Ecology and Epidemiology

Variation in Pathogenicity, Virulence, and Aggressiveness of *Septoria nodorum* in Florida

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ABSTRACT

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Pathogenicity, virulence, and aggressiveness of 282 isolates of *Septoria nodorum*, causal agent of glume blotch of wheat, were determined on eight wheat cultivars of varying resistance. Cultivar reactions, measured as percentage necrosis of seedling leaves, were classified into 253 different resistance patterns. Ninety-five isolates were pathogenic to all eight cultivars; 85, to seven; 54, to six; 32, to five; 11, to four; four, to three; and one, to two cultivars. An isolate was considered pathogenic if it caused necrosis in a greenhouse test. Virulence of the isolates varied; maximum necrosis induced in the cultivars after 12 days ranged from 13 to 80%. Isolates from commercial fields were less variable in pathogenicity and more virulent than those from research plots. Aggressiveness, measured as the time to produce the first necrosis on seedling leaves of the cultivar Potomac, varied from three to 10 days after inoculation. Pathogenic and virulent types were present in differing frequencies and distributions in subpopulations defined in terms of geographic origin and year of isolation.

Additional key words: *Triticum aestivum* L. em. Thell, host resistance.

Glume blotch, caused by the fungus *Septoria nodorum* (Berk.) Berk. (perfect stage *Leptosphaeria nodorum* Müller), is a major factor limiting yields of wheat (*Triticum aestivum* L. em. Thell) in Florida (12). Florida farmers currently grow relatively susceptible, high-yielding, soft red winter wheat cultivars and apply zinc ion-maneb complex fungicides to control glume blotch (1,12). Efforts to improve resistance and yield in wheat cultivars have been based on selection of tolerant cultivars that yield well despite infection (4,18). Scharen and Kupinsky (19) have reported forms with enhanced resistance expressed as fewer lesions, less chlorosis and necrosis, and a lower disease index.

Races of *S. nodorum* have not been characterized, because single genes that give high levels of resistance have not been found in wheat (3,19). However, some cultivar-isolate interactions were revealed in studies by Scharen et al (17,18) that indicate identifiable pathogenic types in *S. nodorum*. It has been recommended that a mixture of the most virulent cultures available be used in screening programs for resistance (3,18). Researchers have used one or a composite of a few cultures in their inoculum (5,10,15,19). Cultivar-isolate interactions may be masked by the use of few isolates or mixtures of isolates whose pathogenicity has not been characterized.

Our purposes were to characterize the pathogenic variability of *S. nodorum* in the wheat-growing regions of Florida and to elucidate the role of pathogen variation in the apparent loss of resistance to glume blotch in breeding lines developed for Florida growers (R. D. Barnett, *personal communication*). We defined and determined the pathogenicity, virulence, and aggressiveness of isolates of *S. nodorum* from Florida and studied factors affecting these characteristics. Subpopulations were described in terms of time, location, and host of origin.

MATERIALS AND METHODS

The population of *S. nodorum* occurring on wheat in Florida was sampled by isolating the fungus from naturally infected wheat during the spring in 1978 and 1979. Isolations made in 1978 were from 50 cultivars and lines in 10-m, four-row plots planted in an advanced soft red winter wheat disease nursery at the Agricultural Research and Education Center (AREC) at Quincy and in Agricultural Research Centers (ARC) at Marianna and Jay. In 1979, the disease nurseries contained 51 entries, some of which differed from those of 1978. Five leaf segments or glumes containing pycnidia were collected from each plot.

In 1979, additional 3.7-m, 30-row plots of seven cultivars used for greenhouse testing of isolates (see below) were planted and sampled at Quincy AREC. Five leaf pieces with glume blotch lesions were taken from the approximate centers of each large plot. Forty-one commercial wheat fields in three counties (Escambia, Santa Rosa, and Gadsden) and two large research plantings in a fourth county (Alachua) were also sampled in 1979 (Fig. 1).

Areas of fields covering up to 40 ha were sampled by taking leaf pieces randomly along two transects through each field. Three isolates per field were selected at random. Two isolates from each large plot and one from each entry in the wheat nurseries were obtained. Isolates were grouped into subpopulations based on geographic area and year. Only data from subpopulations containing at least 15 isolates (including isolates from Escambia, Santa Rosa, and Gadsden counties; Jay ARC in 1978 and 1979; Quincy AREC and Marianna ARC in 1979; and large plots at Quincy AREC in 1979) were used in most analyses.

