Effect of Wheat Spindle Streak Mosaic Virus on Yield of Winter Wheat in New York

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ABSTRACT

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In 1987-88 and 1988-89, field plot experiments were undertaken to assess the effects of wheat spindle streak mosaic virus (WSSMV), a soilborne virus transmitted by *Polymyxa graminis*, on winter wheat yields in New York. Two experimental approaches, reinfestation of fumigated plots with nonfumigated soil and a natural gradient of disease incidence, were used to produce different levels of disease. To minimize problems of covarying soil factors, yields of susceptible cultivars were compared with resistant cultivars in each experiment. The most reliable estimates of WSSMV effect were obtained with the disease gradient method when average disease incidence varied greatly between blocks and replication was high (12 blocks). Based on this approach, the grain yield of the susceptible cultivar Frankenmuth was reduced by an average of 14 kg/ha for every 1 percent increase in plants infected by WSSMV, a 1.4-t/ha (32%) reduction when all plants were infected. Yields of the breeding line NY6432-10 did not decline, despite a high incidence of plants infected with the virus in both years. When data from 1980–1989 regional yield trials were compared with temperature data, significant correlations were detected between long spring periods of temperatures conducive to WSSMV and lower yields of the susceptible cultivars Frankenmuth and Augusta relative to the yield of the highly resistant cultivar Geneva. Relative yield of Frankenmuth decreased by an average of 0.45% per day as net days in the optimal temperature range (2–11 C) increased from 20 to 45. Yield reductions for other cultivars screened over the past decade closely paralleled their relative resistance to, or tolerance of, WSSMV as demonstrated in field plot experiments. These results indicate that WSSMV has significantly reduced the yield of susceptible cultivars in New York over the past decade and that yield reduction is related to the percentage of plants infected with the virus and the duration of spring temperatures conducive to disease development.

Wheat spindle streak mosaic virus (WSSMV) infects winter wheat, *Triticum aestivum* L., throughout the midwestern and eastern regions of North America (21). Although WSSMV is now considered to be a strain of wheat yellow mosaic virus (WYMV), the present study includes only this strain of WYMV; thus, it will be referred to as a WSSMV (21). In New York, this soilborne virus was found in more fields and at a higher incidence than any other virus of winter wheat (7). Estimates of the effects of WSSMV on yield of winter wheat vary from 3 to 87% (1,5,10,15,22). One reason for year-to-year and site-to-site variability is the effect of temperature on WSSMV. Slykhuis (15,16) showed that in controlled-environment chambers the optimal temperature (soil and air) range for wheat spindle streak mosaic (WSSM) symptom development was 4–13 C. In Ontario, Canada, years with severe WSSM had a total of 65 or more days (including spring and fall) with mean air temperatures in this range (15). Since fall transmission took place in as little as 10–17 days (16,18), and every year reported by Slykhuis (15) had more than 30 fall days in the optimal range, fall temperatures were not as critical as spring temperatures in determining the year-to-year severity of WSSM. Rossiter (11) noted that in Rock Springs, Pennsylvania, mean spring soil temperatures at a 5-cm depth were consistently 2 C higher than air temperatures. He thus revised the optimal range for WSSM development to a mean air temperature of 2–11 C, which roughly corresponded to the soil temperature range of 4–13 C identified by Slykhuis.

A second factor complicating assessment of the effects of WSSMV on yield is the difficulty of conducting controlled experiments in the field. Because the virus is difficult to transmit mechanically, and its vector, *Polymyxa graminis* Led. (19), is an obligate parasite, most yield experiments have relied on naturally occurring, symptomless plants as controls. However, symptomatic plants are found more readily in low, poorly drained areas of fields (1,7), and thus soil moisture effects may be confused with WSSMV effects. Some investigators have tried to avoid this problem by selecting symptomatic and asymptomatic plants from within similar soil environments (5,15,22) or by using fumigation (4,10,11).

A 2-yr study was designed to assess the effects of WSSMV on wheat yields in New York. Two experimental approaches, reinfestation of fumigated plots with nonfumigated soil and naturally occurring gradients of disease incidence, were used to produce different levels of disease. To minimize the problem of covarying soil factors, yields of susceptible cultivars were compared with resistant cultivars in each experiment. Finally, 1980–1989 regional temperature data were compared with regional yield data in order to assess WSSMV-related reductions in New York over the past decade.

