Effect of Early Season Powdery Mildew on Development, Survival, and Yield Contribution of Tillers of Winter Wheat

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Accepted for publication 29 July 1992.

ABSTRACT

Everts, K. L., and Leath, S. 1992. Effect of early season powdery mildew on development, survival, and yield contribution of tillers of winter wheat. Phytopathology 82:1273-1278.

The formation, survival, and development of primary and secondary tillers of winter wheat (*Triticum aestivum*) are influenced by stresses the plant encounters during its growth. Three and two cultivars of winter wheat were planted near Clayton, North Carolina, in 1989 and 1990, respectively. Levels of powdery mildew (*Blumeria graminis* f. sp. *tritici*) were established by triadimenol seed treatment and presence or absence of rows of susceptible wheat inoculated with powdery mildew. Presence of primary and secondary tillers was determined four times during the growing season, and the contribution of each tiller to yield was assessed at harvest. There were positive correlations between the presence of some tillers and the amount of powdery mildew previously present in a plot both years of the study. In the 1989–1990 and 1990–1991 seasons, there was a delay in tiller initiation where seed had been treated with triadimenol. However, tillers of plants treated with triadimenol were more likely to survive to harvest and produce heads. Yield increased on all cultivars in both years when wheat was grown from triadimenol-treated seeds and decreased when plots were bordered by rows of wheat susceptible to powdery mildew. Increased yields were associated with reduced tiller initiation and increased survival of primary and secondary tillers. Kernel weight in 1989–1990 and kernel number in 1990–1991 also contributed to increased yields.

When powdery mildew of wheat, caused by *Blumeria graminis* (DC.) E. O. Speer f. sp. *graminis* Ém. Marchal (≡*Erysiphe graminis* DC. f. sp. *tritici* Ém. Marchal), occurs early in the growing season, development and growth of the host can be affected. The occurrence, mechanism, and extent of yield loss due to early season powdery mildew vary with environment and susceptibility of the cultivar examined (1,3,7–11,13,17,19,21,23). Early season infection by powdery mildew has long been known to reduce tiller survival in barley (2). More recently, Bowen et al (1) and Leath and Bowen (13) showed that the magnitude of early infection by *B. g. tritici* is correlated negatively with tiller number at harvest in winter wheat in North Carolina. Early season disease is also critical because it depletes carbohydrate reserves that contribute to grain fill, especially when plants are stressed (4). This is reflected in the fact that early season infection decreases kernel weight in barley (2) and wheat (1,13). Jenkyn (8) concluded low levels of powdery mildew in barley could result in reduced grain size but that high levels could also reduce head number.

Control of early season powdery mildew by triadimenol seed treatment or fall application of a foliar fungicide can increase yields of winter wheat. In Ohio, triadimenol seed treatment reduced area under the disease progress curve (AUDPC) by 38, 13, and 29% in 1985, 1986, and 1987, respectively, compared to carboxin-thiram seed treatment (16). Yield was increased in 1986 and 1987 by 11 and 3%, respectively. In commercial fields, yield increase may have been higher because of the absence of interplot interference. Plants grown from seed treated with triadimenol in North Carolina yielded 95.2%, whereas plants from untreated seed yielded 83.3% of the nearly disease-free plots treated with multiple foliar fungicide applications (16). Although controlling early season powdery mildew may increase tiller number, grain weight, and reduce late season mildew, because of physiological compensation, early season disease control may also decrease some yield components. For example, mildew control may result in decreased kernel size because kernel number per unit of area (tiller number × kernels per head) is increased proportionally more by control than yield per area is increased.

Early season growth in wheat is important in producing tillers, establishing total green leaf area, and establishing carbohydrate reserves, which contribute to the ability of cereals to compensate for reductions in yield components such as tillers per area or kernels per head (4). This occurs, in part, because more tillers form than produce heads, and, as unproductive tillers die, assimilates move from them to the main stem (6). Ishag and Taha (6) found in Sudan that an average of 3.2–4.5 tillers formed per wheat plant; however, less than one tiller per plant (0.4) survived. Primary and secondary tillers contributed 19% to final yield, whereas the main stem contributed 81%.

Primary and secondary tillers of wheat develop from axillary buds at the base of each leaf and are produced sequentially. The coleoptilar tiller (T_0) will form at approximately 0.8 phyllochrons. The tiller in the axil of the first leaf of the main stem (T_1) will form approximately midway between phyllochrons 2 and 3, and the tiller in the axil of the second leaf (T_2) will be produced approximately 0.75–1 phyllochron later (12). Secondary tillers form in the axil of the leaves on primary tillers. The first secondary tiller is designated T_{10}; it is initiated after T_3. If the environment is unfavorable, a tiller will not be produced, but if conditions improve, subsequent tillers will develop. Environmental conditions after tiller formation may influence the number of tillers that survive to produce heads. As a result, the presence or absence of individual tillers is indicative of the history of stress a wheat plant encountered during its growth. Powdery mildew is one such stress.

The objectives of this study were to examine if a low tiller number at harvest, associated with early season powdery mildew, is due to reduced tiller initiation or survival, and to examine the contribution of the various orders of tillers at different disease severities to yield.

