

# Incidence of *Septoria nodorum* in Wheat Seed and Its Effects on Plant Growth and Grain Yield

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## ABSTRACT

Babadoost, M., and Hebert, T. T. 1984. Incidence of *Septoria nodorum* in wheat seed and its effects on plant growth and grain yield. *Plant Disease* 68: 125-129.

*Septoria nodorum* was found in 98.5% of wheat seed samples in North Carolina. Infected seed gave rise to seedlings with infected coleoptiles, which resulted in significant reduction in seedling growth and grain yield. Pycnidia developed in diseased coleoptiles shortly after seed was planted in the fall and on the lower leaves in the spring. The fungus survived and remained virulent in stored seed for more than 2 yr. There was no correlation between percent seed infection and percent germination. This study indicated that seed infected by *S. nodorum* could play an important role in epidemics of glume blotch.

Additional key words: *Leptosphaeria nodorum*, *Triticum aestivum*

*Septoria nodorum* (Berk.) Berk. (perfect state *Leptosphaeria nodorum* Muller) was first reported as a seedborne fungus in wheat (*Triticum aestivum* L. em Thell) in Canada in 1945 (17). Seed has since been found to be a source of inoculum in several wheat-growing areas of the world (22). Within the United States, this fungus has been reported to be seedborne in North Carolina (23), Georgia (6), and Pennsylvania (8).

Burhardt (5) and Obst (20) considered seed to be the main source of inoculum for annual disease occurrence. Shipton et al (22) noted that the role of seedborne inoculum in the disease cycle depends on the longevity of inoculum in or on seed. Von Wechmar (24) reported that *S. nodorum* was almost eliminated from seed stored under dry conditions for 12 mo. Similarly, Krüger and Hoffman (16) found that viability of the fungus in seed was nearly zero after 2 yr and that the rate of decline increased with increasing storage temperature. However, Machacek and Wallace (18) reported that it took more than 7 yr to obtain seed free of *S. nodorum*. Furthermore, Cunfer (7) found that *S. nodorum* not only survived beyond 24 mo in seed stored at 5 and 25 C but also that detection of seed infection

increased during storage, apparently because of decreased competition from other seed fungi.

Inasmuch as the importance of seed as a source of inoculum of *S. nodorum* and on development of glume blotch is not fully resolved, this study was conducted to investigate the significance of the seedborne phase of the fungus in wheat in North Carolina.

## MATERIALS AND METHODS

**Incidence and survival of the fungus in seed.** Wheat seed samples were collected from most of the wheat-growing areas in North Carolina during 1979 and 1980 and assayed for *S. nodorum* on oxgall agar-NUV (19). The 139 samples assayed included 70 collected in 1979 and 69 collected in 1980. Samples represented 13 wheat cultivars (Table 1).

Samples of six lots of infected seed, including two lots of cultivar Coker 747 and one lot each of cultivars Arthur 71, McNair 1003, McNair 1813, and Oasis, were stored under five conditions

beginning 3 mo after harvest in 1979. Samples were assayed for *S. nodorum* before storage. Storage conditions were 1) 13% moisture and 10 C, 2) 13% moisture and 20 C, 3) 21% moisture and 10 C, 4) 21% moisture and 20 C, and 5) 14.5% moisture and 10–27 C. Samples of 100 g from each lot were tied in fiberglass insect screen (Phifer Wire Products, Tuscaloosa, AL) and stored 2.5 cm above 250-ml saturated solutions of either MgCl<sub>2</sub> or NaCl in 600-ml glass jars. Saturated solutions of MgCl<sub>2</sub> and NaCl provided, respectively, 13 and 21% moisture in the seed. Half of the jars were incubated at 10 C and the other half at 20 C. Also, a 700-g sample of each lot was stored in paper bags in a seed warehouse with temperatures of 10–27 C. Moisture content of the seed stored in the warehouse was 14.5% at about 20 C. Moisture content of the seed was determined by differences in weights before and after drying at 105 C for 24 hr (21).

