Crop Residues

Maize Debris Increases Barley Yellow Dwarf Virus Severity in North Carolina Winter Wheat

Christina Cowger,* Randy Weisz, Joseph M. Anderson, and J. Ray Horton

ABSTRACT

In the eastern United States, wheat (*Triticum aestivum* L.) is often planted with minimal or no tillage into maize (Zea mays L.) residues. We conducted a field experiment in the North Carolina Piedmont to compare the effects of three maize residue treatments (unchopped, chopped, and removed) on Fusarium head blight (FHB) in two winter wheat cultivars. While FHB levels were too low for meaningful comparisons, severe epidemics of barley/cereal yellow dwarf virus (YDV) did develop in 2 yr out of 3. In those 2 yr, YDV symptoms of discoloration and stunting were greater ($P \leq 0.001$), and yield was lower ($P \leq 0.01$), in plots with maize residue than in plots without maize residue. In the third year, when planting was late because of a severe fall drought, no YDV epidemic developed, and there were no differences in wheat yield due to maize residue treatment ($P = 0.25$). In the first 2 yr, leaf samples from all plots were assayed for viruses using a multiplexed reverse transcription polymerase chain reaction (RT-PCR) method. The most common YDV serotypes were MAV, PAV, and RPV, which were each detected in at least 46 and 74% of samples in the 2 yr, respectively. Our finding of greater YDV severity in association with surface residue is consistent with the reported aphid preference for high-intensity yellow colors, which we hypothesize attracted aphids preferentially to residue-covered plots in the fall. Our results support a recommendation of seed or seedling insecticide treatment when planting wheat into heavy unincorporated maize residue in the U.S. Piedmont.

Yellow dwarf viruses are transmitted to cereals by aphids and can cause yield losses of up to 31% in naturally infected wheat crops (McPherson et al., 1986; Pike, 1990). The YDVs have a broad host range, including more than 100 species of grasses (Burnett et al., 1995). Maize is of epidemiological significance in many areas, serving as a primary or important source of YDV inoculum in the Mediterranean and southern England (Lister and Ranieri, 1995). Fall aphid flights and resulting fall virus infections are considered to have the most serious negative effects on plant growth and yield, as stunting and yield loss are negatively correlated with the age of the plant at infection (Goulart et al., 1989; Gray et al., 1998).

Five kinds of YDVs have been identified in North America. The most recent classification system developed by a working group of the International Committee on the Taxonomy of Viruses divides the YDVs into two species: *Luteovirus*, which includes the Barley yellow dwarf virus serotypes PAV, MAV, SGV, and RMV, and *Polerovirus*, which includes the Cereal yellow dwarf virus serotypes RPV (Lister and Ranieri, 1995).

C. Cowger, USDA-ARS, Dep. of Plant Pathology, North Carolina State Univ., Raleigh, CB7616, Raleigh, NC 27695; R. Weisz, Dep. of Crop Science, North Carolina State Univ., Raleigh, NC 27695; J.M. Anderson, USDA-ARS, Lilly Hall of Life Sciences, Agronomy Dep., Purdue Univ., West Lafayette, IN 47907-2054; J.R. Horton, North Carolina Dep. of Agriculture & Consumer Services, Border Belt Tobacco Research Station, 86 Border Belt Drive, Whiteville, NC 28472-6828. Received 14 Sept. 2009. *Corresponding author (Christina.Cowger@ars.usda.gov).

Published in Agron. J. 102:688–696 (2010)
Published online 27 Jan. 2010
doi:10.2134/agronj2009.0357

Polymerase chain reaction (PCR) tests have been developed to distinguish the five serotypes (Deb and Anderson, 2008; Malmstrom and Shu, 2004; Robertson et al., 1991).

In the southeastern U.S. wheat production area, surveys of aphid YDV vector species have been conducted in Virginia and South Carolina, but not in North Carolina or other southeastern states. Four main aphid species were found colonizing South Carolina winter wheat samples (Chapin et al., 2001; Gray et al., 1998): the greenbug *Schizaphis graminum* (Rondani), the bird cherry-oat aphid *Rhopalosiphum padi* (L.), the English grain aphid *Sitobion avenae* (Fab.), and the rice root aphid *R. rufiabdominalis* (Walker). Chapin et al. (2001) found that *R. padi* was the primary species responsible for YDV epidemics in South Carolina coastal plain wheat, as only the abundance of *R. padi*, and not of other aphid species, was significantly correlated with YDV incidence and yield loss. They concluded that infection foci are established by relatively small numbers of *R. padi* alates in the late fall and early winter, and then infections are spread within fields by *R. padi* colonies in February and March. Chapin et al. (2001) found that *R. maidis*, the maize leaf aphid, was also capable of transmitting YDV, but was not abundant in South Carolina.

By contrast, in eastern Virginia, *R. maidis* was the most abundant fall aphid on wheat in 1979, followed by *S. graminum* and *R. padi* (McPherson and Brann, 1983). *Sitobion avenae* did not become abundant until the spring.

The most recent published survey of YDV serotypes in the U.S. Southeast was based on samples from 1991, 1996, and 1997, primarily gathered in South Carolina, with a smaller number of samples from North Carolina and Kentucky, and

Abbreviations: AIC, Akaike Information Criteria; BCE, blocking with correlated errors analysis; CE, correlated error analysis without blocking; YDV, yellow dwarf virus; FHB, Fusarium head blight; OLS, ordinary least squares; PCR, polymerase chain reaction; RT-PCR, reverse transcription polymerase chain reaction.

analyzed by ELISA (Gray et al., 1998). PAV was the predominant serotype in South Carolina samples in all years, and was the sole serotype detected in 94% of 228 YDV-infected samples analyzed. Either alone or in combination with RPV, PAV was also found in 44% of 70 samples analyzed from the North Carolina Piedmont (10 samples from Rowan County and 60 from Davie County), while 29% of the 70 samples were found to contain RPV alone. None of the 70 North Carolina samples contained MAV, and only 3% of the 228 YDV-positive samples from South Carolina contained MAV.