MATERIALS AND METHODS

Cultivars. Hart, a soft red winter wheat cultivar (14), and Geneva, a soft white winter wheat cultivar (20), consistently incurred less than 2% incidence of WSSMV infection in field plot experiments and commercial fields (8,9). Harus demonstrated moderate resistance in Ontario (13) and New York (8,9). Houser incurred an intermediate (2–30%) incidence, whereas Frankenmuth, Augusta, and the breeding line NY6432-10 consistently showed greater than 40% incidence of WSSMV infection (8,9).

Fumigation experiment, 1987-1988. An experiment was conducted at the Cornell Agronomy Farm in Aurora, New York, using soil fumigation followed by reintroduction of nonfumigated soil. The site was plowed, harrowed, and then covered with 4.5-

m-wide strips of clear, 4-mil polyethylene plastic. Brom-O-Gas (methyl bromide plus chloropicrin; Great Lakes Chemical, West Lafayette, IN) was released under the plastic at a rate of 49 g/m^2. Plots were kept covered for 4 days, after which the plastic was removed and the soil allowed to aerate for several days before planting. Following fumigation, all hand work was performed wearing disposable plastic boots, and all field equipment was steam-cleaned before entering the area.

Seed was treated with 2 ml/kg Vitavax 200 (carboxin plus thiram) and planted on 16 September at a rate of 167 kg/ha in six-row plots 1.25 × 4.0 m. The site in Aurora was chosen because it had a history of WSSM. The soil, a Honeoye silt loam, was tiled and well drained; it had been in a corn, oat, and wheat rotation for the previous 15 yr—the last wheat crop was planted in 1985. Before planting, 227 kg/ha of 6:24:24 (N-P-K) starter fertilizer was broadcast; a topdressing of 33 kg/ha of nitrogen was applied at crop green-up in spring. Six replications were included in a blocked, split-plot design with three cultivars (Geneva, Hart, and Houser) as main-plot treatments and two inoculation regimes (reintroduction of 1–2 cm of nonfumigated soil in each seed furrow versus covering seed with 1–2 cm of fumigated soil) as subplot treatments. On 14 October 1987, plants from 0.5-m sections of two rows of each plot were counted. On 6 April 1988, one 0.5-m section of each outside row was dug, and plants were counted to determine winter survival.

At second-node detectible, or growth stage (GS) 32 on the scale of Zadoks et al (23), 40 tillers were removed randomly from the center four rows of each plot. These tillers were rated for WSSM symptoms, divided randomly into four batches, and assayed by enzyme-linked immunosorbent assay (ELISA) (7) to confirm symptom ratings. Plots were trimmed to 3.0 m in length and harvested with a mechanical combine. Grain yields and test weights were adjusted to 13.5% moisture for analysis.

In order to estimate the effects of WSSMV independent of non-WSSMV factors in the soil inoculum, a single degree of freedom linear contrast was calculated as follows:

$$LI = (Hs_i - Hs_n) - 0.5(G_i - G_n + Ht_i - Ht_n)$$

where *Hs*, *G*, and *Ht* represent the yields of cultivars Houser, Geneva, and Hart, respectively, and subscripts *n* and *i* represent noninoculated and inoculated plots, respectively. Whereas the undefined soil inoculum presumably contained pathogens, weeds, and other factors that could have affected yield, the linear contrast *LI* factored out these non-WSSMV effects by comparing the effect of soil inoculum on the susceptible cultivar Houser with the effect of soil inoculum on the highly resistant cultivars Geneva and Hart. A similar approach was used by Campbell et al to estimate wheat yield reductions by soilborne wheat mosaic virus (2). Contrasts were calculated and tested with the PROC ANOVA procedure of the Statistical Analysis System (12).

Disease gradient experiment, 1987-1988. Plots of the cultivars Frankenmuth, Augusta, Geneva, and Harus were planted in four randomized complete blocks adjacent to the fumigated experiment at Aurora on 16 September, 1987. Plot size and fertility practices were identical to those of the fumigated experiment, with the exception of the spring top-dressing, which was applied at 67 kg/ha of nitrogen.

At second-node detectible (GS 32), 40 tillers were removed randomly from the center four rows of each plot, and the number of tillers that was infected by WSSMV was determined as follows: each 40-tiller sample was divided into four or more batches (maximum of 11 tillers), and each of these batches was assayed by ELISA. If a batch with streaking symptoms had a positive WSSMV ELISA, all of the tillers in it were considered to be infected. No tillers of any batch with a negative ELISA were considered to be infected. Asymptomatic batches with positive WSSMV ELISA (occurred in less than 7% of asymptomatic batches) were considered to contain one infected plant plus a fraction calculated from the overall proportion of batches of this type in the experiment.