MATERIALS AND METHODS

Plot establishment. Factorial experiments were conducted in the 1989–1990 and 1990–1991 growing seasons at the Central Crops Research Station near Clayton, North Carolina. The experiments were arranged in randomized complete block designs with five replications grouped within years. Factors were cultivar, seed treatment, and inoculation.

Wheat (*Triticum aestivum* L. em. Thell) was sown on 9 October 1989 and 16 October 1990 with a small plot grain drill. The plots were 5.02 × 2.13 m with 0.18 m of row spacing. Plots were bordered on two sides with 1.67 m of barley (*Hordeum vulgare* 'Anson') and with 1.52-m alleys on each end for reducing interplot interference.

Before sowing in 1989 and 1990, we applied fertilizer 12-6-24 (N-P-K) at a rate of 448 kg/ha. Liquid nitrogen was applied on 7 November 1989 and 22 February 1990 at a rate of 34 kg/ha. Liquid nitrogen was applied on 29 January 1991 at a rate of 42 kg/ha. Because of heavy rains, sandy soil, and subsequent leaching, a second application was applied on 5 February 1991 at a rate of 28 kg/ha.

Three wheat cultivars that differed in their susceptibility to powdery mildew were used in 1989–1990. Saluda (PI 480474) is susceptible, Coker 747 (CI 17923) is moderately susceptible, and Coker 983 (NSG 187415) is resistant to powdery mildew. In 1990–1991, Coker 983 was not sown because the level of powdery mildew it sustained the year before was too low to be useful in the study.

Seed was either treated with triadimenol at a rate of 0.259 g/kg of seed (Baytan 30F, Mobay Corp., Kansas City, MO) or left untreated. Plots either had single rows of the susceptible cultivar, Saluda, planted at the end of and perpendicular to them or did not have this cultivar planted near them. These rows were planted one day after the plots were seeded. Saluda wheat growing in 10-cm-diameter pots was inoculated with powdery mildew isolates, Yuma and Pm4, on 26 October 1989 and 26 October 1990; these isolates are virulent to Coker 747 and Saluda (14). Ten days later, infected plants were placed at the middle of each spreader row, and the following day these plants were shaken over their respective spreader row (spores settled onto plants within the row). Before harvest (2 June 1990 and 31 May 1991), the spreader rows were removed.

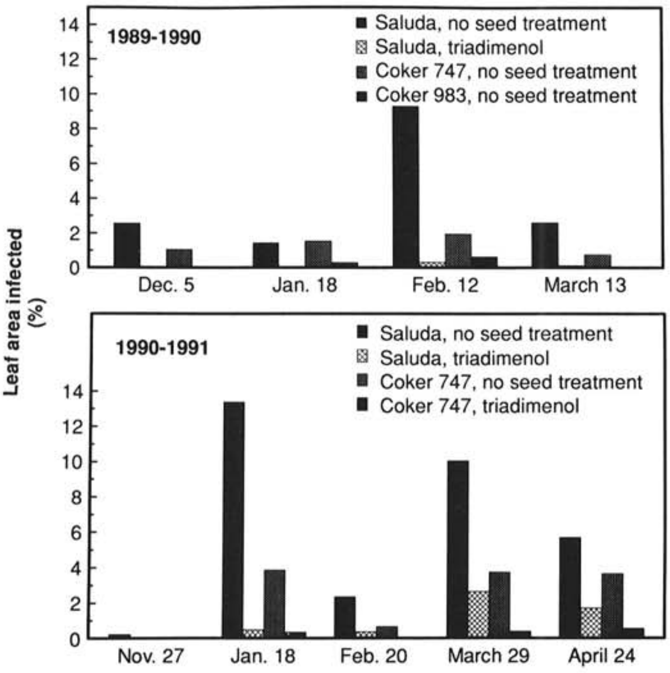

Fig. 1. Severity of early season powdery mildew on winter wheat plants Saluda, Coker 747, and Coker 983 in 1989–1990, and Saluda and Coker 747 in 1990–1991 at Central Crops Research Station near Clayton, North Carolina. The percentage of a leaf infected with powdery mildew was assessed on the top two leaves of 10 main stems from each plot except on 29 March 1991, when incidence and severity were assessed on four 0.5-m row sections selected randomly from each plot.

Tiller assessment. Plants in 0.5-m sections of rows in 1989–1990 and 0.75-m sections of rows in 1990–1991 were dug and taken to the laboratory four times during the growing season. Plants were collected on 5 December 1989, 18 January, 12 February, and 13 March 1990. During the 1990–1991 growing season, samples were collected on 27 November, 18 January, 20 February, and 24 April. The number of leaves on the main stem was expressed as Haun stage (5). Presence and number of tillers at each leaf node were assessed according to the method of Klepper et al (12). We assessed disease on 10 plants selected randomly from the sample on each date by rating the percentage of severity (0–100%) visually on the top two fully expanded leaves on the main stem of each plant. To determine if the presence of tillers at various dates was correlated to the amount of powdery mildew currently or previously present in the plot, we calculated the correlations between percentage of powdery mildew infection and