Each sample was assayed for survival of *S. nodorum* 9, 18, and 24 mo after storage. After 24 mo, isolates of *S. nodorum* from all samples were tested for virulence by inoculating them onto 4-wk-old seedlings of Coker 747. Seedlings were sprayed to runoff with a suspension of about 10<sup>6</sup> conidia per milliliter of water, placed in a mist chamber for 72 hr, and maintained in a glasshouse, where the temperature fluctuated between 12 and 40 C. Seedlings were examined for disease development after 14 days. Also, seed from each sample stored for 24 mo were sown in a sandy loam soil in a glasshouse at temperatures ranging from

Table 1. Incidence of *Septoria nodorum* in wheat seed from North Carolina<sup>a</sup>

Wheat cultivar	No. of samples	No. of samples in each infection class <sup>b</sup>				
		0	1–10	11–25	26–50	50–100
Abe	7	0	4	2	1	0
Arthur 71	28	0	12	10	6	0
Coker 747	42	1	8	21	10	2
McNair 1003	25	1	2	6	14	2
Oasis	8	0	3	4	1	0
Roy	12	0	3	1	5	3
Other cultivars <sup>c</sup>	17	0	4	3	8	2
Total	139	2	36	47	45	9

<sup>a</sup> Combined data from 1979 and 1980, 70 samples in 1979 and 69 samples in 1980 in 20 counties.

<sup>b</sup> Infection class is based on the percentage of infected seed. Samples in class 1–10, for example, would contain 1–10% infected seed.

<sup>c</sup> Other cultivars included Coker 68-15, Delta Queen, McNair 1813, Pioneer, Potomac, Southern Belle, and Sullivan.

Paper 8873 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh 27650.

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Accepted for publication 8 August 1983.

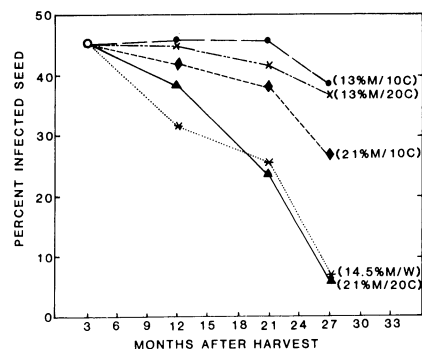
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4.5 to 30 C. Fifty seedlings of each sample were examined for coleoptile infection by *S. nodorum* 4 wk after sowing.

**Seed infection and germination.** Thirteen samples of seed of Coker 747 infected by *S. nodorum* were tested for germination. Twelve samples, from inoculated plants, contained 35–88% infected seed; the other sample, from a commercial field, contained 7% infected seed.

Seed were tested according to Association of Official Seed Analysts (AOSA) procedures (1) and also by sowing them 2.5 cm deep in a sterilized sandy loam soil. Seed sown in the sandy loam soil



**Fig. 1.** Survival of *Septoria nodorum* in infected seed stored under five storage conditions. Seed was kept at room temperature for 3 mo after harvest, then stored under indicated storage conditions for 24 mo. (13%M/10C) = seed with 13% moisture content at 10 C, (13%M/20C) = seed with 13% moisture content at 20 C, (21%M/10C) = seed with 21% moisture content at 10 C, (21%M/20C) = seed with 21% moisture content at 20 C, and (14.5%M/W) = seed with 14.5% moisture content at 10–27 C.

**Table 2.** Effect of seed infection by *Septoria nodorum* on germination in wheat

Seed sample <sup>a</sup>	Infected seed <sup>b</sup> (%)	Percent germination	
		AOSA	Soil
1	88	92	83
2	76	95	82
3	71	94	87
4	58	94	88
5	58	93	84
6	55	95	86
7	50	94	84
8	48	92	84
9	45	94	86
10	45	92	89
11	40	92	88
12	35	94	87
13	7	97	85

<sup>a</sup>Samples 1–12 were from a field inoculation experiment and sample 13 was from a naturally infected lot. All samples were cultivar Coker 747.

<sup>b</sup>Data represent average of four replicates, each with 100 seeds. Seed was assayed on oxgall agar-NUV (19).