Yellow dwarf virus is controlled by applications of insecticide to seeds or young plants, avoidance of early planting, and use of tolerant or resistant cultivars (Burnett et al., 1995; Flanders et al., 2006; Francki et al., 2001; Royer et al., 2005). Early autumn sowing may increase yield potential (Plumb and Johnstone, 1995), but it also increases the risk of YDV infection (Plumb, 1992). Delayed planting reduces YDV incidence, presumably by reducing aphid-day accumulation (Kieckhefer et al., 1995), essentially the number of aphids × days on the plant. However, delays lengthy enough to be effective also reduce yield, increase the risk of being unable to plant due to wet soil (Chapin et al., 2001; Flanders et al., 2006), and increase the risk of late spring-freeze damage. The critical time for control of YDV infection is at early plant growth stages, especially before tillering (Plumb and Johnstone, 1995). Inconsistent results have been obtained when measuring correlation between visual symptoms and yield reductions (Chapin et al., 2001; Weisz et al., 2005), a fact that may hamper breeding for resistance.

There is limited and contradictory information on the effect of previous crop and residue management on aphid populations and YDV severity in small grain crops. A study of spring wheat in South Dakota found that conservation tillage (≥30% cover of various crop residues) led to higher populations of *R. padi* in spring small grains than did preplant tillage (Hesler and Berg, 2003). On the other hand, a study in Oklahoma indicated that *S. graminum* populations were significantly lower in plots of winter wheat with moderate to heavy surface wheat residues than in those with low residue levels (Burton and Krenzer, 1985). In the same vein, more YDV infection was found in barley (*Hordeum vulgare* L.) planted after incorporating residues by plowing than after noninversion tillage or direct drilling (no-till) in a UK study (Kendall et al., 1991); the authors suggested the difference might be due to effects on the survival of predatory arthropods that feed on aphids. Similarly, in a study of spring wheat in Germany, a positive relationship was observed between mulching with chopped barley residues, maintenance of spider populations, and reduction of aphid densities (Schmidt et al., 2004). It has also been found that mulches, that is, different materials applied to cover the soil around crop plants, can reduce the number of alighting aphids and the incidence of aphid-transmitted virus diseases (Döring and Chittka, 2007). Aluminum mulch has been found to be especially effective (e.g., Brust, 2000), with black material also decreasing aphid landing rates and infestation.

Aphids have been found to prefer the color yellow to green or other colors, with yellow particularly triggering the alighting response (Döring and Chittka, 2007). In a study of trap colors preferred by cereal aphids, *R. padi* and *Metopolophium dirhodum* (Walker) were found to favor yellow, followed by bright green, while *Sitobion* nr. *fragariae* (Walker) found yellow and bright green equally attractive (DeBarro, 1991). Yellow is recommended as a good color for insect traps (Döring and Chittka, 2007; Southwood and Henderson, 2000). The preference for yellow appears to be at least as dependent on brightness or light intensity as on actual color (Döring and Chittka, 2007), as yellow has a higher reflectance in the longer wavelengths (green to red spectrum) and a lower reflectance in the shorter wavelengths (UV to blue spectrum). High light intensity is also known to favor YDV symptom expression, as are relatively cool temperatures (15–18°C) (D'Arcy, 1995).

Our experiment was designed to study the effects on Fusarium head blight (FHB, or scab) severity of three different common techniques for managing maize residue before sowing winter wheat in the North Carolina Piedmont region. Most growers either remove maize residue for silage, "bush-hog" or chop residue to reduce particle size, or leave the "standing" whole maize stalks in place. As "no-till" or minimum tillage is common in this region, we wished to learn whether chopping the residue would reduce the risk of FHB, especially in light of the damaging Southeastern FHB epidemic of 2003 (Cowger and Sutton, 2005). Levels of FHB were never high enough to allow conclusions regarding that disease, but the experiment produced interesting data regarding the effect of maize residue on YDV severity and wheat yield.

MATERIALS AND METHODS

Experimental Design and Cropping Details

A field experiment was conducted at the Piedmont Research Station (35°42′ N, 80°37′12′′ W, 214 m elevation) in three growing seasons, 2005–2006, 2006–2007, and 2007–2008, which are hereafter termed 2006, 2007, and 2008, respectively. In each year, the experiment was planted in a Hiwassee clay loam (fine, kaolinitic, thermic Rhodic Kanhapludult). This location is in the North Carolina Piedmont region, where heavy clay soils predominate. Yellow dwarf virus is a common and damaging disease of wheat in this region.

In each year, maize was planted and harvested in the field before planting wheat. In 2006, there were two experiments. The first experiment was planted into high-biomass (later-maturing) maize residue. In the second experiment, wheat was planted into low-biomass (earlier-maturing) maize residue. In 2007 and 2008, a single hybrid of maize was planted. To compare residue treatments, plots were prepared in one of three manners: (i) maize residues "bush-hogged" (chopped) to reduce particle size, (ii) whole maize stalks left standing, and (iii) maize residue removed by raking and bagging.

In each year, the experiment had a split split-plot design. Whole plots were two soft red winter wheat cultivars, NC Neuse and Coker 9295, that had similar, late maturities. NC Neuse is moderately susceptible to YDV, and Coker 9295 is susceptible to YDV. Planting dates were within the recommended period for timely planting (Weisz, 2004) in the first 2 yr. In the third year, the wheat was planted 1 mo late due to a severe drought, and emergence was slow.

Subplots were either irrigated or not irrigated; irrigation was applied from approximately 1 wk before wheat anthesis through 2 wk following anthesis to encourage FHB development. In 2006, irrigation was only applied to wheat plots in the high-biomass strips. Sub-subplots were of the three maize residue treatments described above. In 2006, sub-subplots were 37 m^2, while in 2007 and 2008 they were 74 m^2. There were six replicates each in the high- and low-biomass experiments in 2006, six replicates in 2007, and five replicates in 2008. Preplant N was applied at recommended rates to assure good tillering and fall growth.

Virus Disease Assessment, Sampling, and Characterization

At wheat anthesis in 2006 and 2007, visual symptoms of YDV were assessed on a whole-plot basis by a single observer. Percent of canopy stunted (YDV_{stunt}) and percent of canopy discolored (YDV_{color}) due to YDV were separately recorded for each plot. A YDV epidemic did not develop in 2008 (see below).

