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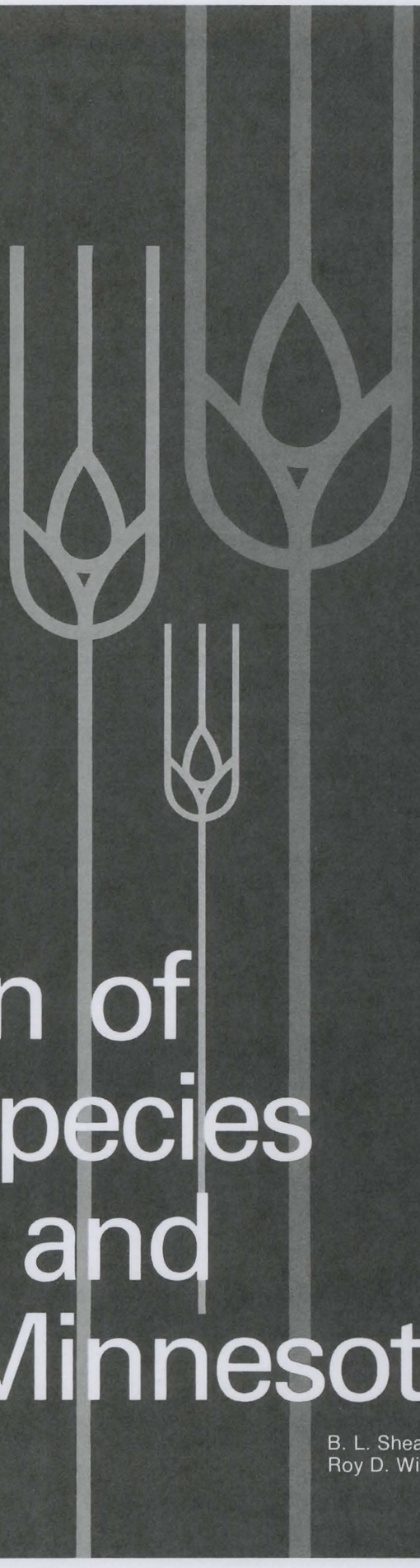

Sporulation of Septoria Species On Wheat and Barley in Minnesota

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Introduction

Necrotic spots and blotches on leaves of spring and winter wheats are a serious problem in Minnesota, as well as elsewhere in the world. The semi-dwarf wheats may be especially susceptible (61). The cause of this necrosis is not fully understood, but it has been attributed to genetic factors, to pathogenic bacteria (38), and to fungi (26).

Species of *Septoria* are some of the most important fungi that cause necrosis of wheat and barley leaves (26,28,36,55,56,57). In Minnesota *Septoria avenae* Frank f. sp. *triticea* T. Johnson and *S. nodorum* (Berk.) Berk. parasitize both crops (52) and *S. tritici* Rob. ex Desm. parasitizes wheat (48,50).

Little is known of the relative importance of the three *Septoria* spp. in Minnesota except they commonly occur (50). When these fungi occur singly on leaves they incite typical symptoms: for *S. avenae* f. sp. *triticea* (31) the lesions are ovate in shape and are straw or buff-colored with an off-white center bearing pycnidia; for *S. nodorum* (2,56) the lesions are rectangular in shape, and have off-white centers with dark brown edges, with or without pycnidia; for *S. tritici* the lesions are irregular to circular in shape, light-brown in color, and contain pycnidia (56).

The lesions caused by the *Septoria* spp. frequently coalesce with each other, or with lesions caused by other pathogens, to form a general necrosis of the leaves (28,50), making it impossible to critically evaluate, by means of symptoms alone, the seasonal occurrence of the pathogens or their relative importance.

The biology of the *Septoria* spp. on wheat is generally well known. *Septoria* belongs to the Sphaeropsidales. *Septoria nodorum* was first described in 1845 and *Leptosphaeria nodorum* Muller is recognized as its perfect stage (56). *Septoria tritici* was first recognized in 1842 (56) and its perfect stage is *Mycosphaerella* graminicola (Fuckel) Schroeter (43). *Septoria avenae* f. sp. *triticea* was recognized in 1947; its perfect stage is *L. avenaria* Weber f. sp. *triticeae* T. Johnson (31). Information about S. *nodorum* and *S. tritici* has been extensively reviewed (26,36,47,56,62). There is little information about *S. avenae triticea*, but that which is available indicates that its epidemiology is basically similar to that of the other two species.

Most observations of the life cycles of the three *Septoria* spp. have been on the imperfect stages. Little is known of the importance of the perfect stages (56) and, in fact, the perfect stage of *S. tritici* was not known until 1976 (43). These fungi survive by means of pycnidiospores in pycnidia in crop debris on the soil surface (20,51). If the crop debris is incorporated into the soil, the fungi are destroyed by soil microorganisms (20,51). During wet weather the spores are extruded from the pycnidia in a mucilaginous matrix (51) and dispersed by splashing rain (44,65). New pycnidia may also form in the moist infected tissue (20,44,65). Once dispersed, the fungi can infect all of the aerial parts of the plant (31,56), and the pycnidia formed in the infected tissue are a secondary source of inoculum.