<sup>c</sup>Data represent average of four replicates, each with 100 seeds. AOSA = germination evaluated by procedures of Association of Official Seed Analysts, 1981 (1). Soil = germination evaluated in sandy loam soil under glasshouse conditions.

were kept in a glasshouse, where temperatures fluctuated between 19 and 38 C and examined for germination after 14 days.

**Seedling infection.** Seed from two lots of Coker 747 from a field inoculation experiment, one lot with 22% infection and one with 80% infection, were used in this experiment. Also, seed with 11% field infection were inoculated 24 hr before sowing by immersing in a spore suspension of *S. nodorum* containing  $10^6$  spores per milliliter and applying a vacuum (–68 kPa) for 10 min. After inoculation, the seed were dried at room temperature for 24 hr. *S. nodorum* was detected on 100% of the inoculated seed when assayed on oxgall agar-NUV (19).

To examine seedling infection in the field, seed were sown 2.5 cm deep in rows 30 cm apart in a Dothan loamy sand at the Central Crops Research Station near Raleigh, NC, on three dates—23 October (early-season), 6 November (midseason), and 20 November (late-season).

Samples of seedlings were taken from the early-, midseason, and late-season plantings 19, 20, and 34 days after sowing, respectively. One hundred seedlings were dug randomly from each plot and examined for disease incidence on the coleoptiles. Diseased seedlings were rated for disease severity according to the Horsfall and Barratt rating scale (12) and examined for pycnidial production. Diseased and healthy plants then were dried at 60 C for 72 hr and weighed.

Diseased parts of other seedlings from the same plots were sampled, cleared, and fixed in formalin-propionic acid-propanol (FPP) for 10–20 days (13). Sections 5–10 mm long were dehydrated in an isopropyl series and infiltrated and imbedded in Paraplast (Sherwood Medical Industries, St. Louis, MO). Sections 12  $\mu$ m thick were cut with a rotary microtome, mounted on slides with Haupt's adhesive, and stained with modified Triarch's stain (Triarch Incorporated, Ripon, WI) without crystal violet. Transverse and longitudinal sections were examined with a standard light microscope. Sections of diseased samples were also examined for cellulose by the I-KI and H<sub>2</sub>SO<sub>4</sub> method, for pectin by the ruthenium red method, and for lignin and gum by the phloroglucinol test (13).

**Disease development.** The role of seedborne inoculum of *S. nodorum* in development of glume blotch in Coker 747 wheat was studied in the field.

Seed inoculated with *S. nodorum* and uninoculated were sown in a Dothan loamy sand on 23 October (early-season), 6 November (midseason), and 20 November (late-season). Seed were inoculated 24 hr before each sowing. Plants were examined frequently for disease development during the growing season and rated for disease severity 16 days before harvest. Plants from a 2.23-

m<sup>2</sup> area in the center of each 3.35-m<sup>2</sup> plot were harvested and total yield and weight of 1,000 kernels were measured.

Two seed lots from a field inoculation experiment, one with 11% seed infection and the other with 80% seed infection, were used in 1981. In addition, some of the seed with 11% field infection were inoculated with *S. nodorum*. Seed were sown in a Dothan loamy sand on 23 October (early-season), 6 November (midseason), and 20 November (late-season). Seed were inoculated 24 hr before each sowing.

Development of disease on the plants was followed by frequent examination from emergence until harvest. Plants were rated for disease severity 22 days before harvest. Also, the number of emerged heads per meter of row was determined by counting plants in four areas, each 25 cm long, in the two middle rows of each plot (total length 1 m/plot). Areas were selected at a distance of 50 cm from each end of the rows. Two middle rows in each plot, with an area of 1.86 m<sup>2</sup>, were harvested and total yield and weight of 1,000 kernels were measured.