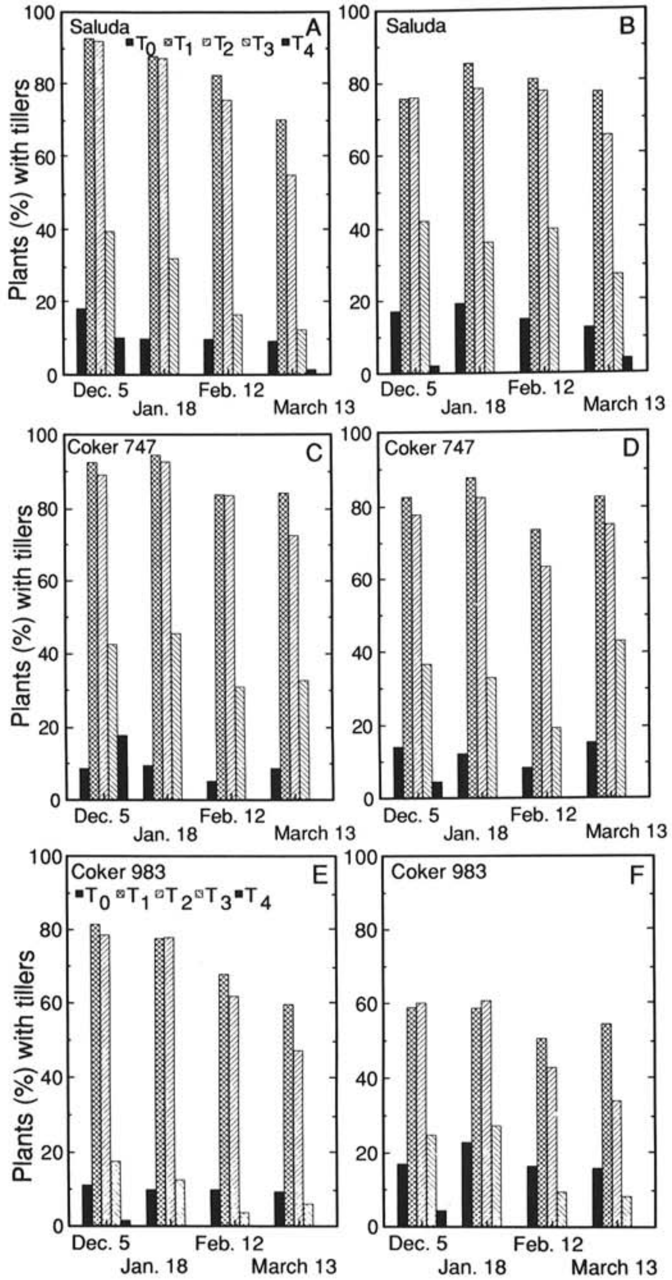

Fig. 2. The percentage of plants (*Triticum aestivum*) with primary tillers T_0, T_1, T_2, T_3, or T_4 (December through March 1989–1990) on Saluda grown from **A**, untreated seed or **B**, seed treated with triadimenol; **C**, Coker 747 grown from untreated seed or **D**, seed treated with triadimenol; and **E**, Coker 983 grown from untreated seed or **F**, seed treated with triadimenol.

the presence of individual tillers. The contribution of each tiller to yield was determined in 1990 by removing heads from each tiller (main stem, T_0, T_1, T_2, etc.) in 0.5-m sections of rows just before harvest and by threshing and weighing seed from each tiller group separately. In 1991, the contribution of each tiller to yield was determined by removing heads from each tiller in a 0.75-m section of a row, counting the heads, and threshing, counting, and weighing seed from each tiller group.

Survival of tillers, excluding the main stem tiller, was calculated in 1991 by dividing the percentage of tillers present per plant within a plot during May by the percentage of tillers present in November 1990 (maximum number T_0) or January 1991 (maximum number of T_1, T_2, T_3, T_{10}, and T_4). The contribution of each order of tiller to yield in 1990 was calculated by dividing the kernel weight contributed by each tiller group (T_1, T_2, etc.) by the kernel weight of all tillers in a 0.5-m section of a row.

Before harvest in 1990, the number of tillers per meter of row was counted, and 10 randomly selected heads per plot were collected for determination of the number of kernels per head and 500-kernel weight. Total grain weight (kg/ha) was determined by harvesting the center one-third (1.7 × 2.1 m) of each plot, from which no samples had been removed, with a small plot combine and adjusting values to 13.5% moisture.

An analysis of variance was performed (SAS statistical package, SAS Institute, Inc., Cary, NC) on data expressed as percentage of tiller survival, grain weight contributed from the main stem, primary and secondary tillers, and tillers per plant. The Hartley test (18) was used to determine if the treatment variances were equal. If variances were not equal ($P = 0.05$), data were transformed by calculating the arcsin of the square root of the proportion of the value. Analysis of variance was then performed on the transformed data. When the treatment variances of the percentage of plants that had different orders of primary and secondary tillers in 1989–1990 were examined, transformations were frequently necessary. In 1990–1991, when a larger segment of row was sampled, treatment variances were lower and data transformation was not warranted, or, when transformed, the results were similar.

