat cultivars. The increase in the WSSMV concentration as determined by ELISA was negatively correlated with plant root and shoot growth and development. A primary effect of WSSMV infection was stunting and reduction of the number of tillers. The increase in the WSSMV concentration corresponded with the tillering stage of growth. The poor vigor of infected tillers was amply illustrated during the 1984–1985 season, when many WSSMV-infected plants were unable to survive severely low temperatures in late January. Healthy plants of Florida 301 and Coker 797 also suffered some loss of tillers, but the stress of low temperature was markedly greater on WSSMV-infected plants. The WSSMV concentration in roots 35 days after planting was an indicator of the subsequent loss of tillers, as shown by the high correlation of these two factors (Table 3). ELISA values and root and shoot dry weights 63 days after planting were also highly predictive of yield components, with the exception of test weight. Loss of tillering capacity is the primary factor in yield reduction by WSSM. Plants were severely affected by mid-February and were unable to produce many new tillers in spring.

ELISA detected moderate WSSMV concentrations in shoots of both resistant cultivars 97 days after planting. ELISA detected WSSMV in roots of all cultivars planted in unfumigated soil 35 days after planting (Fig. 2). The WSSMV concentration subsequently increased rapidly in both roots and shoots of susceptible cultivars, but only very slowly in the roots of the resistant cultivars. *P. graminis* cysts were also found in roots of all cultivars. Therefore, the resistance of Stacy and Coker 916 is related to a reduction of WSSMV concentration and distribution within the plant. Resistance may also be related to ingress of the

TABLE 3. Pearson correlation coefficients between biomass and enzyme-linked immunosorbent assay (ELISA) determinations for all cultivars at three dates after planting

Days after planting		Root weight	ELISA (shoot)	ELISA (root)	Yield	Straw weight	Number of tillers
35	Shoot weight	0.69[a]	—[b]	−0.24 NS	0.23 NS	0.45	0.20 NS
	Root weight		—	0.01 NS	0.03 NS	0.16 NS	0.07 NS
	ELISA (shoot)			—	—	—	—
	ELISA (root)				−0.76	−0.75	−0.70
63	Shoot weight	0.91	−0.45	−0.54	0.57	0.69	0.52
	Root weight		−0.55	−0.58	0.57	0.69	0.52
	ELISA (shoot)			0.89	−0.68	−0.54	−0.60
	ELISA (root)				−0.72	−0.62	−0.60
97	Shoot weight	0.89	−0.65	−0.59	0.79	0.87	0.74
	Root weight		−0.53	−0.48	0.76	0.87	0.67
	ELISA (shoot)			0.78	−0.49	−0.41	−0.52
	ELISA (root)				−0.53	−0.33*	−0.48

[a] NS = not significant; * = significant at $P = 0.05$; all other values are significant at $P = 0.01$.

[b] ELISA values for the shoot on this date were all zero.

TABLE 4. Milling and baking qualities of grain from three wheat cultivars affected by wheat spindle streak mosaic virus, 1984–1985

Cultivar	Soil treatment[w]	Adjusted flour yield (%)	Milling quality score	Protein[x] (%)	AWRC[y]	Softness equivalent	Baking quality score
Stacy	Fumigated	70.5	95.5 B[z]	12.4	54.6	51.3	87.1 D[z]
	Unfumigated	70.4	95.0 B	12.1	54.5	49.6	87.0 D
Florida 301	Fumigated	71.9	100.0 A	10.9	52.7	51.0	100.0 A
	Unfumigated	68.9	89.7 D	13.1	54.1	55.8	90.9 C
Coker 797	Fumigated	69.4	91.7 C	11.5	54.7	55.4	92.8 C
	Unfumigated	60.1	59.7 F	14.6	59.1	60.2	63.6 F
Least significant difference ($P = 0.05$)		0.77	1.07	2.32	2.74		

[w] All plants in fumigated soil were healthy; Florida 301 and Coker 797 in unfumigated plots were 100% infected with wheat spindle streak mosaic virus.

[x] A lower score contributes to better baking quality.

[y] Alkaline water-retention capacity; a lower score contributes to better baking quality.

[z] Differences in letters following the scores represent departures in quality.