Wheat cultivars and lines infected naturally were rated for relative resistance and susceptibility to glume blotch in 1978. The wheats were evaluated at growth stage 10.1–10.5 (Feekes' scale [13]). Each was assigned a rating of R (resistant: very few lesions, 1–2 mm in diameter, without pycnidia); MR (moderately resistant: lesions 2–10 mm in diameter, without pycnidia); MS (moderately susceptible: lesions 10–20 mm in diameter, with few pycnidia, mostly in centers of lesions); or S (susceptible: lesions 20 mm or larger in diameter, with abundant pycnidia).

Eight winter wheat cultivars were selected for screening isolates of *S. nodorum* in the greenhouse. Three soft red cultivars were selected because they varied in susceptibility to glume blotch at different locations (Table 1). Four other cultivars adapted to Florida were included because of their consistent field reactions to *S. nodorum*: Oasis, known to have tolerance to glume blotch and resistance under field conditions; Coker 77-19, also resistant in the field; McNair 1813, widely grown in Florida and moderately susceptible in the field; and Potomac, which varied in reaction to *S. nodorum* in 1978 but previously was observed to be very susceptible in the field. The eighth cultivar, Moking, a hard red winter wheat, was reported by Krupinsky et al (11) to be the most resistant of more than 6,000 wheat lines tested.

Isolation. Leaf pieces or glumes with lesions containing pycnidia were placed on microscope slides on filter paper or paper-towel disks in petri dishes. The filter paper was kept moist until cirri were extruded from pycnidia (after about 24 hr). Infected leaf pieces or glumes on which pycnidia were not visible were surface sterilized by soaking them for 1 min in a solution of 10% Clorox (0.5% NaOCl) containing one drop of Tween 20 (polyoxyethylene sorbitan monolaurate) per 100 ml of solution. The tissue was then plated onto yeast-malt agar (YMA) made with 2 g of malt extract, 2 g of yeast extract, 2 g of dextrose, 10 g of Difco agar, and 500 ml of distilled water. Mature pycnidia formed in the tissue or in the agar medium, and cirri were extruded after 2–5 days.

Portions of the cirri were transferred to plates of 1% water agar. Glass needles with tips approximately the diameter of the spore (about 3 µm) were used to separate spores from the cirrus and transfer single spores to plates of YMA, thus establishing cultures of single-spore isolates.

Maintenance of isolates. Pycnidia formed 5–10 days after single spores were plated. A portion of a cirrus from one pycnidium per isolate was transferred to a YMA slant before being transferred to soil.

Samples (2–3 g) of Dothan sandy loam (15–20% clay, pH 5.3 in 0.01 M CaCl₂, pH 6.0 in distilled water) from Jay ARC were placed in 13 × 100 mm tubes plugged with cotton and autoclaved twice (20 min with a 24-hr interval). Spores were harvested from 5- to 12-day-old cultures on YMA by flooding petri plates or slants with sterile distilled water. One-milliliter samples of the suspension were transferred to the soil preparations, which were shaken lightly to allow the suspensions to penetrate the soil. The soil cultures were stored in the dark at 6–7 C and remained viable for at least 22 mo.

Inoculation. To produce inoculum, a small portion of the soil (about 0.1 g) was suspended in 1 ml of sterile distilled water and dispensed onto YMA plates. The plates were incubated for 5–10

days at 20 C under constant cool-white fluorescent light. Spores were harvested by flooding plates with distilled water, swirling to dislodge cirri, and decanting the spore suspension into beakers.

In preliminary greenhouse tests with 12 isolates and 2-, 4-, 6-, and 8-wk-old wheat plants, growth stage did not affect susceptibility. Seedlings were used for the rest of the experiments because of ease of handling and the short growing period.

Wheat seedlings were grown in a greenhouse at 22 C (range 18–30 C) without supplemental lighting and were inoculated when the first and second leaves were fully expanded (10–14 days). Wheat was planted in clusters of five plants per cultivar, four cultivars per pot in 12.5-cm (5-in.) plastic pots containing an autoclaved soil mix of sandy loam soil, peat, and perlite (3:2:1, v/v).

Cultivars were inoculated with 15–20 ml of a spore suspension (usually 5 × 10⁵ spores per milliliter) to which one drop of Tween 20 had been added per 100 ml of suspension. Inoculum was applied at 0.5–0.6 kg/cm² pressure onto all leaf surfaces with an atomizer. Runoff did not occur.