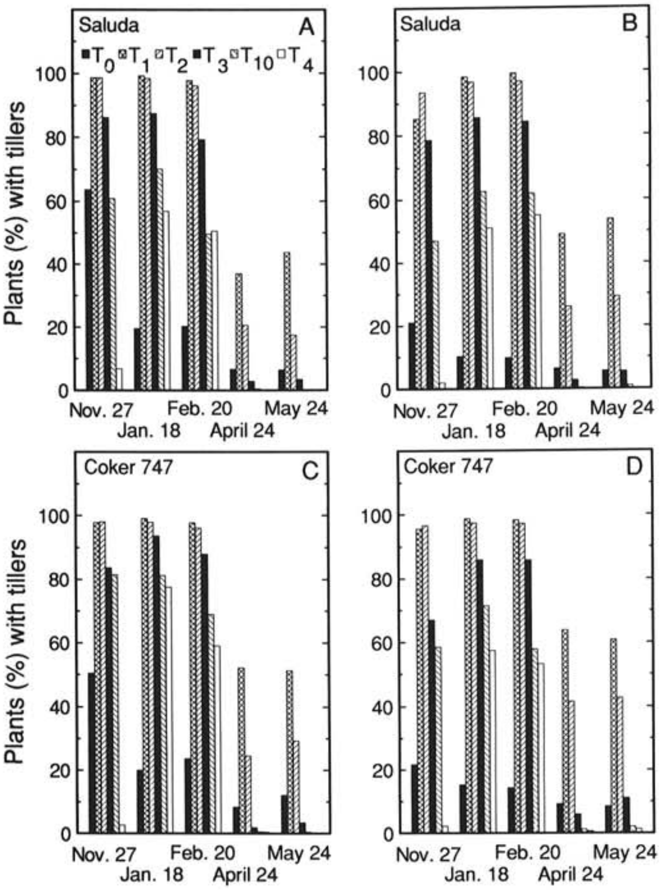

Fig. 3. The percentage of plants (*Triticum aestivum*) with tillers T_0, T_1, T_2, T_3, T_{10}, or T_4 (November through May 1990–1991) on Saluda grown from **A**, untreated seed or **B**, seed treated with triadimenol; and **C**, Coker 747 grown from untreated or **D**, seed treated with triadimenol.

RESULTS

Mildew establishment. Powdery mildew first was observed in plots on 14 November 1989 and 26 November 1990, 19 and 31 days after infected plants were placed in the center of spreader rows, respectively. During the 1989–1990 growing season, powdery mildew severity was less in plots of Saluda and Coker 747, where wheat was grown from seed treated with triadimenol, than in plots where wheat seed was not treated. Severity of powdery mildew in plots of Coker 983 was less than 10% during January through March. In December and January, there was a significant seed treatment × spreader row interaction in Coker 747; powdery mildew was more severe in plots that had inoculated spreader rows, if seed planted to the plots had not been treated with triadimenol. However, throughout the 1990–1991 growing season, there were no significant differences in mildew severity on the main stem between plots with or without spreader rows. When Saluda was treated with triadimenol in 1990–1991, mildew severity was reduced significantly during January through April (Fig. 1). Powdery mildew severity in Coker 747 plots, where seed had been treated with triadimenol, was also reduced significantly in January and April 1991 compared with plots where seed had not been treated.

Presence of tillers. Many more tillers were present in all cultivars early in the season than in March 1990 or May 1991 (Figs. 2,3). We also observed reduced tiller initiation in plots where seed had been treated with triadimenol compared with plots where seed had not been treated in 1989–1990 (Fig. 2). There were significantly fewer T_2 and T_4 on Saluda and T_2 on Coker 983 on 5 December 1989 in plots where seed had been treated with triadimenol than where seed was untreated. On 18 January, fewer T_1 and T_2 on Coker 983 and T_1 on Coker 747 were present in plots where seed had been treated with triadimenol than in plots where seed had not been treated. During 1990–1991, plants in triadimenol-treated plots did initiate similar numbers of tillers beyond T_0 to plants in plots not treated with triadimenol by later in the growing season.

By January 1990, tillers had begun to die but were more likely to be present in triadimenol-treated plots than in untreated plots. On 18 January, more T_0 and T_3 on Coker 983 were present, and on 12 February this was even more pronounced with T_3 on Saluda. On 13 March 1990, T_4 on Saluda and T_0 on Coker 747 were more frequent in triadimenol-treated plots than in untreated plots (Fig. 3).

TABLE 1. Survival (%) of primary and secondary tillers of three cultivars of winter wheat from December 1989 to March 1990 and from November 1990 (T_0) or January 1991 (T_1, T_2, T_3, T_{10}, and T_4) to May 1991 in Clayton, North Carolina, in relation to triadimenol seed treatment and presence of spreader rows of wheat susceptible to powdery mildew

	No seed treatment		Triadimenol	
Cultivar	Absent[x]	Present[x]	Absent	Present
1989–1990				
Saluda	61 c[y]	61 c	85 ab	95 a
Coker 747	75 c	92 b	102 ab	118 a
Coker 983	56[z]	83	76	84
1990–1991				
Saluda	17 b	14 b	31 a	16 b
Coker 747	27	18	32	41

[x]Spreader row of susceptible wheat present or absent.
[y]Values in rows followed by the same letter are not significantly different according to Fischer's protected LSD, $P = 0.10$.
[z]Fisher's protected LSD was not calculated because $P > 0.10$ for the F statistic associated with these treatments.