For analysis of virus content, wheat leaf samples were collected in 2006 and 2007, but not in 2008. The sampling protocol was as follows: 1 m of wheat at each plot end and both outside rows of each plot were avoided to minimize interplot interference. Twenty flag leaves were blindly chosen from various parts of each plot, and bagged together by plot.

Leaf samples were analyzed for virus content using a multiplexed reverse transcription polymerase chain reaction (RT-PCR) detection method with primers specific to each of eight different wheat viruses (Deb and Anderson, 2008). Those viruses are the five YDV serotypes (RPV, PAV, SGV, MAV, and RMV), as well as wheat streak mosaic virus (WSMV), soilborne wheat mosaic virus (SBWMV), and wheat spindle streak mosaic virus (WSSMV). Although the last three viruses were each detected in some samples, in this report only those results pertaining to the YDV serotypes are included. While the RT-PCR method is not quantitative, band intensity can be visually estimated, and there is some relationship between that intensity and virus titer in the sample.

Briefly, for the RT-PCR method, total plant RNA was extracted from leaf samples, and cDNA was synthesized from it using random primers, as described in Deb and Anderson (2008). Eight pairs of primers, each specific to a particular virus and all functioning with similar annealing and melting temperatures, were used to amplify any viruses present in each sample in a single microfuge tube. Amplified PCR products were analyzed by gel electrophoresis, using ethidium bromide as a stain, and the bands were visualized under UV light. A standard consisting of all eight bands in each of two lanes was run with each group of 21 samples. Band intensity was estimated on a 0 to 5 scale, with 0 being absent and 5 being maximum intensity.

Yield and Test Weight

All wheat plots were harvested in early June with a Wintersteiger Delta combine (Wintersteiger, Salt Lake City, UT) and the grain yields and test weights were measured with a HarvestMaster grain gauge (Juniper Systems, Inc., Logan, UT). Grain yields were adjusted to 135 g kg^{-1} moisture for analysis. Yields were determined by harvesting a strip 1.75 m wide and 12.2 m long from the center of each sub-subplot.

Data Analysis

Initial statistical analysis was conducted for each experiment using classical ANOVA for either a split-plot or a split split-plot design using SAS PROC MIXED (SAS Institute, 2006). In determining treatment effects with classical ANOVA, it is assumed that the model-fit errors are independent and identically distributed with the same variance (IID). However, in these experiments, YDV infections that resulted from natural aphid infestations occurred in 2 of the 3 yr. Because it was unlikely that spatial patterns of aphid colonization would conform to the experimental blocking used in the field (Weisz et al., 2005), it was anticipated that the resultant model-fit errors would be spatially correlated, violating the assumption of independence.

When spatially correlated errors are present, the efficiency of classical ANOVA in estimating treatment comparisons and treatment means has been questioned (Stroup et al., 1994), because the classical use of ordinary least squares (OLS) ignores local patterns of variability. Additionally, when errors are spatially correlated, OLS underestimates the variance of the error terms (Neter et al., 1996); consequently, the resultant t- and F-tests may not be reliable. The statistical analysis we used to overcome this problem has been described in detail by Hong et al. (2005) and specifically by Weisz et al. (2005) in relationship to field experiments where YDV infections occurred. In addition to using classical ANOVA, blocking with correlated errors analysis (BCE) and correlated error analysis without blocking (CE) were implemented in PROC MIXED (2006). These analyses were undertaken for each experiment in 2006 and 2007 for the following variables: grain yield, grain test weight, YDV_{color}, YDV_{stunt}, band intensity of each virus, and the mean of these band intensities ($Mean_{Intensity}$). For each variable of interest, we first ran classical ANOVA, then ran six BCE models (using spherical, exponential, and Gaussian spatial functions with and without nugget effects), and finally ran six CE models (also using spherical, exponential, and Gaussian spatial functions with and without nugget effects). The Akaike Information Criteria (AIC) (Akaike, 1974) of each of the 13 models were compared, and the model with the lowest AIC was selected as having the best fit to the data (Littell et al., 2002). This best-fit model was then used for estimating treatment effects, and for separation of means. In 2008, when YDV infections did not occur, only classical ANOVA was used to analyze the data.

RESULTS

In 2006 and 2007, when wheat was planted on time, severe YDV epidemics developed in the experiment. In the 2008 experiment, however, no YDV symptoms were visible, evidently because late planting and slow emergence following a severe drought had precluded aphid infestation and virus transmission. In 2007, numerous NC Neuse plots were lost due to a mechanical failure at planting, and thus results are only presented for Coker 9295 in 2007.

Virus Symptoms and Serotype Frequencies

In both 2006 and 2007, the most commonly detected YDV serotypes were MAV, PAV, and RPV (Table 1). Taking the 2 yr together, these serotypes were detected in 78, 74, and 62% of samples, respectively. Band intensities of these serotypes were also higher than those of SGV, indicating that the mean titer of MAV, PAV, and RPV was higher.

Residue management treatment was a significant determinant of yield, YDV_{color}, and YDV_{stunt} in 2006 and 2007 (Tables 2, 3, and 4). Both YDV_{stunt} and YDV_{color} were higher

Table 1. Frequency of yellow dwarf virus (YDV) serotypes detected in wheat leaf samples from a field experiment in Salisbury, NC, comparing three maize residue treatments. In 2006, wheat was planted following either a low-biomass (2006L) or a high-biomass (2006H) maize hybrid, while a single maize hybrid preceded the wheat in 2007 and 2008. No YDV epidemic developed in 2008. Leaf samples from each plot were analyzed for YDV using a multiplexed reverse transcription polymerase chain reaction (RT-PCR), and bands were visualized under UV light.

YDV serotype	Percentage of samples in which serotype was detected				Mean band intensity† (0–5 scale)		
	2006L (n =70)‡	2006H (n = 72)	2007 (n = 72)	Mean (n = 214)	2006L	2006H	2007
	%						
MAV	79	64	92	78	4.1	3.8	3.1
PAV	69	58	94	74	4.0	3.7	3.5
RPV	66	46	74	62	3.9	3.5	2.5
SGV	11	1	32	15	1.4	4.0	1.0
RMV	0	0	3	1	none	none	0.8

† Bands were visually scored for intensity using a 0 to 5 scale. Samples were only included in calculation of means if they produced bands.