## RESULTS

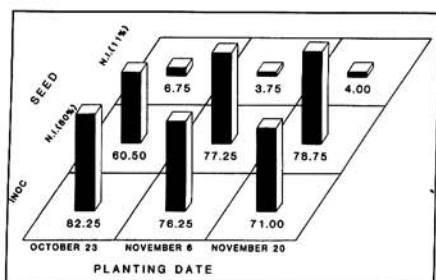
**Incidence and survival of the fungus in seed.** *S. nodorum* was found in 98.5% of the seed samples (100% in 1979 and 97% in 1980) assayed (Table 1). Sixty-six percent of the samples had 11–50% infected seed. Furthermore, the fungus survived longer than 27 mo in stored seed (Fig. 1). Seed with a moisture content of 13% maintained a higher percentage of infected seed than seed with a moisture content of 21%, and seed stored at 10 C maintained a higher percentage of infected seed than seed stored at 20 C. The fungus survived in more than 20% of seed with 88% original infection in all storage conditions 27 mo after harvest.

*S. nodorum* isolated from stored seed caused disease in inoculated seedlings. Furthermore, infected seed stored for 27 mo and sown in sandy loam soil gave rise to seedlings with infected coleoptiles. Symptoms were observed only in seedlings grown from seed stored with 13% moisture content at 10 and 20 C and from the seed stored with 21% moisture content at 10 C.

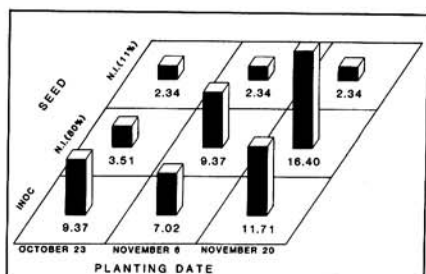
**Seed infection and germination.** There was no correlation between percent seed infected and percent seed germinated (Table 2).

**Seedling infection.** Plants grown from infected seed had infected coleoptiles (Fig. 2). Treatments with inoculated seed (100% of seed carrying *S. nodorum*) and naturally infected seed (80% infection) had significantly more diseased seedlings than the treatment containing seed with 11% infection.

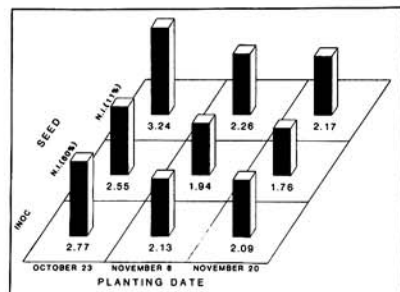
Severity of disease on coleoptiles was influenced by the percentage of infected seed and sowing date (Fig. 3). When seed were sown early, significantly more



**Fig. 2.** Disease incidence on coleoptiles of winter wheat caused by seedborne *Septoria nodorum*. Bars represent percent seedlings infected. INOC = inoculated seed with 100% infection, N.I.(80%) = naturally infected seed with 80% infection, and N.I.(11%) = naturally infected seed with 11% infection. Interactions among seed inoculum levels and planting dates are highly significant ( $P = 0.001$ ). LSD = 5.88 using the Waller-Duncan  $k$ -ratio  $t$  test ( $k$ -ratio = 100).



**Fig. 3.** Disease severity of winter wheat seedlings grown from seed infected by *Septoria nodorum*. Bars represent percent coleoptile area diseased. INOC = inoculated seed with 100% infection, N.I.(80%) = naturally infected seed with 80% infection, and N.I.(11%) = naturally infected seed with 11% infection. Interactions among seed inoculum levels and planting dates are highly significant ( $P = 0.002$ ). LSD = 3.27 using the Waller-Duncan  $k$ -ratio  $t$  test ( $k$ -ratio = 100).