TABLE 2. Analysis of variance of the natural logarithm of area under the powdery mildew curve (lAUPMC), yield components, and yield data from three wheat cultivars grown with or without triadimenol seed treatment and with or without spreader rows of susceptible wheat inoculated with powdery mildew and planted at the end of plots near Clayton, North Carolina, in 1989–1990

		Mean square				
Factor	df	lAUPMC[y]	Tillers per meter of row	Seed per 10 heads	Kernel weight	Yield
Replicate	4	7.3**[z]	454.4*	3,732.4*	1.0	969,803**
Cultivar (C)	2	38.2**	4,451.5**	16,158.5**	22.8**	1,151,485*
Seed treatment (ST)	1	172.9**	114.8	5,264.1	15.3**	6,709,359**
Spreader row (SR)	1	0.1	350.4[+]	1,197.1	1.1	7,756,428**
C × ST	2	9.2[+]	744.5**	436.2	1.5*	313,907*

[y] AUPMC was calculated on the basis of four visual assessments of powdery mildew severity on the top two fully expanded leaves of 10 main stem tillers per plot.

[z] +, * and ** represent significant treatment effects at the $P = 0.10$, $P = 0.05$, and $P = 0.01$ levels of probability, respectively.

In November 1990, there were significantly fewer T_0 and T_1 in plots of Saluda treated with triadimenol than in plots where seed had not been treated. However, by April and May of 1991, more T_1 were present in plots where Saluda seed was treated with triadimenol than in untreated plots. Also, more T_2 were present in May 1991 in plots grown from triadimenol-treated seed compared to untreated seed.

There were positive ($P \leq 0.05$) correlations between the presence of some tillers in December or January and powdery mildew severity on the two uppermost leaves of the main stem in all cultivars examined in 1989–1990. For example, in Saluda plants grown from untreated seed, powdery mildew severity on 5 December was positively correlated with the presence of T_4 and T_5 on 18 January. Likewise, in Saluda plants grown from seed treated with triadimenol, powdery mildew severity on 5 December was positively correlated with the presence of T_5 on 12 February and T_{10} on 13 March. However, powdery mildew severity in March in plots of treated Saluda was negatively correlated with the presence of T_4 in March.

The severity of powdery mildew on 5 December, 18 January, and 12 February in plots of untreated Coker 983 was positively correlated with the presence of T_{10} and T_4 on 18 January and T_5 on 13 March, respectively. In plots of Coker 747 grown from seed treated with triadimenol, powdery mildew severity on 5 December was positively correlated with the presence of T_4 in March.

There were positive correlations ($P \leq 0.05$) between powdery mildew severity in November 1990 and January and February 1991 and presence of some tillers. Powdery mildew severity in January on plants of Saluda grown from untreated seed was positively correlated to the presence of T_3, T_{10}, and T_4 in January. In November and January, disease severity of Coker 747 plants grown from untreated seed was positively correlated to the presence of T_0 and T_{10}, respectively. In addition, powdery mildew severity on untreated Saluda plants in April was positively correlated to the presence of T_0 in May. Powdery mildew severity on untreated Saluda in April was positively correlated to the presence of T_0, T_1, and T_2 in May. Only the severity of powdery mildew (on plants of Coker 747 from untreated seed) in January was negatively correlated with the presence of T_1 in February.

Inoculated spreader rows of susceptible wheat significantly affected the presence of T_2 on Saluda in April and May of 1991. In May, T_2 was present on 17% of plants in plots with spreader rows compared to 30% of plants where there were no spreader rows. Coker 747 grown from seed treated with triadimenol in 1991 had fewer T_0, T_3, and T_{10} in November of 1990 than plots where seed was not treated. However, at subsequent sampling dates, seed treatment did not significantly affect the number of tillers present.

Survival of tillers. Significantly more tillers were initiated than survived and produced heads at harvest during both growing seasons. During 1989–1990, survival was calculated by dividing the percentage of plants with each order of tiller in March by the percentage of plants with each order of tiller in December (Table 1). Total tiller survival was calculated as the sum of survival of all tillers in March.

TABLE 3. Components of yield from three cultivars of winter wheat at Clayton, North Carolina, 1990, where varied levels of powdery mildew resulted from triadimenol seed treatment and spreader rows

Cultivar and	No seed treatment		Triadimenol	
yield component	Absent[x]	Present[x]	Absent	Present
Saluda				
Kernels per 10 heads	312[y]	308	346	290
500-kernel weight (g)	14.28 b[z]	15.02 b	16.22 a	16.30 a
Tillers per meter of row	86	90	105	102
Coker 747				
Kernels per 10 heads	269	251	285	277
500-kernel weight (g)	15.2	15.2	15.5	16.0
Tillers per meter of row	126 ab	134 a	111 b	131 a
Coker 983				
Kernels per 10 heads	298	324	335	340
500-kernel weight (g)	13.1 b	13.3 b	14.0 a	14.1 a
Tillers per meter of row	107	114	118	108

[x] Spreader row of susceptible wheat present or absent.

[y] Fisher's protected LSD could not be calculated because the overall F test for the model was not <0.05.

[z] Values followed by the same letter within a row are not significantly different according to Fisher's protected LSD.

In Saluda, survival of T_2 was influenced by seed treatment (61% survived where seed had not been treated compared to 85% where seed was treated with triadimenol). Survival of all tillers also was influenced by seed treatment; 5.7 tillers per plant survived versus 4.5 when seed had been treated or untreated, respectively.