TABLE 5. Milling and baking quality scores of grain from five wheats affected by wheat spindle streak mosaic virus, 1985–1986

Cultivar	Soil treatment	Milling quality score[x]	Baking quality score[y]
Stacy	Fumigated	94.3 C[z]	83.3 E[z]
	Unfumigated	97.5 B	93.2 C
Coker 916	Fumigated	93.8 C	87.6 D
	Unfumigated	90.5 C	95.5 B
Florida 301	Fumigated	100.0 A	100.0 A
	Unfumigated	96.2 B	107.6 A
Florida 302	Fumigated	95.0 B	81.4 E
	Unfumigated	88.3 D	82.8 E
Coker 797	Fumigated	94.3 C	89.0 D
	Unfumigated	92.5 C	86.4 D

[x] Composite score based on flour yield and endosperm separation index.

[y] Composite score based on protein content, alkaline water-retention capacity, and softness equivalent.

[z] Differences in letters following the scores represent departures in quality.

vector, but this aspect was not investigated quantitatively in this study.

Skaria et al (6) discussed the association of reduced concentration of barley yellow dwarf virus, as determined by ELISA, with reduced symptom expression. They suggested that ELISA data may measure resistance more accurately than visual observation of symptoms in some cultivar-virus isolate combinations. In the current study, ELISA values for roots and shoots early in the season were well correlated with yield reduction (Table 3). ELISA may be useful to evaluate germ plasm for WSSM resistance. Grain test weight was erratically correlated with ELISA values and biomass weight at the three sampling dates. Severely diseased plants had fewer tillers than healthy plants and thus had more water available during grain filling.

Milling and baking qualities were reduced sharply in 1985, when 1,000-kernel weight and test weight were severely lowered by WSSM (Tables 1 and 4). Effects on quality were more erratic in 1986; these qualities were little affected by WSSM, probably because 1,000-kernel weight and test weight were less affected (Tables 2 and 5). Florida 302 had the largest differences between treatments for these two components, and this was reflected in the milling quality score (Table 5). WSSM affects milling and baking qualities in relation to its reduction of 1,000-kernel weight and test weight, rather than its effects on yield.

WSSM can cause significant yield losses on susceptible wheat cultivars in the southeastern United States. Resistant cultivars sustained no significant yield loss during two years of field trials when natural WSSM pressure was high. ELISA detected WSSMV in roots before symptoms developed and reduction in plant biomass began. The ELISA values were highly correlated with reductions in biomass and yield.

LITERATURE CITED

1. Bays, D. C., Cunfer, B. M., and Demski, J. W. 1985. Occurrence of wheat spindle streak mosaic virus on winter wheat in Georgia. Plant Dis. 69:1094-1096.
2. Gonsalves, D., and Ishii, M. 1980. Purification and serology of papaya ringspot virus. Phytopathology 70:1028-1032.
3. Larsen, H. J., Brakke, M. K., and Langenberg, W. G. 1985. Relationships between wheat streak mosaic virus and soilborne wheat mosaic virus infection, disease resistance, and early growth of winter wheat. Plant Dis. 69:857-862.
4. Lister, R. M. 1978. Application of the enzyme-linked immunosorbent assay for detecting viruses in soybean seed and plants. Phytopathology 68:1393-1400.
5. Nguyen, H. T., and Pfeifer, R. P. 1980. Effects of wheat spindle streak mosaic virus on winter wheat. Plant Dis. 64:181-184.
6. Skaria, M., Lister, R. M., Foster, J. E., and Shaner, G. 1985. Virus content as an index of symptomatic resistance to barley yellow dwarf virus in cereals. Phytopathology 75:212-216.
7. Slykhuis, J. T. 1970. Factors determining the development of wheat spindle streak mosaic caused by a soil-borne virus in Ontario. Phytopathology 60:319-331.
8. Slykhuis, J. T. 1974. Differentiation of transmission and incubation temperatures for wheat spindle streak mosaic virus. Phytopathology 64:554-557.
9. Slykhuis, J. T. 1975. Seasonal transmission of wheat spindle streak mosaic virus. Phytopathology 65:1133-1136.
10. Zadoks, J. C., Chang, T. T., and Konzak, C. F. 1974. A decimal code for the growth of cereals. Weed Res. 14:415-421.