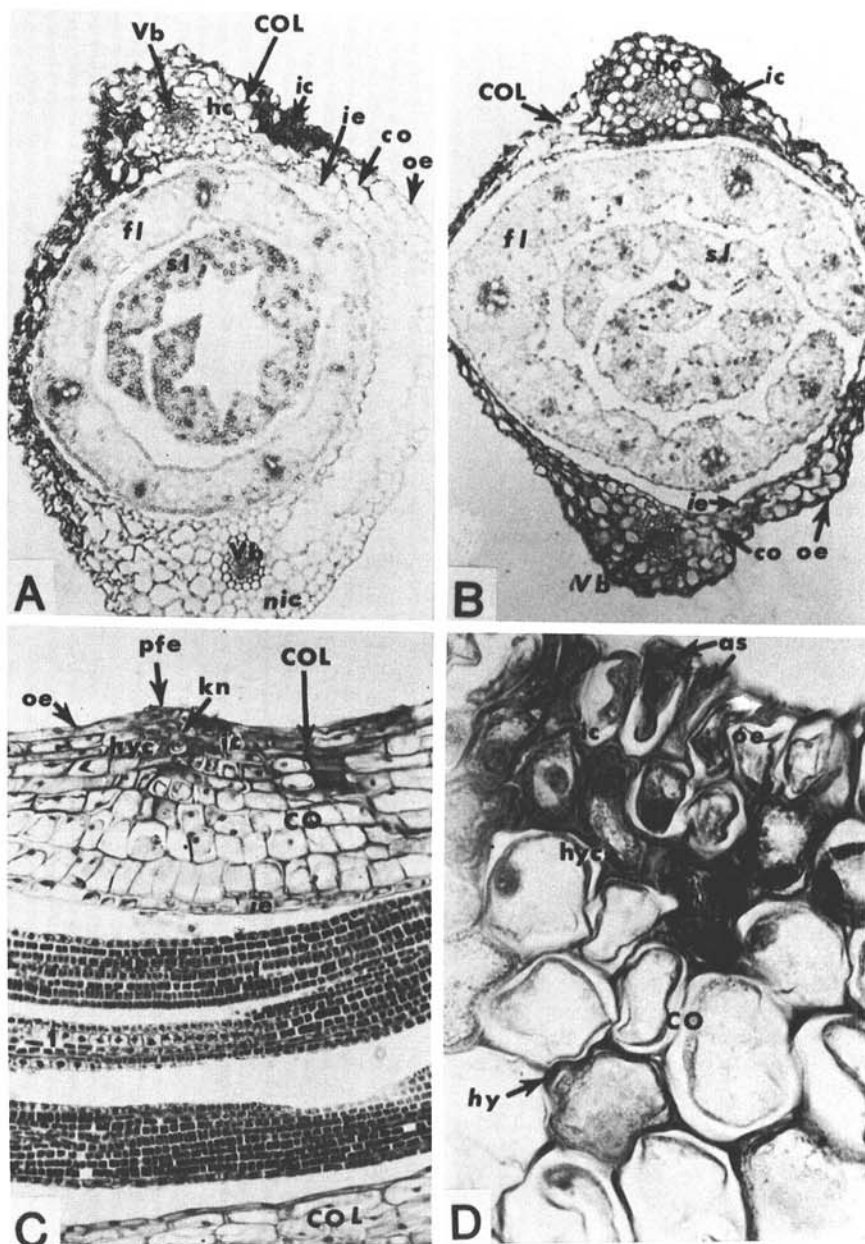
**Fig. 4.** Effect of seedborne *Septoria nodorum* on growth of winter wheat seedlings. Each bar represents dry weight of 100 seedlings in grams. Seedling samples were taken 19 days after early-season sowing (23 October), 20 days after midseason sowing (6 November), and 34 days after late-season sowing (20 November). INOC = naturally inoculated seed with 100% infection, N.I.(80%) = naturally infected seed with 80% infection, and N.I.(11%) = naturally infected seed with 11% infection. Interactions among seed inoculum levels and planting dates are not significant. For comparison of seed inoculum means (2.33, 2.08, 2.56), LSD = 0.13 using the Waller-Duncan  $k$ -ratio  $t$  test ( $k$ -ratio = 100). Planting date means showed a significant linear decrease from early to late planting dates.

disease developed in plants from inoculated seed than in plants from naturally infected seed. In the midseason and late-season sowings, plants from naturally infected seed with 80% infection were significantly more severely diseased than plants grown from inoculated seed or naturally infected seed with 11% infection. Late-season sowing resulted in more severely diseased plants than early-season or midseason sowing did. Pycnidia were produced on infected coleoptiles and on seed.