Coker 747 tillered later in 1989–1990 (there were more tillers in March than in December) and more primary and secondary tillers survived ($F = 2.78$, $P = 0.07$) in plots when wheat was grown from triadimenol-treated seed than from untreated seed. Survival of T_0 in Coker 747 was reduced when spreader rows were present. Plants of Coker 983, whether grown from treated or untreated seed, did not differ significantly in primary and secondary tiller survival.

In 1990–1991, a model including cultivar, seed treatment, and spreader row ($F = 1.95$, $P = 0.08$) indicated that cultivar and seed treatment influenced tiller survival. Coker 747, which tended to tiller later and was slightly more resistant than Saluda, had greater tiller survival (28% of primary and secondary tillers of Coker 747 survived to harvest, compared to 20% of Saluda). Survival of primary and secondary tillers of Saluda and Coker 747 where a spreader row was absent was greater ($P = 0.10$) when seed was treated with triadimenol in 1989–1990 (Table 1). Survival of Saluda was greater in plots where seed had been treated with triadimenol and where spreader row was absent than in plots where seed had not been treated in 1990–1991.

Contribution of main stem and secondary tillers to yield. Cultivar significantly influenced disease and yield as well as total yield components in 1989–1990 (Table 2). The number of tillers per meter of row of Saluda ($F = 2.70$, $P = 0.063$) (main stem primary and secondary) present at harvest in 1990 was greater in plots grown from treated seed (Table 3). Coker 747, grown in the presence of spreader rows, had more tillers present at harvest

TABLE 4. Number of heads per row, mean number of kernels per head, and mean weight per kernel of cultivars Saluda and Coker 747 grown from seed treated with triadimenol or untreated in plots with or without a spreader row at harvest in 1991

	Heads per meter of row				Kernels per head			
	No seed treatment		Triadimenol		No seed treatment		Triadimenol	
Spreader row	Absent[x]	Present[x]	Absent	Present	Absent	Present	Absent	Present
Saluda								
Main stem	61.5[y]	63.6	58.8	57.2	26.3	24.1	29.6	29.2
T_0	4.5	3.1	3.2	2.9	14.1	11.7	15.3	12.3
T_1	27.9	26.6	35.6	26.1	19.6 ab	15.3 bc	21.3 a	13.3 c
T_2	12.2 b[z]	9.3 b	22.6 a	10.9 b	18.8	13.3	19.7	17.4
T_3	2.1	1.3	5.1	1.1	17.5	16.8	20.5	23.2
T_{10}	0.0	0.3	0.3	0.8	...	8.0	8.0	17.3
T_4	0.0	0.3	0.0	0.0	...	16.0	...	...
Coker 747								
Main stem	56.7	64.6	57.2	55.1	24.1	22.9	25.6	25.6
T_0	9.6	4.8	4.0	5.3	12.0	9.7	16.0	12.7
T_1	33.8	27.7	30.3	35.6	16.5	15.5	18.5	16.9
T_2	19.7	15.7	19.9	26.1	15.4	15.5	19.2	16.2
T_3	2.7	1.6	6.1	5.3	19.2	12.0	15.8	16.5
T_{10}	0.3	0.3	1.3	0.8	11.0	14.0	16.6	8.7
T_4	0.0	0.0	1.1	0.3	...	...	18.5	17.0

[x] Spreader row of susceptible wheat present or absent.
[y] Fisher's protected LSD could not be calculated because the overall F test was not <0.05.
[z] Numbers followed by the same letter are not significantly different according to Fisher's protected LSD.

in plots where seed was treated with triadimenol than when seed was treated with triadimenol but no spreader row was present. Five-hundred kernel weight of Saluda and Coker 983 was significantly greater when wheat was grown from seed treated with triadimenol. The number of seeds per 10 heads was not affected by seed treatment or presence of spreader row. Yield and components of yield were not significantly affected by cultivar × seed treatment, seed treatment × spreader row, or higher order interactions. T_3 of Coker 983 grown from seed treated with triadimenol where a spreader row was absent contributed significantly more to yield (2.5%) than plants grown from untreated seed (0.2%) or where a spreader row was present (0.4%).

In 1990–1991, the number of main stem tillers per meter of row (and, therefore, plants) of all treatments was similar at harvest (Table 4). Neither cultivar, seed treatment, nor spreader row influenced the number of main stem tillers, the number of kernels that formed, or the weight of the kernels on the main stems. However, within the cultivar Saluda, triadimenol seed treatment increased the number of T_2 present at harvest. The number and weight of kernels borne on T_1 of Saluda were also decreased in plots where a spreader row was planted. Within Coker 747 at harvest, there were no significant differences in number of primary and secondary tillers, number of kernels, or kernel weight when plants were grown from triadimenol-treated seed or in plots that were bordered by a spreader row of wheat susceptible to powdery mildew.

Loss in tiller number and subsequent compensation also varied in both years of the study. Despite high levels of disease, total tiller number of Saluda in untreated plots with no spreader row was higher at harvest in 1991 (108 tillers per meter of row) than in 1990 (86 tillers per meter of row). However, fewer kernels per head formed (26.3 on main stem tillers) in 1991 compared with 1990 (31.2). Kernel weight was greater in 1991 (15.5 g/500 main stem kernels) than in 1990 (14.3 g/500 kernels). The period of tiller formation for Coker 983 was longer than Saluda in 1989–1990; we often found Coker 983 plants with T_6 and, occasionally, T_7 or T_8. In 1990–1991, we never found the higher order tillers.