‡ Serotype data missing for two samples.

in plots with maize residue than in plots without maize residue in 2006 (Fig. 1 for high-biomass plots; the same results and means differences were found in the low-biomass plots, and thus data are not shown) and 2007 (Fig. 2). In addition, the 2006 and 2007 yields were highest in plots where the residues had been removed (Fig. 1 and 2).

In the 2006 low-maize-biomass plots and in 2007, residue management did not have an effect on the band intensity of RPV, PAV, MAV, or the three serotypes averaged together (Tables 3 and 4). In the 2006 high-maize-biomass plots, residue management did have a significant effect on RPV band intensity. The RPV band intensities were highest in plots with maize residues (intensity means of 2.21 and 1.88 for the standing-stalk and chopped treatments, respectively) compared to those in which residues had been removed (mean of 0.75). Interpretation of band intensities for PAV and MAV in the 2006 high-biomass plots is less certain. There was no effect of residue management on these intensities in the nonirrigated plots. However, in the irrigated plots, PAV and MAV band intensities were lowest in the residue-removed treatment (0.58 and 1.00, respectively), intermediate in the chopped treatment (1.67 and 2.01, respectively), and highest in the standing-stalk treatment (3.25 and 3.67, respectively). It is unclear why there were differences between irrigation treatments, and why in the irrigated plots PAV and MAV had higher band intensities in the standing-stalk treatment than in the chopped treatment.

In the 2006 high-maize-biomass plots, PCR band intensities of PAV and MAV were strongly correlated ($r = 0.96$, $P = 0.0001$), but neither PAV nor MAV were strongly correlated with RPV ($r \le 0.26$, $P \ge 0.03$). In the 2006 low-maize-biomass plots, however, PAV, MAV, and RPV band intensities were all correlated ($r \ge 0.89$, $P = 0.0001$). In 2007, PAV and MAV were again strongly correlated ($r = 0.93$, $P = 0.0001$), and each was also less strongly correlated with RPV ($r = 0.77 – 0.79$, $P = 0.0001$).

Yield and Test Weight

In both 2006 and 2007, residue management had a significant effect on yield (Tables 2, 3, and 4). Yields were significantly higher in the plots with maize debris removed than in plots with either chopped or standing maize residue (Fig. 1 and 2). In 2006, yields in chopped and standing residue plots did not differ from each other (Fig. 1; 2006 low maize-biomass results were similar to the high biomass test, data not shown). In 2007, yields from plots with residue removed and those from chopped-residue plots were not significantly different, and both treatments outyielded standing-stalk plots (Fig. 2).

In the 2006 high maize-biomass plots, yield across both cultivars had a significant negative correlation with YDV_{stunt} and a weaker although significant correlation with YDV_{color}

Table 2. Analysis of variance results for the 2006 experiment following high maize biomass. Variables are yield, test weight (Tst Wt), percent of canopy with symptoms of YDV discoloration (YDV_{color}), percent of canopy with symptoms of YDV stunting (YDV_{stunt}), RPV, PAV, and MAV band intensity, and the mean of these three virus band intensities ($Intensity_{Mean}$). The experiment had a split split-plot design with wheat cultivar (C) as the main plot, irrigation (I) as the subplot, and residue management (RM) as the sub-subplot. The covariance structure of the best-fit model for each analysis is indicated.

Variable	Best-fit model†	C	I	I × C	RM	RM × C	RM × I	RM × C × I
Yield	CE Nugget Gaussian	ns‡	*	ns	***	ns	ns	ns
Tst Wt	BCE	ns	**	ns	ns	ns	ns	ns
YDV_{color}	IID	***	ns	ns	***	ns	ns	ns
YDV_{stunt}	CE Nugget Spherical	ns	ns	ns	***	ns	ns	ns
RPV	IID	ns	ns	ns	*	ns	ns	ns
PAV	CE Nugget Gaussian	ns	ns	ns	ns	ns	**	ns
MAV	CE Nugget Gaussian	ns	ns	ns	*	ns	*	ns
$Intensity_{Mean}$	CE Nugget Exponential	ns	ns	ns	*	ns	*	ns

* Significant at the 0.05 level.

** Significant at the 0.01 level.

*** Significant at the 0.001 level.

† Models tested included classical analysis of variance with independent and identically distributed errors, IID; blocking with correlated errors analysis, BCE; and correlated errors analysis without blocking, CE.

‡ ns, not significant.

Table 3. Analysis of variance results for the 2006 experiment following low maize biomass. Variables are yield, test weight (Tst Wt), percent of canopy with symptoms of YDV discoloration (YDV_{color}), percent of canopy with symptoms of YDV stunting (YDV_{stunt}), RPV, PAV and MAV band intensity, and the mean of these three virus band intensities ($Intensity_{Mean}$). The experiment had a split-plot design with wheat cultivar (C) as the main plot, and residue management (RM) as the subplot. The best-fit covariance structure for each analysis is indicated.

Variable	Best-fit model†	C	RM	C × RM
Yield	CE Nugget Gaussian	***	***	ns‡
Tst Wt	IID	ns	ns	ns
YDV_{color}	CE Nugget Gaussian	***	***	ns
YDV_{stunt}	CE Nugget Spherical	ns	***	ns
RPV	CE Nugget Gaussian	ns	ns	ns
PAV	CE Nugget Gaussian	ns	ns	ns
MAV	CE Nugget Gaussian	ns	ns	ns
$Intensity_{Mean}$	CE Nugget Gaussian	ns	ns	ns

*** Significant at the 0.001 level.

† Models tested included classical analysis of variance with independent and identically distributed errors, IID; blocking with correlated errors analysis, BCE; and correlated errors analysis without blocking, CE.

‡ ns, not significant.