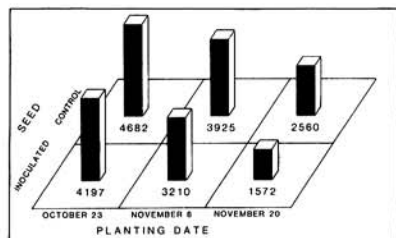
Disease severity and dry weight of

seedlings were negatively correlated, especially for seedlings from seed with 80% infection (Fig. 4). In each of the three sowings, seedlings grown from seed with 80% infection weighed significantly less than those grown from seed with 11% infection. Furthermore, in the late-season sowing, weight of the plants from seed with 80% infection was significantly less than plants from inoculated seed.

*S. nodorum* hyphae grew from seed and infected the seedling by penetrating the coleoptile (Fig. 5A). Heavy infection resulted in cell death and eventual



**Fig. 5.** (A) Cross section of wheat seedling. COL = coleoptile, oe = outer epidermis, co = cortex, ie = inner epidermis, vb = vascular bundles, fl = first leaf, sl = second leaf, ic = infected cells with *Septoria nodorum*, nic = noninfected cells, and hc = hypersensitive cells around vascular bundles (3) ( $\times 110$ ). (B) Cross section of wheat seedling showing a coleoptile (COL) with severely infected region of outer epidermis (oe), cortex (co), and inner epidermis (ie) and noninfected true leaf region (fl = first leaf, sl = second leaf) ( $\times 90$ ). (C) Longitudinal section of wheat seedlings showing coleoptile (COL) and true leaf region (l). Outer epidermis (oe), cortex (co), and inner epidermis (ie) of coleoptile are shown; pfe = point of fungal entry, ic = infected cells, hyc = hyperplastic area, and kn = swollen area (knob) ( $\times 120$ ). (D) Longitudinal section of infected coleoptile showing outer epidermis (oe) and cortex region (co). Hyperplastic area (hyc), hyphae (hy) of *S. nodorum* between the cells, and infected cells (ic) with accumulated substance(s) are indicated ( $\times 960$ ).



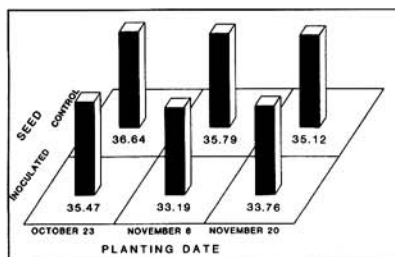
**Fig. 6.** Effect of seedborne *Septoria nodorum* on yield of winter wheat in 1980-1981. Bars represent yields (kg/ha). Seed was inoculated by immersing in a *S. nodorum* spore suspension of  $10^6$  spores per milliliter. *S. nodorum* was present on 100% of inoculated seed and on 0% of control seed. Interactions among seed sources and planting dates are not significant. Mean yield of the plants from inoculated seed is significantly lower than that of plants from control seed. Plant date means showed a significant linear decrease from early to late planting dates.

destruction of the entire coleoptile (Fig. 5B). Swollen parts of the coleoptile (knobs) resulted from development of hyperplastic areas (Fig. 5C,D). Infection was not observed in the vascular bundles. The inner epidermis of coleoptiles was infected but the region of the true leaves, adjacent to the inner epidermis of coleoptiles, was not infected (Fig. 5A-C). A substance(s) that stained reddish green accumulated in infected cells. The substance(s) did not react in histochemical tests for cellulose, pectin, lignin, or gum.

**Disease development.** Inoculated and infected seed gave rise to seedlings with infected coleoptiles in the field experiments conducted in 1980 and 1981. Symptoms such as brown flecks and knobs developed on the coleoptiles and some seedlings became distorted. Fertile pycnidia were observed on the coleoptiles 19 days after sowing seed. Brown lesions with pycnidia appeared on lower leaves of the seedlings in the fall. These lesions were mostly on senescent leaves. More pycnidia were observed on lesions exposed to sunshine than on lesions in shaded areas.

Although lower leaves were diseased, there were no noticeable symptoms of the disease on upper parts of the plants until flowering. No part of the plants had more than 10% infected area, and no correlation was found between degree of seed infection and disease severity of the upper leaves, stems, or spikes. Similarly, the number of heads per unit area did not significantly differ among treatments.