Plant height was determined at hard-dough (GS 87) by taking four readings in the two center rows of each plot. Spike density was measured at the same GS by counting spikes in a 30 × 45 cm frame placed at each end of each plot. Grain yields and test weights were determined as described in the fumigated experiment above.

Incidence of WSSMV infection is often affected by soil drainage characteristics (1,7). To avoid mistaking the effects of soil moisture with the effects of WSSMV, therefore, yield and yield components of individual plots of susceptible cultivars were adjusted as follows:

$$A_i = S_i\,(R_{tot}\ /\ R_i)$$

where A_i and S_i represent adjusted yield and actual yield, respectively, of a susceptible cultivar in block *i*; R_{tot} equals mean yield of resistant cultivars in all blocks; and R_i equals mean yield of resistant cultivars in block *i*. Adjusted yields and yield components were regressed against incidence of WSSMV infection using the SAS PROC REG procedure (12).

Disease gradient experiment, 1988-1989. Experimental plots were planted at the Aurora Agronomy Farm on 16 September. Soil type and fertility practices were the same as those used in the disease gradient experiment in 1987-88. The last wheat crop at this site had been planted in 1986. The experiment was designed in 12 randomized complete blocks with cultivars (Frankenmuth, Geneva, Harus, and NY6432-10) as treatments. Blocks were oriented perpendicular to any observable drainage gradient.

In early October, plants from 1 m of the outside row of each plot were counted. In early April, the same 1-m sections of row were dug and counted to determine winter survival. Plant height was recorded at harvest by measuring 10 randomly selected plants from each plot, and straw was weighed and adjusted for moisture by drying a subsample from each plot. All other yield components were measured as in 1987-88.

Geneva, Harus, and Frankenmuth plots were rated for incidence of WSSMV infection following a procedure similar to that used in the disease gradient experiment in 1988. WSSM symptoms on plants of the breeding line NY6432-10 were much less distinct in 1989, and ELISA results suggested that the initial visual assessment included many false negative ratings. For this reason, NY6432-10 plots were resampled and assayed using a standard dilution series of a known-infected source of the same cultivar on each ELISA plate. Absorbance values were found to vary in a linear manner ($r^2 = 0.98$) within the range of dilutions used (1:1–1:16 in a preparation from uninfected tissue). Thus, a WSSMV rating was calculated by comparing sample absorbance values with the best-fit line from the regression analysis of the standard dilution series on each plate. Statistical analyses followed the same procedures described for the 1987-88 disease gradient experiment.

Regional temperature and yield data, 1979–1989. Regional air temperature data were obtained through the Department of Soil, Crop, and Atmospheric Sciences, Cornell University (1979–1986 data) and through Cornell Cooperative Extension's CENET on-line weather data records (1987–1989 data). Running daily means were calculated by averaging the current day's mean air temperature with that of the previous 2 days, a procedure designed to simulate the lower degree of fluctuation typical of soil temperatures (D. G. Rossiter, *personal communication*). The number of fall and spring days in the optimal range for WSSM development (2–11 C) was tallied and compared across locations and years.

Yield data for the 1980–1989 seasons were obtained from regional plant breeding nurseries at various sites in New York. The mean yields of various cultivars were converted to a percentage of the yield of the cultivar Geneva at each site, and these values were regressed against the net number of spring days in the optimal range for WSSM development (see above) at the weather station nearest to the experimental site.

RESULTS

Fumigation experiment, 1987-1988. Streaking on young, emerging leaves of Houser, the most susceptible cultivar in this experi-

TABLE 1. Winter survival, grain yield, and test weight of winter wheat cultivars grown in fumigated soil with and without reintroduction of soil with wheat spindle streak mosaic virus (WSSMV) at the Aurora Agronomy Farm in 1987-1988

Cultivar	Treatment	Winter survival (%)	Grain yield (t/ha)	Test weight[a] (g/L)	WSSM (% plants infected)
Houser	*i*[b]	91.1	4.95	700	8.8
	n[c]	105.5	5.25	713	2.1
Geneva	*i*	96.6	4.95	738	1.2
	n	89.7	4.49	730	0.4
Hart	*i*	82.6	4.95	760	2.9
	n	81.5	4.73	756	0.0
LI[d]		−18.4	−0.64*	−18*	

[a]Means of six replications. Grain yield and test weight were adjusted to 13.5% moisture.

[b]*i* = seed was covered with 1 cm nonfumigated, infectious soil from the same site.

[c]*n* = seed was covered with fumigated soil using a hoe.