Table 4. ANOVA results for the 2007 experiment; data from one wheat cultivar (Coker 9295). Variables are yield, test weight (Tst Wt), percent of canopy with symptoms of YDV discoloration (YDV_{color}), percent of canopy with symptoms of YDV stunting (YDV_{stunt}), RPV, PAV, SGV, and MAV band intensity, and the mean of these four virus band intensities ($Intensity_{Mean}$). The experiment had a split-plot design with irrigation (I) as the main plot, and residue management (RM) as the subplot. The best-fit covariance structure for each analysis is indicated.

Variable	Best-fit model†	I	RM	I × RM
Yield	IID	ns‡	**	ns
Tst Wt	IID	***	ns	ns
YDV_{color}	IID	ns	***	ns
YDV_{stunt}	IID	ns	***	ns
RPV	IID	*	ns	ns
PAV	IID	ns	ns	ns
SGV	IID	ns	ns	ns
MAV	IID	ns	ns	ns
$Intensity_{Mean}$	IID	ns	ns	ns

* Significant at the 0.05 level.

** Significant at the 0.01 level.

*** Significant at the 0.001 level.

† Models tested included classical analysis of variance with independent and identically distributed errors, IID; blocking with correlated errors analysis, BCE; and correlated errors analysis without blocking, CE.

‡ ns, not significant.

(Fig. 3A). Irrigated plots had significantly lower yields than nonirrigated plots (Table 2; 5.51 vs. 5.38 Mg ha^{-1}), and significantly lower test weights as well (Table 2; 711.8 vs. 720.1 kg m^{-3}). In the 2006 low maize-biomass plots, however, yield was more closely related to $YDV_{color\ r}$ than to YDV_{stunt} (Fig. 3B).

Similarly, in 2007, yield of Coker 9295 had a significant negative correlation with YDV_{color} (data not shown; $r = -0.48$, $P = 0.003$). Irrigation had no effect on yield ($P \geq 0.05$), but did affect test weight (704.9 vs. 744.5 kg m^{-3} for irrigated and nonirrigated, respectively).

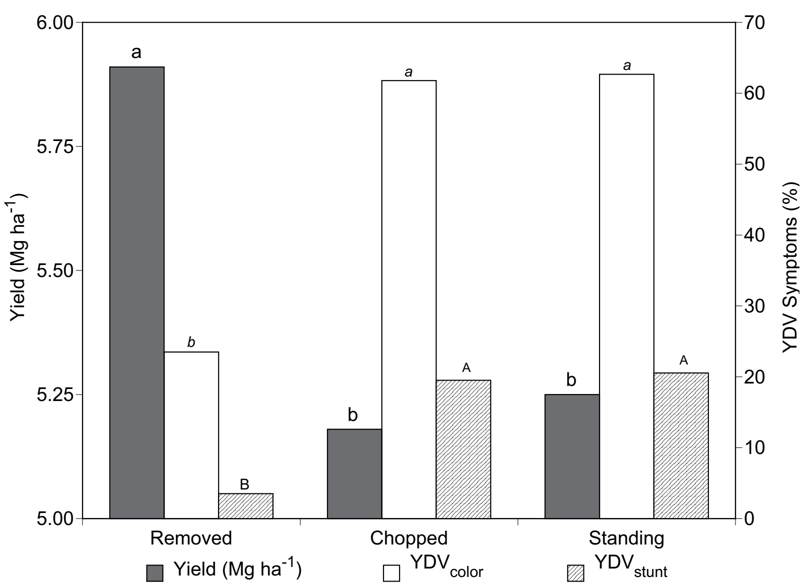

Fig. 1. Least-square means for wheat yield and YDV symptoms (YDV_{stunt} = visual estimate of percentage of plants with YDV-caused stunting and YDV_{color} = visual estimate of percentage of plants with YDV-caused discoloration) by maize residue management treatment in a Salisbury, NC, field experiment in 2006. Data are from two wheat cultivars (NC Neuse and Coker 9295) planted following a high-biomass maize crop (2006H in Table 1). Maize residue treatments: "removed" = maize residue removed by raking and bagging; "chopped" = maize residues chopped to reduce particle size; and "standing" = whole maize stalks. Least-square means for yield, YDV_{stunt} and YDV_{color} associated with the same letter were not statistically different ($P \geq 0.05$).

In 2008, when no YDV epidemic developed, residue treatment did not affect yield (Table 5; $P = 0.25$). NC Neuse significantly outyielded Coker 9295 (5.82 and 5.11 Mg ha^{-1}, respectively). Yields of both cultivars were higher without irrigation than with it (5.62 and 5.31 Mg ha^{-1}, respectively), as were test weights (772.6 and 754.7 kg m^{-3}, respectively).

DISCUSSION

Our data show that in YDV-conducive years, YDV epidemics developed more strongly in plots with maize residue than in plots without residue, and the virus disease was associated with yield reductions in comparison to plots where maize debris had been removed. Chopping the maize residue did not lead to YDV severity lower than that in standing-stalk plots, nor to yields equal to those in no-debris plots. The absence of both a YDV epidemic and a residue-management effect on yield in 2008 supports the inference that the lower yields from wheat planted into maize residue in 2006 and 2007 were primarily due to YDV damage. This is the first detailed survey of YDV serotypes in the Piedmont region of North Carolina.

We hypothesize that the maize debris in two-thirds of our experimental plots attracted YDV-transmitting aphids to those plots. As discussed above, most aphid species, including cereal aphids, prefer the color yellow to green, even seeking out plants with yellow leaves in preference to those with green leaves (Döring and Chittka, 2007; Wilkinson et al., 2002). Yellow triggers the alighting reflex in aphids. Maize residues are obviously not a true yellow, but rather a light yellow-tan color, and they are bright in fall sunlight. It is also possible that decaying maize residues provide olfactory stimuli that assist with host-finding (Döring and Chittka, 2007; Pettersson, 1993). Residues may also provide warmth and shelter for aphids. Although we did not perform aphid counts, we cannot imagine mechanisms other than larger aphid populations that would account for the more severe YDV epidemics in the plots with residue. Regardless of mechanism, however, the finding of an association between surface maize residues, YDV, and yield loss has important practical implications.