In the 1980-1981 field experiment, plants grown from inoculated seed produced significantly less yield with lower seed weight than plants grown from uninoculated seed in all sowings (Figs. 6 and 7). Yield reductions of plants from late-season and midseason sowings were significantly higher than those from midseason and early-season sowings, respectively. Seed weights of plants from midseason and late-season sowings were



**Fig. 7.** Effect of seedborne *Septoria nodorum* on seed weight of winter wheat in 1980-1981. Bars represent weight of 1,000 kernels in grams. Seed was inoculated by immersing in a *S. nodorum* spore suspension of  $10^6$  spores per milliliter. *S. nodorum* was present on 100% of inoculated and on 0% of control seed. Interactions among seed sources and weight of plants from inoculated seed is significantly lower than that from control seed. For comparison of planting date means (36.05, 34.49, 34.44), LSD = 1.09 using the Waller-Duncan *k*-ratio *t* test (*k*-ratio = 100).

significantly lower than those of plants from early-season sowing. Interactions among seed sources and planting dates were not significant.

By contrast, in the 1981-1982 experiment, significant differences occurred only among planting dates. Yield and seed weights of plants from the late-season sowing were significantly lower than those of plants from either early-season or midseason sowing.

## DISCUSSION

Survival of *S. nodorum* in wheat seed stored for more than 27 mo agrees with reports by Cunfer (7) and Machacek and Wallace (18) that the fungus survived in wheat seed for more than 2 yr. The results do not agree with Von Wechmar's report (24) that seed infection was almost eliminated within 12 mo. In this study, *S. nodorum* not only survived in seed for more than 2 yr but also remained virulent. Survival of *S. nodorum* in wheat seed may be influenced by degree of seed infection, storage conditions, presence of other seedborne microorganisms, and wheat cultivar.

In the warehouse, seed samples that initially had 88% infection still had 29% infected seed after 27 mo, whereas samples with seed infection of 50% or less were almost free of the fungus after this period. The fungus survived in a higher percentage of seed with low moisture content and stored at low temperatures. This indicates that differences among reports on longevity of *S. nodorum* in seed could be related, to a large degree, to storage conditions.

Yield loss caused by seed infection is not clearly understood. Burhardt (5) was able to increase yield by 370 kg/ha with seed treatment. Early severe seedling infection by *S. nodorum* has been reported to reduce tiller production, contribute to dwarfing of culms and ears, and lead to gross infertility (22). Although in this study, infection of lower

leaves occurred after coleoptile infection, there was no significant difference in the number of heads in the plots of different treatments. Yield loss appeared to be due primarily to reduction in seed weight. Further reduction in yield occurred when seed was sown late in the fall. This could be because of colder conditions that favored disease development (3,9,10,15). Another factor that may affect yield is the toxin ochracine, which has been reported to be produced by *S. nodorum* (4). Growth of roots and shoots of wheat seedlings grown from seed infected by *S. nodorum* was significantly reduced compared with seedlings grown from uninfected seed (2). Reduction in root growth may cause dwarfing of heads and/or reduction in seed weight.

It is not clear how infected seed may lead to spread of the organism. Histological studies indicated that even in the case of severe infection of the coleoptile, the region of true leaves remained free of infection for 6 wk from the time of sowing seed, but this region may be infected later. Pycnidia were produced on diseased coleoptiles shortly after sowing seed in the fall and on lower leaves of the plants throughout the growing season. However, the disease did not develop on the upper parts of the plants until the flowering stage. This was probably due to dry environmental conditions during the 2 yr of this study; commercial fields in the area had very little glume blotch this period. The observations also agree with reports that wheat plants are most susceptible to glume blotch disease at flowering time (11,14,20). Thus, seedborne inoculum could play an important role as a source of initial inoculum for glume blotch development in wheat in North Carolina.

Because *S. nodorum* survives and remains pathogenic in wheat seed for more than 2 yr and causes reduction in plant growth and yield, even without spread to the foliage, it may be profitable to control seedborne inoculum of the fungus.

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