Yield. In 1989–1990, grain yield of Saluda, Coker 747, and Coker 983 was greater in plots where there was no spreader row and in plots where seed had been treated with triadimenol (Table 5). Increased yields reflected increased tiller survival in plots of Saluda where seed had been treated with triadimenol and increased kernel weight in Saluda and Coker 983 at harvest.

In 1990–1991, total grain yield of Saluda and Coker 747 was higher in plots where seed had been treated with triadimenol. Grain yield was lower when plants were grown in the presence of a spreader row. Increased yields in 1990–1991 were due in part to increased survival and kernel weight of the primary tillers in Saluda.

TABLE 5. Yield (kg/ha) of three cultivars of winter wheat grown from seed treated with triadimenol or left untreated and plots with or without a spreader row at the Central Crops Research Station near Clayton, North Carolina, in 1990 and 1991

	No seed treatment		Triadimenol	
Year and cultivar	Absent[y]	Present[y]	Absent	Present
1989–1990				
Saluda	3,628 b[z]	2,946 c	4,729 a	3,750 b
Coker 747	4,195 b	3,589 c	4,815 a	4,129 b
Coker 983	3,810 b	3,253 c	4,409 a	3,604 bc
1990–1991				
Saluda	3,770 b	2,919 c	4,650 a	3,793 b
Coker 747	3,666 b	3,068 c	4,479 a	3,804 b

[y] Spreader row of susceptible wheat present or absent.
[z] Values within a row followed by the same letter are not significantly different according to Fisher's protected LSD, $P = 0.05$.

DISCUSSION

Yield components affected by early season disease may vary from year to year because of the influence of the environment and host genotype on the ability of the wheat plant to form tillers. For example, tiller formation was greater in 1990–1991 despite the application of nitrogen in November 1989. Nitrogen application is usually associated with increased tillering; however, other factors, such as mean temperature, differed between the 2 yr (2.6 C in December 1989–1990, 10.5 C in December 1990–1991).

The positive correlation between early season powdery mildew and presence of some tillers, as well as the presence of more tillers on Coker 747 plants grown in plots where rows of susceptible wheat were present, indicates that tiller initiation was increased in response to disease stress. However, these additional tillers could not be supported on limited plant resources, and, therefore, often failed to survive and develop. Increased initiation of tillers can negatively affect yield, because at uniform plant densities formation of more tillers results in lower average head size and fewer kernels per head. Because most tillers that are initiated do not survive, they deplete carbohydrate reserves. Because early season powdery mildew increases tiller formation, yield losses may occur even in years when tiller number at harvest is not affected by disease.

Lim and Gaunt (15) demonstrated that spring barley was unable to compensate with increased grain number and size (later developing yield components) for reduced growth and development because of an early season epidemic of powdery mildew. However, they also found that early season disease did not affect tiller initiation. Their results may differ from ours because spring barley develops tillers over a short period of time, whereas winter wheat develops tillers and grain over a longer period.

Triadimenol, by delaying or reducing tiller formation, may increase both heads per meter and kernels per head indirectly. This is because fewer tillers form initially on plants grown from treated seed, and those that form have less competition and are more likely to survive. As a result, fewer plant resources are wasted on tillers that will not ultimately survive to produce heads. Reduced tiller initiation also resulted in more tillers surviving to harvest in Canada. Simons and Hunt (22) found that the proportion of tillers that produced heads decreased with increasing tiller number. They concluded that cultivars with high tiller initiation have a high proportion of small tillers that are not as likely to survive and produce heads; conversely, plants producing fewer tillers have a higher percentage of earlier tillers that reach maturity. Simon and Hunt (22) studied tillering in Canada, where tillers are produced much later than in North Carolina. However, we also saw that tiller presence from November through January, when maximum numbers were present, was not correlated to yield.

Survival of T_0 in 1989–1990, kernel weight of T_1 in 1990–1991, and grain yield in both years were lower when plants were grown in the presence of a spreader row of susceptible wheat. However, mildew severity on the main stem tiller did not differ significantly between plots with or without a spreader row. Because mild weather frequently occurs during the winter months in North Carolina, the first wheat leaves to form may become infected and, therefore, senesce early in the growing season, reducing green leaf area at a time when the canopy is relatively open. As winter progresses, temperatures and infection of new leaves decrease. Therefore, plants with similar amounts of disease on the top leaves of the main stem may have lower leaves or primary and secondary tillers that differ in their level of disease. Also, in a study conducted by Jörg et al (10), the severity of powdery mildew on leaves, awns, and culms of primary tillers of spring and winter wheat was greater than on the main stem. Yield reductions in North Carolina may have resulted from early low levels of disease or unrecorded differences in disease on the lower leaves (only the top two fully expanded leaves on the main stem were rated in November to March) and on the primary and secondary tillers. Low levels of powdery mildew have a relatively large effect on photosynthetic rate. Rabbinge et al (20) determined that the effect of *B. g. tritici* on photosynthetic rate of winter wheat was larger than the size of the visual lesion by a factor of 8. Disease severities of 1–5% occur frequently in North Carolina and may have a large effect on tiller growth and development.