[d]*LI* = a linear contrast estimating the effect of WSSMV as follows: $LI = (Hs_i - Hs_n) - 0.5\ (G_i - G_n + Ht_i - Ht_n)$, in which *Hs, G,* and *Ht* represent yields of the cultivars Houser, Geneva, and Hart, and subscripts *n* and *i* represent noninoculated and inoculated plots, respectively. Estimates with an asterisk are significantly less than zero according to a one-tailed *F*-test ($P < 0.05$).

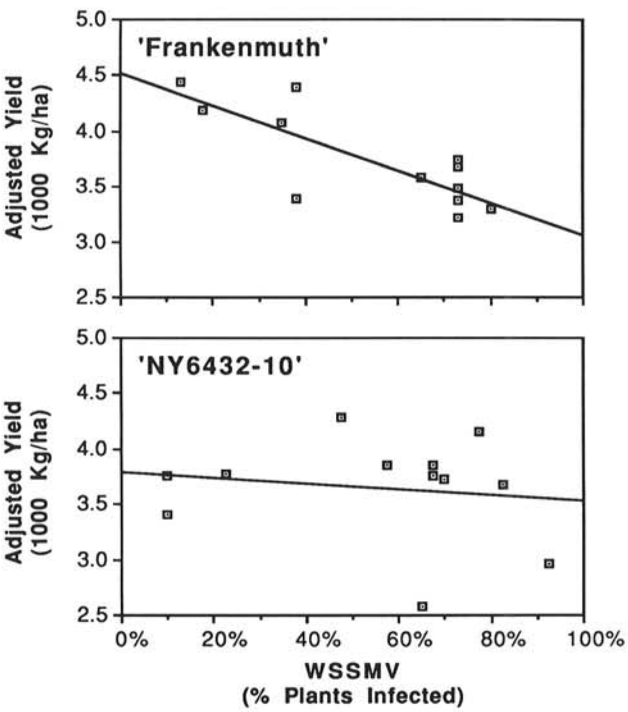

Fig. 1. Relationship of grain yield of winter wheat cultivars Frankenmuth and NY 6432-10 at varying incidences of wheat spindle streak mosaic virus infection in New York in 1989.

ment, was first observed during the last week of April and quickly progressed to include chlorosis and some necrosis as these leaves matured. New foliage continued to emerge with visible streaking for approximately 14 days after initial symptoms were observed. After 6 May (GS 32), when mean temperatures rose and remained above 11 C, newly emerging leaves no longer showed visible streaking, but the chlorotic and necrotic symptoms on previously affected leaves remained. The highest incidence of plants infected was found in inoculated Houser plots (Table 1). Noninoculated plots of all cultivars demonstrated a consistently low incidence of WSSMV infection (mean = 0.8%).

Mean yields for all treatments were between 4.5 and 5.0 t/ha. When grain yield data from all blocks were analyzed, the linear contrast (*LI*) indicated that WSSMV had caused a mean reduction of 0.64 t/ha (12%) in the yield of Houser, an unexpectedly large yield reduction given the relatively low incidence of WSSMV infection observed. However, since the 95% confidence interval for *LI* extended from 0.02 to 1.3 t/ha, there was considerable uncertainty about the magnitude of actual yield loss attributable to WSSMV in this experiment. No significant reduction in winter survival was detected, but test weight was reduced by 18 g/L (3%). The main effect of soil inoculation was not significant for any variable measured, whereas cultivar main effects were significant ($P < 0.05$) for winter survival and test weight.

Disease gradient experiment, 1987-1988. Symptoms on plants of Augusta and Frankenmuth, the most susceptible cultivars in this experiment, were similar to those described for Houser in the fumigation experiment above. Incidence of WSSMV infection in plots of Augusta and Frankenmuth varied from 4 to 74%, whereas plots of the cultivars Geneva and Harus averaged 0 and 1.9% incidence, respectively. Infected plants of the breeding line NY6432-10 produced a distinct but milder chlorosis than that on Augusta and Frankenmuth.

Yields of the resistant cultivars Geneva and Harus averaged 5.6 and 5.8 t/ha, respectively. Yields of the susceptible cultivars Augusta and Frankenmuth averaged 5.6 and 5.1 t/ha, respectively, whereas that of NY6432-10 averaged 5.7 t/ha. When adjusted yields of susceptible cultivars were regressed against incidence of WSSMV infection, negative slopes were found for the cultivars Augusta and Frankenmuth. The average slope of the least squares regression lines of these relationships represented a grain yield reduction of 4.2 kg/ha for every 1% increase in plants infected by WSSMV, a 0.42-t/ha (12%) reduction when all plants are infected. Yield of NY6432-10 did not change significantly in relation to an increase in incidence. However, the limited replication of this experiment greatly reduced the power of statistical tests.