After the inoculum had dried (about 30 min), the plants were placed in a clear plastic chamber inside the greenhouse, where they received intermittent mist (2.5 sec every 5 min) for 1-hr periods four times during the day and once at night. The temperature inside the mist chamber at midday was typically 2–3 C higher than that in the greenhouse. Inoculations were not performed if greenhouse temperatures exceeded 30 C. Plants were removed to the greenhouse bench after 48 hr. To evaluate symptom expression, necrosis on leaves was compared visually with published disease assessment keys (8) 12–14 days after inoculation.

Assessment of pathogenicity, virulence, and aggressiveness. Pathogenicity, virulence, and aggressiveness of each isolate of *S. nodorum* were determined on five seedlings of each cultivar. Aggressiveness (the number of days for necrosis to appear) of 103 isolates was measured after inoculation on Potomac, the most
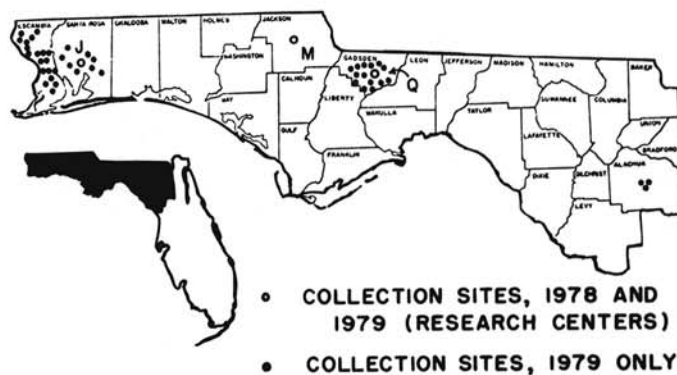

Fig. 1. Collection sites for *Septoria nodorum* in principal wheat-growing areas of Florida in 1978 and 1979. Advanced wheat-breeding nurseries are represented by open circles (o): J = Jay Agricultural Research Center (ARC); M = Marianna ARC; Q = Quincy Agricultural Research and Education Center. (●) Represent commercial wheat fields.

TABLE 1. Disease ratings[a] of cultivars from advanced soft wheat disease nursery at Agricultural Research and Education Center, Quincy, and Agricultural Research Centers, Jay and Marianna, Florida, 1978

Entry	Location[b]		
	Quincy	Marianna	Jay
Oasis	MR	MR	MR
Coker 76-35	R	MS	MS
Potomac	S	R	MS
McNair 1813	MS	MS	MS
Doublecrop	S	MR	R
Coker 77-19	R	MR	MR
Coker 77-25	S	S	S