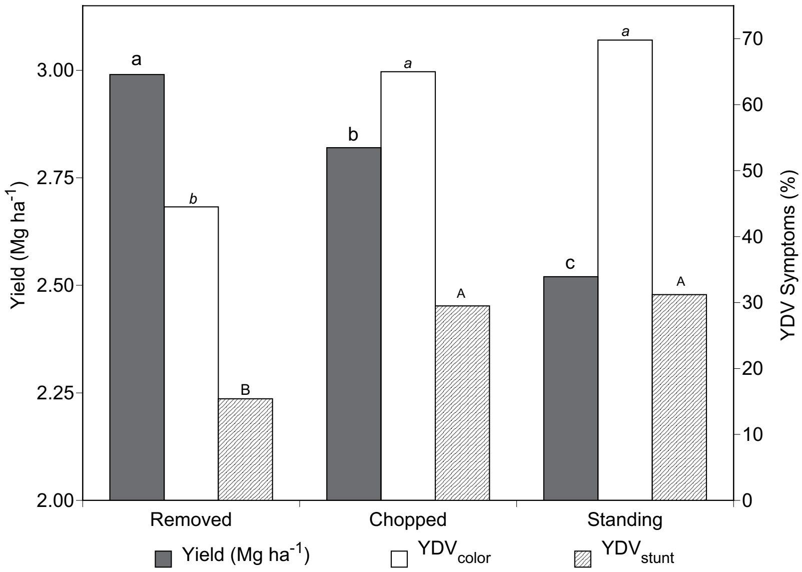

Fig. 2. Least-square means for wheat yield and YDV symptoms (YDV$_{stunt}$ = visual estimate of percentage of plants with YDV-caused stunting and YDV$_{color}$ = visual estimate of percentage of plants with YDV-caused discoloration) by maize residue management treatment in a Salisbury, NC, field experiment in 2007. Data are from plots of a single cultivar (Coker 9295). Maize residue treatments: "removed" = maize residue removed by raking and bagging; "chopped" = maize residues chopped to reduce particle size; and "standing" = whole maize stalks. Least-square means for yield, YDV$_{stunt}$ and YDV$_{color}$ associated with the same letter were not statistically different ($P \geq 0.05$).

In 2006, we saw that wheat yield was more closely related to stunting in the high-biomass maize residue than in the low-biomass residue. As YDV-related stunting is more common following fall infections, this suggests that fall-arriving aphids were more strongly attracted to parts of the field containing larger masses of debris that provided stronger visual signals. The hypothesis that at least somewhat different aphid populations transmitted YDV to the high- and low-biomass plots in 2006 is supported by the differences in serotype correlations: PCR band intensities of PAV were strongly correlated with those of MAV in the high-biomass plots, but neither of those was correlated with RPV, while band intensities of all three serotypes were correlated in the low-maize-biomass plots. This would be consistent with one aphid population primarily colonizing the high-biomass plots in the fall, and a different population arriving later in the low-biomass plots, either from the high-biomass plots, from outside, or both. In 2007, MAV and PAV band intensities were also highly correlated, and each was less correlated with RPV, once again suggesting differences in vector populations. The English grain aphid, *S. avenae*, transmits PAV and MAV efficiently, whereas *R. padi* and *R. maidis* generally do not transmit MAV efficiently (Li et al., 2001). This suggests *S. avenae* may have been primarily responsible for fall YDV transmission in 2006 (mainly initially to the high-corn-biomass plots) and 2007, whereas *R. padi* may have played a role in transmission to the low-maize-biomass plots in 2006. Of course, direct observational studies would be needed to confirm these hypotheses.

Our results are at odds with findings mentioned above that surface residues are associated with lower YDV severity in small grains (Kendall et al., 1991; Schmidt et al., 2004). Without aphid counts, we cannot directly compare our results with those of Burton and Krenzer (1985) or Hesler and Berg (2003), who found that surface residues decreased and increased aphid populations, respectively. In our experiment, we infer that any benefit provided by the maize residues in supporting aphid predators was outweighed by the aphid-attracting and/or -harboring properties of the residues. Our residue results are congruent with those of Hesler and Berg (2003), who also found *R. padi* was the dominant aphid species, as did Chapin et al. (2001) in South Carolina.

We considered possible alternative explanations for the effect of tillage treatment on yield, mechanisms other than the attraction of aphids and the concomitant severity of YDV. One possibility would be the residues tying up N, leading to differences among tillage treatments in the availability of this nutrient. However, in the first 2 yr our experiment followed a dry maize season, and it

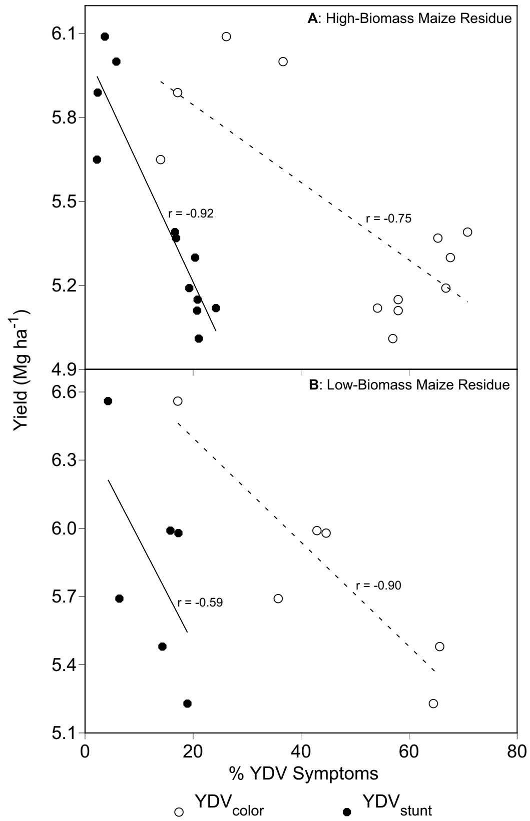

Fig. 3. Correlations of wheat yield and virus symptoms (YDV$_{stunt}$ = visual estimate of percentage of plants with YDV-caused stunting and YDV$_{color}$ = visual estimate of percentage of plants with YDV-caused discoloration) in Salisbury, NC, field experiment in 2006. Data are from two wheat cultivars (NC Neuse and Coker 9295) planted following (A) a high-biomass maize crop, and (B) a low-biomass maize crop (respectively, 2006H and 2006L in Table 1).