Disease gradient experiment, 1988-1989. In 1989, symptom development progressed more quickly than in 1988. Chlorotic streaking appeared on emerging leaves of susceptible cultivars by 20 April and persisted for approximately 26 days (through GS 36). Once mean air temperatures rose above 11 C, severe mosaic symptoms remained on affected leaves; however, these tissues no longer contained levels of WSSMV detectible by ELISA. After a cool period in early June, some streaking was also observed on flag leaves, but plants were not assayed by ELISA

TABLE 2. Regression analyses of the relationships of yield and yield components with incidence of wheat spindle streak mosaic virus (WSSMV) infection in wheat cultivar Frankenmuth at the Aurora Agronomy Farm in 1988-1989[a]

	Winter survival (%)	Spikes per m^2	Plant height (cm)	1,000-kernel wt (g)	Test weight (g/L)	Grain yield	Straw yield
Intercept	95	626	110	34.3	838	4.51[b]	5.45[b]
Slope	0.037	0.502	−0.042	−0.052	−0.481	−0.014	−0.007
% Reduction[c]	3.8	8.0	−3.8	−15.1	−5.7	−31.7	−12.6
r^2	0.04	0.02	0.12	0.37	0.22	0.64	0.06
Significance	0.53	0.69	0.13	0.01	0.06	<0.01	0.22

[a]Data from individual plots of the susceptible cultivar, Frankenmuth, were adjusted using the relative values of the resistant cultivars, Geneva and Harus, in the same block.

[b]Grain and straw yields expressed as 1,000 kg/ha and adjusted to 13.5% moisture and dry weight values, respectively.

[c]Change in yield component associated with a 100% incidence of WSSMV infection.

TABLE 3. Number of spring and fall days with running daily mean[a] air temperature between 2 and 11 C[b] at five sites[c] in New York

Season	1 September to 30 November					1 March to 31 May				
	Aur	Bat	Ithaca	Lkprt	Tully	Aur	Bat	Ithaca	Lkprt	Tully
1978-79	38	32	39	39	39	37*[d]	38*	38*	40*	34*
1979-80	39	36	42	40	46	36	41	35	36	42*
1980-81	44	43	43	47	29	34**	45**	36*	37**	40
1981-82	54	54	53	52	53	31*	23	34	34	19
1982-83	33	34	36	30	35	56*	50*	58*	50*	46*
1983-84	43	38	47	40	40	39*	37*	40*	41*	40
1984-85	36	32	40	38	37	28*	21	31*	30*	30*
1985-86	38	na	44	30	na	31*	29*	34	33*	25
1986-87	42	38	43	40	45	32*	37*	38*	38*	na
1987-88	44	44	49	39	na	41*	41	34*	41	na
1988-89	47	46	46	na	na	44	43	43	45	na

[a]Running daily means calculated by averaging mean temperature of current day with that of the two previous days. Scattered days of optimal temperatures interspersed in warmer periods at the end of spring are not included.
[b]Optimal range for wheat spindle streak mosaic development adapted from Slykhuis (15,16) and Rossiter (11).
[c]Aur = Aurora, Bat = Batavia, Lkprt = Lockport. In 1987–1989, data from Geneva and Freeville were substituted for temperatures from Batavia and Ithaca, respectively.
[d]* = Periods of spring temperatures in optimal range were broken by five or more consecutive days with above-optimal temperatures. ** = Two above-optimal periods in one spring.

at this stage. Incidence of WSSMV infection at the Aurora site was similar to that in 1988; Geneva and Harus plots averaged only 0.5 and 2.6%, respectively, and Frankenmuth plots varied from 13 to 80%.

Grain yields of all cultivars were lower in 1989 than in 1988, with Geneva and Harus averaging only 4.4 and 4.3 t/ha, respectively, at the Aurora site. Adjusted yield of the susceptible cultivar, Frankenmuth, declined 32% in association with an increase from 0 to 100% in incidence of WSSMV infection (Fig. 1), and this slope was highly significant ($P < 0.01$). Of the individual yield components that were measured, 1,000-kernel weight showed the largest reduction attributable to WSSMV infection (Table 2), but the estimated reduction of this parameter (15%) did not account for the total 32% reduction in grain yield.