[a] Ratings based on symptoms caused by *Septoria nodorum*. S = susceptible; MS = moderately susceptible; MR = moderately resistant; R = resistant. Ratings refer to whole plants.
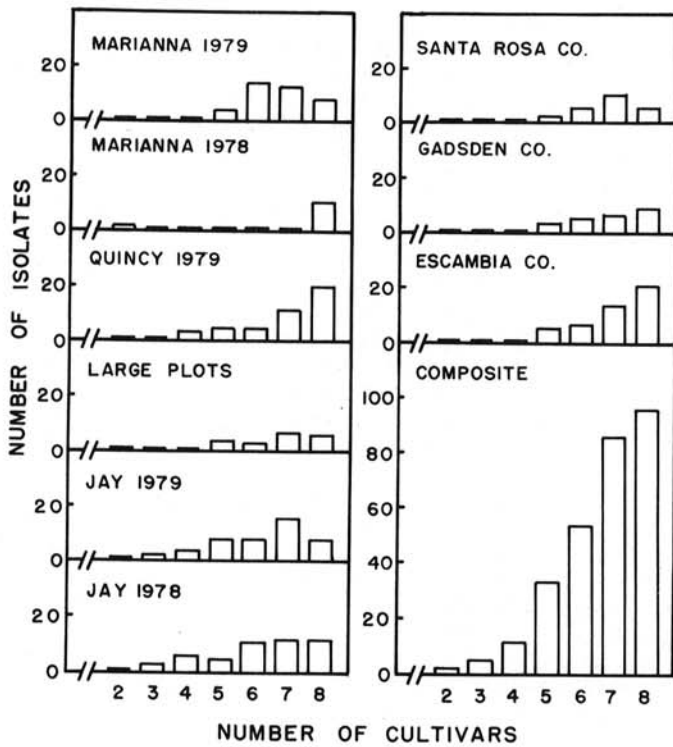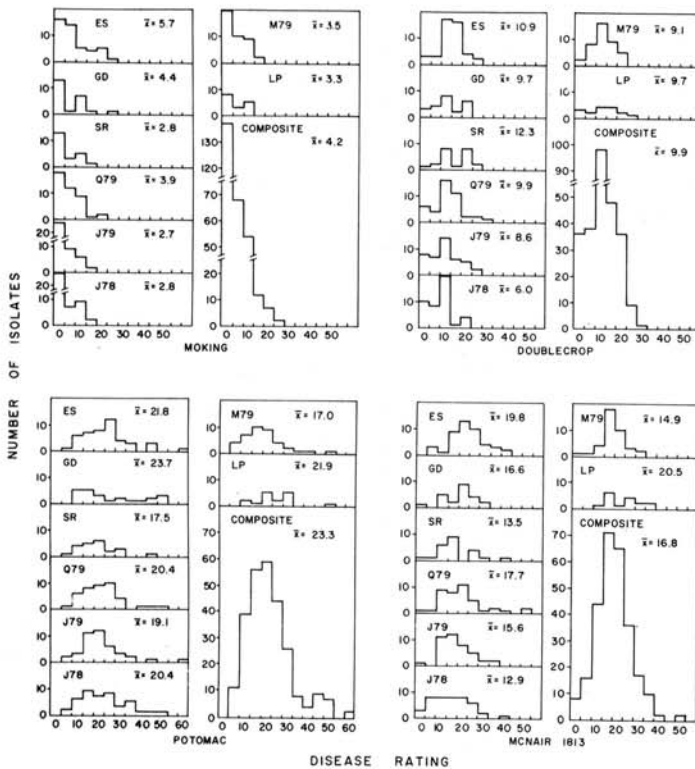
Fig. 2. Number of isolates of *Septoria nodorum* from nine locations and in composite samples that were pathogenic to given numbers of test wheat cultivars. Solid horizontal bars represent values of zero (no isolates).

Figs. 3. Range and mean of virulence of population samples of *Septoria nodorum* to wheat cultivars Moking, Potomac, McNair 1813, Doublecrop, Oasis, Coker 77-19, Coker 77-25, and Coker 76-35. Disease ratings are arc sine transformations. Each horizontal increment within a bar represents one isolate-cultivar combination, the mean of data from five plants. Subpopulations are represented by ES = Escambia County; GD = Gadsden County; SR = Santa Rosa County; Q79 = Quincy Agricultural and Education Center (AREC) 1979; J79 and J78 = Jay Agricultural Research Center, 1979 and 1978; M79 = Marianna 1979; LP = large plots, Quincy AREC.

susceptible cultivar. Virulence was measured by comparing the percentage leaf necrosis on each cultivar. Pathogenicity was determined by the number of cultivars on which an isolate caused necrosis and the order of susceptibility of cultivars to individual isolates. The relationship between pathogenicity and virulence was examined by comparing the number of cultivars on which an isolate caused necrosis to the virulence rating of each isolate on Potomac, McNair 1813, and Coker 76-35.

A standard host-isolate combination was established for use with each set of plants inoculated to detect the effect of variation in greenhouse conditions on symptom expression. The isolate J78-33 (from entry 33 of the wheat nursery at Jay ARC in 1978) was consistently highly virulent on Potomac in preliminary tests with inoculum concentrations as low as 10^4 spores per milliliter.

The optimal spore concentration, leaf position, and time after inoculation for evaluating isolate-cultivar combinations were determined. Seedlings of cultivars Potomac and McNair 1813 were inoculated at the three-leaf stage with suspensions of 10^4, 10^5, 5×10^5, and 10^6 spores per milliliter of J78-33, incubated in the greenhouse, and evaluated.

Cultivar of origin, colony color and virulence. Isolates were grouped according to the wheat cultivar from which they were obtained in the field, regardless of location. Sufficient isolates for comparison were obtained from four cultivars: McNair 1813, McNair 1003, Holley, and Omega 78. Mean necrosis caused by isolates within each group was calculated for each cultivar. Group means on each cultivar and overall cultivars were compared.

Colony color was assessed 8–10 days after single spores were transferred to YMA. Virulence of isolates of different colors on YMA (color of mycelium and discoloration of medium) was compared. Isolates were separated into a groups based on four colors that occurred most frequently: pink, white, yellow, and gold.