Table 5. ANOVA results for wheat yield and test weight (Tst Wt) from the 2008 experiment, a split split-plot design with wheat cultivar (V) as the main plot, irrigation (I) as the subplot, and residue management (RM) as the sub-subplot. The covariance structure of the best-fit model for each analysis is indicated.

Variable	Best-fit model†	C	I	I × C	RM	RM × C	RM × I	RM × C × I
Yield	IID	*	**	ns‡	ns	ns	ns	ns
Tst Wt	IID	***	***	ns	ns	ns	ns	NS

* Significant at the 0.05 level.

** Significant at the 0.01 level.

*** Significant at the 0.001 level.

† Models tested included classical analysis of variance with independent and identically distributed errors, IID; blocking with correlated errors analysis, BCE; and correlated errors analysis without blocking, CE.

‡ ns, not significant.

seems likely that carry-over N was abundant. Moreover, none of the plots exhibited signs of N stress at any time, with the wheat in all three tillage treatments appearing healthy throughout the fall and winter of each year. Thus, this explanation is unpersuasive.

Our serotype frequencies differed substantially from those found by Gray et al. (1998) in the South Carolina coastal plain. They found that PAV was the sole serotype in 94% of 228 YDV-infected samples, and none of 70 North Carolina Piedmont samples contained MAV (Gray et al., 1998). By contrast, MAV was the serotype most frequently detected in our 214 samples, taking both years together. The predominance of MAV, PAV, and RPV in this experiment is consistent with analyses of several dozen samples collected from various cultivars in different experiments across North Carolina, including in the Coastal Plain, in the years 2005–2008 (data not shown). These samples were analyzed using the same RT-PCR methodology used in this experiment.

The discrepancy between our serotype frequencies in 2006–2008 and those in collections from the early 1990s could be due to changes over time in frequencies of vectors and/or serotypes. Also, different sampling protocols and the different detection methodology in the earlier study (ELISA) may explain some of the differences. For example, Creamer and Falk (1990) showed that plants doubly infected with MAV and RPV contained transcapsidated virions, or MAV RNA in RPV protein capsids. These "disguised" MAV particles would not have been detected using the ELISA methodology of the earlier study.

It is unclear why irrigation reduced yield and test weight in 2006 and 2008, and test weight in 2007. Scab was not present in the 2008 experiment, when the negative influence of irrigation on yield and test weight was greatest, and mean scab incidence and severity were below 10% in both the 2006 and 2007 experiments. No other diseases were significantly present to be enhanced by irrigation and thus diminish yield.

In conclusion, our results suggest that light-colored unincorporated maize debris on red-clay Piedmont soils attracts aphids to emerging winter wheat crops in preference to immediately adjacent wheat plants not surrounded by maize debris. These results would likely be applicable outside North Carolina in other states where growers follow similar production practices. We hypothesize that fields with heavy maize debris attract aphids when wheat plants are small and maize residues provide a strong visual and/or olfactory cue. Heavy fall aphid infestations increase the risk of YDV and stunting-related yield losses. When planting wheat into maize residue with low or no tillage, growers may wish to consider treating seed or seedlings with an insecticide (Flanders et al., 2006), especially if the maize residue is abundant, the wheat cultivar is susceptible to YDV, and/or planting is early or "on-time."

ACKNOWLEDGMENTS

Many thanks to the staff of the Piedmont Research Station for excellent management of the field experiment; to the editor and reviewers for useful comments; to S. Bambara for helpful consultation; and to those who provided technical support: C. Gatlin, T. Gray, E. Hrebenuyuk, P. Langdon, J. Patton Özkurt, B. Portwood, and B. Tarleton.

REFERENCES

Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19:716–723.

Brust, G.E. 2000. Reflective and black mulch increase yield in pumpkins under virus disease pressure. J. Econ. Entomol. 93:828–833.

Burnett, P.A., A. Comeau, and C.O. Qualset. 1995. Host plant tolerance or resistance for control of barley yellow dwarf, p. 321–343. *In* C.J. D'Arcy and P.A. Burnett (ed.) Barley yellow dwarf: 40 years of progress. APS Press, St. Paul, MN.

Burton, R.L., and E.G. Krenzer. 1985. Reduction of greenbug (Homoptera: Aphididae) populations by surface residues in wheat tillage studies. J. Econ. Entomol. 78:390–394.

Chapin, J.W., J.S. Thomas, S.M. Gray, D.M. Smith, and S.E. Halbert. 2001. Seasonal abundance of aphids (Homoptera: Aphididae) in wheat and their role as barley yellow dwarf virus vectors in the South Carolina Coastal Plain. J. Econ. Entomol. 94:410–421.

Cowger, C., and A.L. Sutton. 2005. The southeastern U.S. Fusarium head blight epidemic of 2003. Available at www.plantmanagementnetwork.org/pub/php/research/2005/fhb/. Plant Health Prog. doi:10.1094/PHP-2005–1026–01-RS.

Creamer, R., and B.W. Falk. 1990. Direct detection of transcapsidated barley yellow dwarf luteoviruses in doubly infected plants. J. Gen. Virol. 71:211–217.

D'Arcy, C.J. 1995. Symptomatology and host range of barley yellow dwarf, p. 9–28. *In* C.J. D'Arcy and P.A. Burnett (ed.) Barley yellow dwarf: 40 years of progress. APS Press, St. Paul, MN.

Deb, M., and J.M. Anderson. 2008. Development of a multiplexed PCR detection method for barley and cereal yellow dwarf viruses, wheat spindle streak virus, wheat streak mosaic virus and soil-borne wheat mosaic virus. J. Virol. Methods 148:17–24.

DeBarro, P.J. 1991. Attractiveness of four colours of traps to cereal aphids (*Hemiptera: Aphididae*) in South Australia. J. Aust. Entomol. Soc. 30:263–264.

Döring, T.F., and L. Chittka. 2007. Visual ecology of aphids–A critical review on the role of colours in host finding. Arthropod-Plant Inter. 1:3–16.