Although plants of NY6432-10 developed symptoms at approximately the same time as plants of Frankenmuth, the chlorotic streaking was, as noted above, difficult to rate visually. The WSSMV-rating scheme based on ELISA absorbance values revealed a sufficient range in disease across the experiment (10–93%) for analysis of yield effects. Regression analysis of this WSSMV rating against adjusted grain yield of NY6432-10 plots suggested that infection by the virus did not significantly ($P > 0.05$) affect grain yield (Fig. 1). Analysis of NY6432-10 grain yield components and straw yield revealed no significant correlations with WSSMV rating.

Temperature data, 1979–1989. Fall temperatures at all sites remained in the optimal range for WSSM development (2–11 C) for extended periods in all years, ranging from 29 to 54 days (Table 3). In no year was this fall period shorter than the 10–17 days that Slykhuis (16) identified as necessary for maximum infection by WSSMV. Spring temperatures exhibited a wider range, from 19 (Tully in 1982) to 52 optimal days (Ithaca in 1983). The periods of cool spring temperatures were broken by periods of warmer-than-optimal temperatures in many years. The work of other investigators (11,17) suggested that temperatures above 11 C increased the total number of days required for WSSM symptom expression. The effect of these warmer periods is illustrated by comparing the number of days at optimal temperatures that were required for symptom expression at the Aurora site in 1988 and 1989. In 1988, a warmer-than-optimal period occurred from 4 April through 8 April, and symptoms did not appear until a total of approximately 30 days had passed in the optimal range. In 1989, no period of warmer temperatures occurred, and symptoms appeared after only 22 days in the optimal range. Warmer-than-optimal periods must, therefore, be taken into account when comparing weather data from different years and sites.

Applying these criteria to the data presented in Table 3, the net number of spring days contributing to WSSM development (total days in the optimal range minus periods of 5 or more days of mean temperature above 11 C) varied widely from site to site and year to year (Table 4). Of the 52 site-by-year combinations recorded, 17 had net spring days equal to or greater than those observed during the Aurora experiments. The majority of these cases were found in the years 1980, 1983, 1988, and 1989. Different sites varied considerably within each year, but no one site appeared to have consistently greater or lesser totals throughout the 11 yr. Eleven site-by-year combinations (most notably those in 1985) had optimal periods of less than the 22–25 net days required for symptom development at Aurora in 1988 and 1989.

TABLE 4. Net spring days with temperatures optimal for wheat spindle streak mosaic development[a] at five sites[b] in New York

Year	Aurora	Batavia	Ithaca	Lockport	Tully	Average
1979	31	31	32	33	29	31
1980	*36*[c]	*41*	35	*36*	*36*	*37*
1981	22	33	29	29	*40*	31
1982	26	23	34	34	19	27
1983	*49*	*42*	*42*	*43*	*39*	*43*
1984	34	31	35	*36*	*40*	35
1985	21	21	24	22	24	22
1986	26	21	34	28	25	27
1987	19	28	29	29	NA[d]	26
1988	*36*	*41*	29	*41*	NA	*37*
1989	*44*	*43*	*43*	*45*	NA	*44*

[a]Total number of days with 3-day running mean air temperatures between 2 and 11 C, minus periods of five or more consecutive days above 11 C.
[b]In 1987–1989, data from Geneva and Freeville were substituted for temperatures from Batavia and Ithaca, respectively.
[c]Numbers in italic type represent periods of net spring days greater than those observed during the 1988 and 1989 experiments in Aurora.
[d]NA = data not available.

Yields of regional winter wheat nurseries, 1980–1989. Longer periods of net spring days between 2 and 11 C were strongly associated with a reduction in relative yield of the susceptible cultivar Frankenmuth when expressed as a percentage of the yield of the resistant cultivar Geneva (Fig. 2). The slope of the least-squares regression line for this relationship was statistically significant ($P = 0.02$) and represented an incremental reduction of 0.45% for each 1-day increase in the period of optimal temperatures for WSSM development. Relative yields of the cultivars Augusta and Houser showed similar trends (Table 5), however, the slopes of these relationships were not statistically significant.

Low yield of the cultivar Geneva in the 1988 Livingston County trial led to large outliers (Studentized residuals > 3.0) in analyses of the relative yield of all three of the susceptible cultivars. A severe common bunt problem was encountered in this trial, and although individual plot ratings were not taken for this disease, it may account for these otherwise-unexplained outliers. When regression analyses were rerun after removing these outliers, the significance levels for the analyses of yield-reduction relationships were reduced considerably. For both Frankenmuth and Augusta this relationship was statistically significant ($P < 0.05$). Slope estimates and statistical analyses of these relationships are presented in Table 5. The relative yields of the breeding line NY6432-10 in these same regional trials revealed no evidence of WSSMV-related yield reduction. The slope of the least-squares regression line for this cultivar was positive, but not statistically significant either with or without the 1988 Livingston county data.