Analyses of variance were performed on percentage necrosis data that were transformed using $Y = $ arc sine (percentage necrosis)$^{1/2}$ or the angular transformation (14), so that variances would be homogeneous. Transformed values are given in degrees. Duncan's new multiple range test was used to compare means.

RESULTS

Differences among cultivars and among isolates in the greenhouse were best detected by inoculating seedlings with 5×10^5 spores per milliliter of inoculum and rating the first or second seedling leaf after 10–14 days. Using the first seedling leaf enabled the rapid detection of significant differences among isolates with relatively low numbers of spores. Inoculum concentrations and leaf positions evaluated were significantly different when as few as one isolate and two cultivars were tested.

The recurrent use of one cultivar-isolate combination (J78-33 and Potomac) was an effective check of variation in greenhouse conditions. If plants of this standard combination did not show at least 30% necrosis by 12 days after inoculation, the other isolates involved were tested a second time.

Pathogenicity. The range of pathogenicity of the isolates differed in each subpopulation. Variation among subpopulations was best evaluated by comparison with the composite sample (Fig. 2). Of the 282 isolates, 95 were pathogenic to all eight cultivars; 85, to seven; 54, to six; 32, to five; 11, to four; four, to three; and one, to two cultivars. Most isolates from Marianna 1979 and Jay 1979 were pathogenic to fewer than eight cultivars.

Isolates differed in pathogenicity if the order of susceptibility of the cultivars to them was different. Inoculations with 282 isolates produced 253 different rankings. Twenty-seven patterns of cultivar ranking were produced by more than one isolate. The most frequent (100 isolates) were those to which Potomac, Coker 77-19, and McNair 1813, in varying order, were the most susceptible, regardless of the order of the other cultivars. The proportions of isolates pathogenic to cultivars ranged from 51% (Moking) to 78% (Coker 77-25), 81% (Coker 76-35), 86% (Oasis), 87% (Doublecrop), 93% (Coker 77-19), 97% (McNair 1813), and 100% (Potomac).

Virulence. Single isolates of *S. nodorum* caused up to 80% necrosis on Coker 77-19, 76% on Potomac, 60% on McNair 1813

and Coker 76-35, 25% on Oasis, 23% on Coker 77-25, 21% on Doublecrop, and 13% on Moking. Of these, no single isolate was the most virulent to more than one cultivar. The most virulent isolates to Moking and Coker 77-25 were from Escambia County; to Doublecrop and McNair 1813, from Quincy 1979; to Oasis, from large plots at Quincy (1979); to Coker 76-35, from Gadsden County; to Coker 77-19, from Jay 1978; and to Potomac, from Quincy 1978 (Fig. 3).

The distributions of virulence values of the composite sample and subpopulations are represented in plots of the number of isolates against the amount of necrosis caused on each cultivar under greenhouse conditions (Fig. 3). The more resistant the cultivar, the more the range of virulence of the isolates shifted toward the low end of the rating scale. Distributions for subpopulations on Moking, Oasis, and others were centered around class 5 or 10. The distributions of isolates tested on Potomac, generally the most susceptible cultivar, were centered around class 20 or 25. The greatest variation in virulence was found in reactions to the more susceptible Potomac, Coker 77-19, and McNair 1813.