Flanders, K., A. Herbert, D. Buntin, D. Johnson, K. Bowen, J.F. Murphy, J.W. Chapin, and A. Hagan. 2006. Barley yellow dwarf in small grains in the Southeast ANR-1082. Alabama Coop. Ext. System, Auburn, AL.

Francki, M.G., H.W. Ohm, and J.M. Anderson. 2001. Novel germplasm providing resistance to barley yellow dwarf virus in wheat. Aust. J. Agric. Res. 52:1375–1382.

Goulart, L.R., H.W. Ohm, and J.E. Foster. 1989. Barley yellow dwarf symptom severity in oat affected by plant growth stage at infection and plot type. Crop Sci. 29:1412–1416.

Gray, S.M., J.W. Chapin, D.M. Smith, N. Banerjee, and J.S. Thomas. 1998. Barley yellow dwarf luteoviruses and their predominant aphid vectors in winter wheat grown in South Carolina. Plant Dis. 82:1328–1333.

Hesler, L.S., and R.K. Berg. 2003. Tillage impacts cereal-aphid (Homoptera: Aphididae) infestations in spring small grains. J. Econ. Entomol. 96:1792–1797.

Hong, N., J.G. White, M.L. Gumpertz, and R. Weisz. 2005. Spatial analysis of precision agriculture treatments in randomized complete blocks: Guidelines for covariance model selection. Agron. J. 97:1082–1096.

Kendall, D.A., N.E. Chinn, B.D. Smith, C. Tidboald, L. Winstone, and N.M. Western. 1991. Effects of straw disposal and tillage on spread of barley yellow dwarf virus in winter barley. Ann. Appl. Biol. 119:359–364.

Kieckhefer, R.W., J.L. Gellner, and W.E. Riedell. 1995. Evaluation of the aphid-day standard as a predictor of yield loss caused by cereal aphids. Agron. J. 87:785–788.

Li, C., D. Cox-Foster, S.M. Gray, and F. Gildow. 2001. Vector specificity of barley yellow dwarf virus (BYDV) transmission: Identification of potential cellular receptors binding BYDV-MAV in the aphid, *Sitobion avenae*. Virology 286:125–133.

Lister, R.M., and R. Ranieri. 1995. Distribution and economic importance of barley yellow dwarf, p. 29–53. *In* C.J. D'Arcy and P.A. Burnett (ed.) Barley yellow dwarf: 40 years of progress. APS Press, St. Paul, MN.

Littell, R.C., W.W. Stroup, and R.J. Freund. 2002. SAS for linear models. SAS Inst., Cary, NC.

Malmstrom, C., and R. Shu. 2004. Multiplexed RT-PCR for streamlined detection and separation of barley and cereal yellow dwarf viruses. J. Virol. Methods 120:69–78.

McPherson, R.M., and D.E. Brann. 1983. Seasonal abundance and species composition of aphids (*Homoptera: Aphididae*) in Virginia small grains. J. Econ. Entomol. 76:272–274.

McPherson, R.M., T.M. Starling, and H.M. Camper, Jr. 1986. Fall and early spring aphid (*Homoptera: Aphididae*) populations affecting wheat and barley production in Virginia. J. Econ. Entomol. 79:827–832.

Neter, J., M.H. Kutner, C.J. Nachtsheim, and W. Isserman. 1996. Applied linear statistical models. 4th ed. Irwin, Inc., Chicago, IL.

Pettersson, J. 1993. Odour stimuli affecting autumn migration of *Rhopalosiphum padi* (L.). Ann. Appl. Biol. 122:417–425.

Pike, K.S. 1990. A review of barley yellow dwarf virus grain yield losses. p. 356–361. *In* P.A. Burnett (ed.) World perspectives on barley yellow dwarf. CIMMYT, Mexico, DF.

Plumb, R.T. 1992. Barley yellow dwarf, p. 41–79. *In* U. S. Singh et al. (ed.) Plant diseases of international importance: Diseases of cereals and pulses. Vol. I. Prentice Hall, Englewood Cliffs, NJ.

Plumb, R.T., and G.R. Johnstone. 1995. Cultural, chemical, and biological methods for the control of barley yellow dwarf, p. 307–319. *In* C.J. D'Arcy and P.A. Burnett (ed.) Barley yellow dwarf: 40 years of progress. APS Press, St. Paul, MN.

Robertson, N.L., R. French, and S.M. Gray. 1991. Use of group-specific primers and the polymerase chain reaction for the detection and identification of luteoviruses. J. Gen. Virol. 72:1473–1477.

Royer, T.A., K.L. Giles, T. Nyamanzi, R.M. Hunger, E.G. Krenzer, N.C. Elliott, S.D. Kindler, and M. Payton. 2005. Economic evaluation of the effects of planting date and application rate of imidacloprid for management of cereal aphids and barley yellow dwarf in winter wheat. J. Econ. Entomol. 98:95–102.

SAS Institute. 2006. SAS Release 9.1.3. SAS Inst., Cary, NC.

Schmidt, M.H., U. Thewes, C. Thies, and T. Tschamtke. 2004. Aphid suppression by natural enemies in mulched cereals. Entomol. Exp. Appl. 113:87–93.

Southwood, T.R.E., and P.A. Henderson. 2000. Ecological methods. 3rd ed. Blackwell Sci., Oxford, UK.

Stroup, W.W., P.S. Baenziger, and D.K. Mulitze. 1994. Removing spatial variation from wheat field trials: A comparison of methods. Crop Sci. 86:62–66.

Weisz, R. 2004. Small grain production guide 2004–05:AG-580. NC Coop. Ext. Serv., North Carolina State Univ., Raleigh.

Weisz, R., B. Tarleton, J.P. Murphy, and F.L. Kolb. 2005. Identifying soft red winter wheat cultivars tolerant to *Barley yellow dwarf virus*. Plant Dis. 89:170–176.

Wilkinson, D.M., T.N. Sherratt, D.M. Phillip, S.D. Wratten, A.F.G. Dixon, and A.J. Young. 2002. The adaptive significance of autumn leaf colours. Oikos 99:402–407.