In North Carolina, the main stem contributes most of the grain yield (57–87%). These figures are similar to data from Ishag and Taha (6). They found 81% of total grain yield at harvest was contributed by the main stem tiller and 19% from T_1 and T_2. The percentage that the main stem and primary and secondary tillers contribute to total yield is a result of tiller initiation, survival, and development, which are influenced by many factors such as cultivar, weather, plant spacing, soil type, and biotic stresses (disease).

In North Carolina, early season disease increases formation of tillers. Even under disease-free conditions, more tillers form than survive; increased tillering depletes carbohydrate reserves, resulting in fewer tillers surviving at harvest and fewer kernels forming per tiller. Yield losses result in spite of late season efforts to compensate with increased seed size.

LITERATURE CITED

1. Bowen, K. L., Everts, K. L., and Leath, S. 1991. Reduction in yield of winter wheat in North Carolina due to powdery mildew and leaf rust. Phytopathology 81:503-511.
2. Brooks, D. H. 1972. Observations on the effects of mildew, *Erysiphe graminis*, on growth of spring and winter barley. Ann. Appl. Biol. 70:149-156.
3. Cox, W. J., Bergstrom, G. C., Reid, W. S., Sorrells, M. E., and Otis, D. J. 1989. Fungicide and nitrogen effects on winter wheat under low foliar disease severity. Crop Sci. 29:164-170.
4. Evans, L. T., Wardlaw, I. F., and Fischer, R. A. 1975. Wheat. Pages 101-149 in: Crop Physiology. L. T. Evans, ed. Cambridge University Press, Cambridge.
5. Haun, J. R. 1973. Visual quantification of wheat development. Agron. J. 65:116-119.
6. Ishag, H. M., and Taha, M. B. 1974. Production and survival of tillers of wheat. J. Agric. Sci. 83:117-124.
7. Jenkins, J. E., and Storey, I. F. 1975. Influence of spray timing for the control of powdery mildew on yield of spring barley. Plant Pathol. 24:125-134.
8. Jenkyn, J. F. 1974. Effects of mildew on growth and yield of spring barley: 1969–1972. Ann. Appl. Biol. 78:281-288.
9. Johnson, J. W., Baenziger, P. S., Yamazaki, W. T., and Smith, R. T. 1979. Effects of powdery mildew on yield and quality of isogenic lines of 'Chancellor' wheat. Crop Sci. 19:349-352.
10. Jörg, E., Weissenfels, D., and Kranz, J. 1987. Disease and pests on the main shoots and tillers of wheat. J. Plant Dis. Prot. 94:509-519.
11. Kingsland, G. C. 1982. Triadimefon for control of powdery mildew of wheat. Plant Dis. 66:139-141.
12. Klepper, B., Rickman, R. W., and Peterson, C. M. 1982. Quantitative characterization of vegetative development in small grain cereal grains. Agron. J. 74:789-792.
13. Leath, S., and Bowen, K. L. 1989. Effects of powdery mildew, triadimenol seed treatment, and triadimefon foliar sprays on yield of winter wheat in North Carolina. Phytopathology 79:152-155.
14. Leath, S., and Heun, M. 1990. Identification of powdery mildew resistance genes in cultivars of soft red winter wheat. Plant Dis. 74:747-752.
15. Lim, L. G., and Gaunt, R. E. 1986. The effect of powdery mildew (*Erysiphe graminis* f. sp. *hordei*) and leaf rust (*Puccinia hordei*) on spring barley in New Zealand. II. Apical development yield potential. Plant Pathol. 35:54-60.
16. Lipps, P. E., and Madden, L. V. 1988. Effect of triadimenol seed treatment and triadimefon foliar treatment on powdery mildew epidemics and grain yield of winter wheat cultivars. Plant Dis. 72:887-892.
17. Lipps, P. E., and Madden, L. V. 1989. Assessment methods of determining powdery mildew severity in relation to grain yield of winter wheat cultivars in Ohio. Phytopathology 79:462-470.
18. Neter J., Wasserman, W., and Kunter, M. H. 1985. Applied Linear Statistical Models: Regression, Analysis of Variance, and Experimental Designs. Richard D. Irwin, Inc., Homewood, IL.
19. Priestly, R. H., and Bayles, R. A. 1982. Effect of fungicide treatment on yield of winter wheat and spring barley cultivars. Plant Pathol. 31:31-37.
20. Rabbinge, R., Jorritsma, I. T. M., and Schans, J. 1985. Damage components of powdery mildew in winter wheat. Neth. J. Plant Pathol. 91:235-247.
21. Royse, D. J., Gregory, L. V., Ayers, J. E., and Cole, H., Jr. 1980. Powdery mildew of wheat: Relation of yield components to disease severity. Can. J. Plant Pathol. 2:131-136.
22. Simons, R. G., and Hunt, L. A. 1983. Ear and tiller number in relation to yield in a wide range of genotypes of winter wheat. Z. Pflanzenzuecht. 90:249-258.
23. Zaharieva, T. D., De Milliano, W. A. J., and Zadoks, J. C. 1984. Powdery mildew on winter wheat in Bulgaria, 1980: Relations between disease incidence, disease severity, and yield. Neth. J. Plant Pathol. 90:41-54.