Since incidence ratings were not taken for individual plots in these regional trials, the possibility exists that some factor other than WSSMV also was affected by periods of cool spring temperatures. If this factor was influential we would expect to see similar trends in all of the cultivars whose yields were compared to Geneva. This, however, was not the case. In fact, the estimated yield reductions closely paralleled the respective levels of resistance to WSSM in field plots and commercial fields (7,8,9). This consistent trend is strong evidence that yield reductions over this decade were, indeed, attributable to WSSMV rather than to other covarying environmental factors.

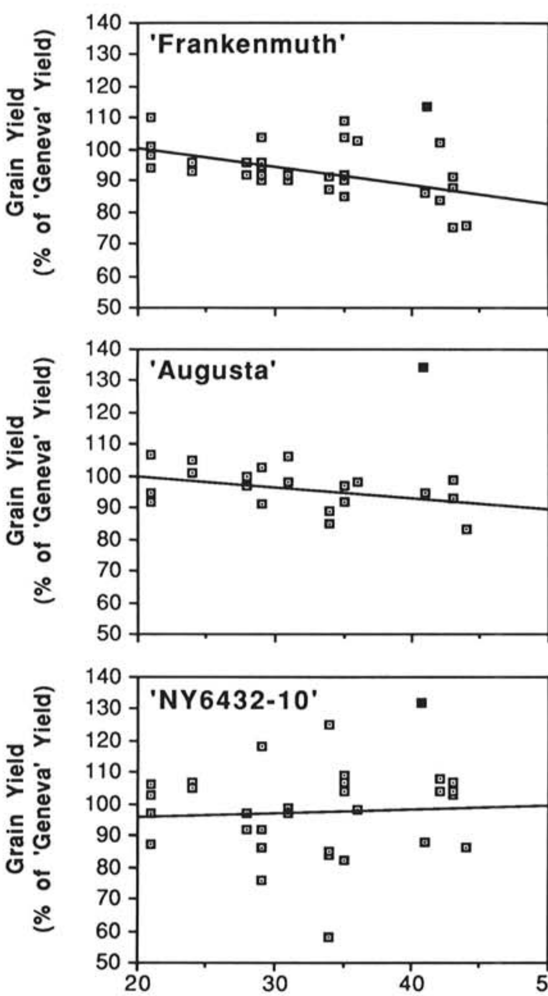

Fig. 2. Relationship of grain yield of winter wheat cultivars Frankenmuth, Augusta, and NY 6432-10 with duration of spring temperatures in the optimal range for wheat spindle streak mosaic development in New York in 1980–1989. Livingston Co. data for 1988 (solid squares) were not included in calculation of best-fit lines. Net days represent 3-day running mean air temperatures between 2 and 11 C.

DISCUSSION

The consistent association of lowered winter wheat yields with increased incidence of WSSMV infection suggests that the virus reduced yields of susceptible cultivars in field plot experiments in New York. During the 1988-89 season this reduction reached a magnitude (up to 32%) comparable to the highest estimates reported from similar wheat-growing regions (10,15,22). Statistically significant reductions were also observed in the cultivar Houser during the 1987-88 season, although estimates of this reduction were less precise.

Experimental approaches using soil fumigation and a natural gradient of disease incidence were both effective in detecting WSSMV-related yield reductions. The latter approach seemed preferable, however, since it assessed yield reductions under conditions similar to those encountered in commercial fields, and it allowed yield reduction to be estimated over a wide range of disease incidence.

Temperature and yield data from the wheat-growing region of New York over the past decade indicate that WSSMV-related yield reductions were not an isolated phenomenon. Temperature patterns conducive to severe WSSM development occurred at a majority of locations in 4 of the past 11 yr in the state. The observed yield reductions of five cultivars during these same years closely paralleled their relative levels of susceptibility to WSSMV and provided further evidence of the detrimental effects of this disease in New York.

By quantifying the effects of disease incidence and spring temperatures, the above results provide the beginning of a descriptive model for the effect of WSSMV on winter wheat yield. In the current study, the parameters for the effects of incidence and spring temperatures were estimated separately. A fully integrated model will require further experiments documenting the incidence/yield reduction relationship over more spring temperature regimes in order to incorporate any interactions between the effects of these two parameters.