Subpopulations from commercial fields differed in some ways from those from research center plots. Subpopulations from commercial fields had more types that were pathogenic to Moking, Coker 77-25, and Doublecrop than did subpopulations from research centers. Isolates from fields in Escambia and Santa Rosa counties were most virulent to the most resistant cultivars. Subsamples from Gadsden County, including large plots at Quincy AREC, were most virulent on the four most susceptible cultivars (Fig. 3). Although commercial fields in Santa Rosa County were close geographically to the Jay ARC, characteristics of the fungal subpopulations were very different. The subpopulation from Jay 1978 had lowest mean virulence on six of the eight cultivars; that from Santa Rosa County had lowest mean virulence on Coker 77-19; and that from Marianna 1979 had lowest mean virulence on Coker 76-35 (Fig. 3).
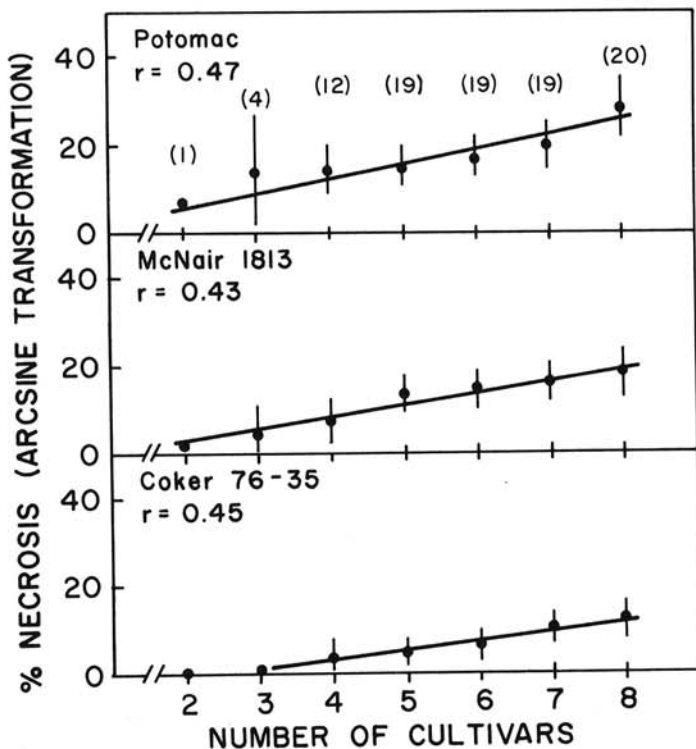
In somes cases, the mean and range of virulence of a subpopulation to a cultivar were correlated with the original field disease assessments. The population from Quincy 1978, where Potomac was susceptible, was highly virulent to Potomac in the greenhouse. A subpopulation with low virulence to Potomac, Marianna 1978, was the one area where Potomac had been rated as resistant. The fungal population from Jay 1978, where Doublecrop was rated as susceptible, was highly virulent to that cultivar in greenhouse tests. However, virulence of subpopulations tested in the greenhouse varied on McNair 1813, which was rated as susceptible to all subpopulations in the field.

In general, an isolate that was pathogenic to more cultivars than another isolate had higher virulence on any one cultivar (Fig. 4). Linear correlations were low ($r = 0.43-0.47$) regardless of the relative resistance or susceptibility of the cultivar.

Aggressiveness. Necrosis was first observed on Potomac after a minimum of four days (10% of isolates) to 10 days (3% of isolates). Most isolates (73%) induced necrosis after 5–7 days. In general, isolates that induced symptoms earliest also induced the highest percentage necrosis after 10–12 days (Fig. 5).

Cultivar of origin and colony color. Isolates from Holley wheat had higher mean virulences than isolates from other cultivars (Table 2). Isolates from other cultivars did not differ in virulence. Isolates from Holley wheat were most virulent on Coker 76-35 and Potomac. Those from Omega 78 were most virulent on Coker 77-25 and least virulent on Coker 77-19. McNair 1813 was the only cultivar on which field isolates taken from McNair 1813 were most virulent, although their virulence did not differ significantly from that of isolates from Holley or Omega 78. Some host specialization of isolates did occur.

Isolates with gold colonies in culture were more virulent than isolates that were white (Table 3). Both were more virulent than pink or yellow isolates. When individual cultivars were examined, gold isolates were more virulent than isolates of all other colors on Potomac and McNair 1813. Gold isolates were more virulent than yellow and pink isolates on Doublecrop and Moking and more virulent than pink isolates on Coker 76-35 and Coker 77-25.

DISCUSSION

Breeding and selection programs that depend on the use of one or two isolates may fail to detect variants in the host population that

Fig. 4. Relationship between pathogenicity and virulence of *Septoria nodorum* on three wheat cultivars. Each graph plots disease (Y = arc sine [percentage necrosis]$^{1/2}$) caused by an isolate on the target cultivar against the number of cultivars to which an isolate was pathogenic. Data points are averages of virulence of all isolates pathogenic to different numbers of the eight cultivars. Values in parentheses are numbers of isolates, from a random sample of 94, pathogenic to a given number of eight cultivars. Vertical lines are 95% confidence intervals for each mean.