The observed estimates of reduction of two yield components (test weight and 1,000-kernel weight) did not equal the entire reduction in grain yield. One yield component not measured in the experiments (i.e., number of kernels per spike) may account for some of this difference. A second factor that complicated detection of reductions in early components was the small sampling unit (two times 30 × 45 cm) used for counts of spikes per square millimeter. Within-treatment variability for these counts was quite high; thus, reductions in this parameter were

TABLE 5. Regression analyses of the relationships of relative yields[a] of five wheat cultivars with net spring days in the optimal temperature range for wheat spindle streak mosaic development,[b] 1980–1989[c]

	Frankenmuth	Augusta	Houser	NY6432-10	Harus
All data					
Slope (%/day)	−0.45	−0.02	−0.14	0.26	−0.14
r^2	0.13	0.00	0.01	0.02	0.02
Significance	0.02	0.47	0.33	0.48	0.27
Data excluding outlier[d]					
Slope (%/day)	−0.58	−0.34	−0.38	0.08	−0.24
r^2	0.25	0.16	0.06	0.00	0.07
Significance	0.002	0.04	0.09	0.82	0.14

[a] Data were obtained from plant breeding regional trials in central and western New York. Yields of all susceptible cultivars are expressed as a percentage of yields of the cultivar Geneva in the same experiment.
[b] Total number of days with 3-day running mean air temperatures between 2 and 11 C, minus periods of five or more consecutive days above 11 C.
[c] Yields for Augusta and Harus were available from 1984–1989 and 1985–1989, respectively.
[d] Analysis repeated after removing data from 1988 Livingston county trial. At this site significant common bunt was observed. Although individual plot ratings were not taken, the cultivar Geneva has had a problem with this disease in the past, and low yields of this cultivar led to otherwise-unexplained outliers in plots of all susceptible cultivars in this trial.

difficult to detect.

Since 1,000-kernel weight and test weight are determined in later stages of plant growth, reduction of these components by WSSMV was somewhat unexpected. However, some symptoms were observed on flag leaves in 1989, and severe chlorosis persisted on leaves immediately below flag leaves. Since photosynthetic activity in these leaves provides carbohydrates for grain filling, it is not surprising that some late components were affected. A further explanation for the effect of WSSMV on 1,000-kernel weight and test weight could be that the virus weakened plants and predisposed them to later-season diseases. In 1989, late-season fungal diseases (particularly Septoria nodorum blotch, leaf rust, and scab) were a significant problem on winter wheat in the state and probably contributed to the low yields of WSSMV-resistant cultivars in the Aurora experiment (4.4 t/ha as compared to 5.7 t/ha in 1988). A similar hypothesis was suggested by Cunfer et al (4).

Several factors may explain other differences between this and previous studies on wheat yield reduction attributable to WSSMV. Cunfer et al (4) reported that reduced winter hardiness and reduced biomass were most responsible for wheat yield reductions attributable to WSSMV in Georgia. However, the environmental conditions present during their study (extended winter periods in the optimal range for WSSM development followed by killing frosts in January) were quite different from the conditions experienced during the present study. Severe frosts are encountered in New York in some years; however, they do not generally reduce winter wheat survival, because locally adapted cultivars remain dormant at these times.

Wiese et al (22) reported WSSMV-related effects (particularly reduced tillering) in Michigan, under environmental conditions much closer to those experienced in New York. Their study involved wheat that was space-planted at 15- × 30-cm intervals (approximately 1/20 of a normal planting density). Under these conditions, reduced tillering of individual plants could not be compensated for by an increase in tillering of healthy plants. In a population of normally spaced wheat plants, plant compensation could result in a lower overall effect on tillering and/or head density.

The performance of the breeding line NY6432-10 in these experiments is strong evidence of tolerance, sensu Cooper and Jones (3), to infection by WSSMV. Symptom severity in NY6432-10 was much milder than in other cultivars, and no evidence of yield effects was observed in field plot experiments or regional trials. In these and related studies involving 13 winter wheat cultivars (8,9), no other cultivars produced notably mild symptoms such as those observed in NY6432-10 plants.

All widely planted cultivars in the state except Geneva and Harus appear to be moderately to highly susceptible to WSSMV infection. Susceptible cultivars incurred an average incidence of 33 and 34% in commercial fields in 1988 and 1989, respectively (7). Many commercial fields, especially those planted to Frankenmuth, showed greater than 80% infection by WSSMV. Thus, it appears that WSSM has been a longstanding problem in New York, and efforts to control the disease should continue to receive attention.

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