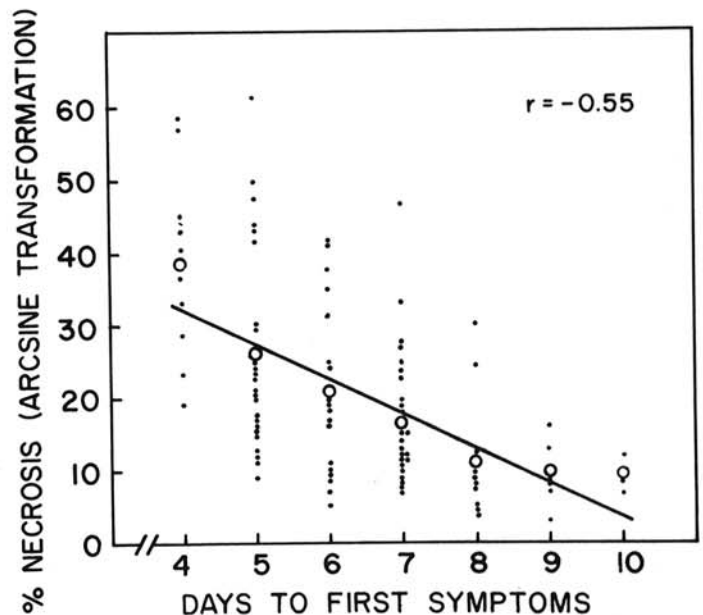**Fig. 5.** Relationship between virulence and aggressiveness of *Septoria nodorum* on the wheat cultivar Potomac. Disease (Y = arc sine [percentage necrosis]$^{1/2}$) caused by an isolate is plotted against number of days after inoculation until first necrosis was observed. Dots (•) represent individual isolates; open circles (o) are means of isolates of the same aggressiveness in a random sample of 103.

are resistant to a given pathogen genotype. Planting plots of promising cultivars near commerical fields owned by cooperating farmers might be an effective addition to strategies for selecting for resistance to glume blotch.

Greenhouse assessments were not always accurate indicators of the performance of a selection under field conditions. Coker 77-25, rated as susceptible in the field in 1978, was resistant in the greenhouse. Coker 77-19, selected because of its resistance in the field, was one of three cultivars most severely infected in the greenhouse.

Scharen and Krupinsky (18) found that no two isolates in a sample of 75 gave identical reactions on a test series of wheat cultivars. In our sample, approximately 90% of the isolates had unique ranking patterns on the test cultivars. No pattern was represented by more than three different isolates.

Although some isolates had identical reactions on the cultivars, and there were differential interactions, the patterns found in this study do not conform to conventional race differentiation. Reactions based on percentage necrosis, a quantitative measure of disease, were not separated into discrete classes. The number of possible rankings (8! = 40,320) was greater than that for eight cultivars rated for presence or absence of symptoms ($2^8 = 256$).

Harrower (6) found that the wheat genotype from which an isolate was obtained might influence the virulence of that isolate to similar host genotypes. The virulence of a subpopulation may increase through adaptation to resistance in the host. The breeding lines were more heterogeneous and may have had greater resistance to glume blotch than McNair 1813, the predominant cultivar in commercial fields, and could be expected to select for higher virulence. The occurrence of more virulent types among isolates from commercial fields may indicate that factors other than host susceptibility affect pathogen virulence in glume blotch of wheat.

Isolates from a given wheat cultivar may reinfect it in several ways: direct infection of coleoptiles from infected seed, as reported by Bateman (2); spread from lower to upper plant parts within a growing season, as suggested by Harrower (6); or spread from debris containing pycnidia, as observed by Holmes and Colhoun (7). Disease resulting from reinfection may be more severe if host specialization occurs. The use of infected straw to ensure the presence of inoculum of *S. nodorum*, a common practice in establishing disease in breeding nurseries (R. D. Barnett, *personal*

TABLE 2. Virulence of groups of isolates of *Septoria nodorum* obtained from specific wheat cultivars to eight test wheat cultivars

Test cultivar	Cultivar of origin	Disease rating[z]
Potomac	Holley	28.0 a
	McNair 1813	20.9 b
	McNair 1003	19.7 b
	Omega 78	18.5 b
Coker 77-19	McNair 1003	19.8 a
	Holley	19.3 a
	McNair 1813	17.0 a
	Omega 78	13.6 b
McNair 1813	McNair 1813	19.4 a
	Holley	18.9 a
	Omega 78	17.0 a
	McNair 1003	12.0 b
Coker 76-35	Holley	18.9 a
	McNair 1813	8.9 b
	Omega 78	8.3 b
	McNair 1003	8.2 b
Coker 77-25	Omega 78	11.6 a
	McNair 1813	8.2 b
	McNair 1003	7.5 b
	Holley	7.4 b
Doublecrop	Omega 78	11.2 a
	McNair 1003	10.9 a
	McNair 1813	10.3 a
	Holley	10.1 a
Oasis	Holley	9.3 a
	McNair 1813	9.1 a
	Omega 78	9.0 a
	McNair 1003	8.1 a
Moking	McNair 1003	5.8 a
	McNair 1813	4.8 a
	Omega 78	4.7 a
	Holley	4.6 a
All cultivars	Holley	14.6 a
	McNair 1813	12.4 b
	Omega 78	11.8 b
	McNair 1003	11.5 b

[z]Ratings are expressed as tranformed values (arc sine [percentage necrosis]$^{1/2}$) of disease on seedlings of each test cultivar. Each value represents the mean of five plants per isolate-cultivar combination. Means followed by the same letter within the subgroup for each test cultivar are not significantly different at $P = 0.05$ according to Duncan's new multiple range test.

TABLE 3. Virulence of groups of isolates of *Septoria nodorum* differing in colony color to eight wheat cultivars

Test cultivar	Colony color	Disease rating[z]
Potomac	Gold	29.0 a
	White	22.0 b
	Pink	17.0 c
	Yellow	16.6 c
McNair 1813	Gold	22.6 a
	White	16.3 b
	Pink	13.8 c
	Yellow	12.0 c
Coker 77-19	White	19.0 a
	Pink	18.2 a
	Gold	17.1 a
	Yellow	17.0 a
Doublecrop	Gold	13.0 a
	White	9.5 ab
	Pink	7.8 bc
	Yellow	6.6 c
Coker 76-35	Gold	9.8 a
	White	8.7 a
	Yellow	6.7 ab
	Pink	5.3 b
Oasis	Gold	8.7 a
	White	8.5 a
	Yellow	6.9 a
	Pink	6.0 a
Coker 77-25	Gold	8.1 a
	Yellow	5.5 ab
	White	5.2 ab
	Pink	4.3 b
Moking	Gold	6.8 a
	White	4.2 ab
	Pink	3.0 b
	Yellow	2.9 b
All cultivars	Gold	14.4 a
	White	11.7 b
	Pink	9.4 c
	Yellow	9.3 c

[z]Disease ratings are transformed (arc sine [percentage necrosis]$^{1/2}$). Each. value represents the mean of five plants per isolate-cultivar combination. Means followed by the same letter within the subgroup for each test cultivar are not significantly different at $P = 0.05$ according to Duncan's new multiple range test.

communication), may result in variable cultivar reactions depending on the origin of that debris. The seed for research center plots is derived from previous plantings there, and a local fungal population may be maintained on the seed. Although commercial farmers may plant the same cultivar each year, their seed must be purchased and, if infected, may introduce more variation into the fungal population of an area.

Colony color was correlated with virulence. Sporulation was generally greater in pink colonies and lower in gold colonies, the most virulent type. Abundant sporulation in culture was not always related to high virulence, in contrast with the sample studied by Scharen and Krupinsky (18), who did not correlate colony color with virulence. Pigmentation of the medium, most striking in gold colonies, has been associated with toxin production by *S. nodorum* (9). Toxins may account for the higher virulence of this group. Rapilly and Skajennikoff (16) found that green colonies were consistently the most virulent, but the proportion of green isolates in our sample (3 of 282) was too small for comparison.

Aggressiveness may be determined by measuring the time to the appearance of symptoms, the time to reach a given disease level, or the time from infection to sporulation. The most aggressive isolates in our sample, based on earliness of symptom expression, did not always cause the most necrosis in a given time period. Variation from the mean amount of necrosis on Potomac was greatest for the most aggressive isolates (first necrosis after 4–6 days). Low correlations between virulence and aggressiveness or pathogenicity are ascribed to isolate-cultivar interactions.

According to Vanderplank (20), a correlation between variation in the pathogen and in the host implies that if the host is changed, as when a new host genotype is brought into cultivation, the pathogen will also change. A "loss" of resistance is often associated with vertical or race-specific resistance; however, the host specialization of *S. nodorum* to wheat cultivars and lines observed in this study and by Harrower (6) shows that pathogen adaptation is not limited to host-pathogen systems in which races can be identified. Frequencies of unique pathogenic types present in the population of *S. nodorum* may change in response to selection pressure as in single-gene systems.

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