The role of wild grasses as sources of inoculum of the three species of *Septoria* is not well understood (48), although they are probably important. *Septoria nodorum* and *S. avenae triticea* both infect barley (*Hordeum vulgare* L.) and a wide range of wild grasses (46,48,52,58,65). The host range of *S. tritici* is more restricted than that of the other two fungi (58,65).

The aerial parts of the host plants are all infected by *Septoria* spp. but there is little or no information on the differential infection of plant parts or of plants of different ages (56). Most of the studies, especially those from Western Europe, are with *S. nodorum* and have concentrated on head infection, though Scharen (44) stressed the need for studies on leaf infection by this pathogen. Most of the work with *S. tritici* has been on leaf infection.

Little attention has been given to the comparative development of the *Septoria* species on different plant parts and the results are usually expressed on a per-

plant basis. Thus the relative contribution of the different plant parts to the development of an epidemic is not known.

There have been only a few attempts to compare natural epidemics of the *Septoria* spp.; most studies have been on epidemics initiated by artificial inoculation. The natural epidemics studied have involved only one species, or, if more than one species was involved, they were grouped under the term "Septoria," and there has been little attempt to determine the relative contribution of each species. Recent studies compared artificial epidemics of *S. nodorum* and *S. tritici* (9,23,32,67), but the epidemiological conclusions from these studies must be accepted with caution because small plots were artificially inoculated with large numbers of spores and plastic bags were placed over the plots to create long periods of high humidity for infection.

The interactions of the *Septoria* spp. in infections caused by a mixture of the species is not well understood. In a natural epidemic of *S. nodorum* and *S. tritici* on winter wheat in England, Jenkins and Morgan (28) observed that *S. tritici* tended to develop on lower leaves early in the season, whereas *S. nodorum* predominated late in the season. Jones and Odebunmi (33) studied infections of *S. nodorum* and *S. tritici* on plants in the heading stage in a glasshouse experiment, and found that symptoms of infection by *S. nodorum* tended to mask those by *S. tritici*.

Regarding the interaction of the *Septoria* spp., Minnesota appears to be unique in that all three Septoria species may be found in the field on single plants. In most other wheat-growing areas of the world, only *S. nodorum* and *S. tritici* are reported to occur together, although *S. avenae triticea* may not have been recognized (56).

Assessing the relative amount of each *Septoria* species present is one of the main difficulties in a study of the species on cereals. Generally the amount of a particular species is indicated by the percentage of the leaf or head covered by symptoms (9,23,26,32,67), but one cannot accurately separate the species by symptoms alone, especially when several *Septoria* species occur together or when other diseases or plant maturity interferes (28,50). Furthermore, because disease severity must be assessed before plants are killed, the contribution of infected, mature plant parts to an epidemic may be ignored. This is a serious deficiency, as the *Septoria* spp. may continue to grow and sporulate in mature plant tissue (20,31,65). In Minnesota, necrosis caused by *Pyrenophora trichostoma* (26) and more recently by bacteria (38), has been found to interfere with the assessment of the *Septoria* spp. when assessment was by symptoms alone (50). In surveys in this state symptoms were considered too inaccurate for distinguishing the *Septoria* spp. on wheat and so the species were identified by spore morphology (50).

Because it is difficult to estimate the relative population of the *Septoria* spp. in cereals from symptoms, the production of spores by each species may be the best method of assessing the populations of the species present. This method of estimating the amount of a fungus species present in a population has not been used to any great extent, especially with *Septoria* spp. Bockmann (4) estimated the resistance of wheat cultivars to *S. nodorum* by the numbers of spores of the fungus produced in the heads.

When the prevalence of a species is indicated by the number of spores present, it is assumed that each spore will produce an infection (68). With the *Septoria* spp. more than one spore may be required to assure that infection will occur, but the data should indicate the number of spores that could be dispersed, as well as the potential for infection. When prevalence is based on spore counts the species that can sporulate rapidly may be favored (28) over those that cause the most damage to the plant. Despite some problems, sporulation should show the main trends in pathogen prevalence (28).

Little attention has been given to the quantitative analysis of data on spore production, but much attention has been given to the analysis of disease severity data. The upper limit of severity is 100 percent and, typically, sigmoid severity curves can be linearized by the ln(x/l-x) transformation, where ln is natural logs and x is the severity of disease expressed as a proportion (63). A plot of ln (x/l-x) against time gives a straight line whose slope is the apparent infection rate, r (63).

In the case of data on spore-production, the maximum number of spores is not known; it will vary depending on environmental conditions. For cereal rusts, Romig and Dirks (41) used the ln (x/l−x) transformation and expressed the cumulative daily spore counts as a proportion of the final cumulative spore count. However, the disadvantage of cumulative spore counts is that the actual number of spores at a particular time in the growing season cannot be read off, since the total represents the number of spores at that particular time plus all those observed previously.

An alternative to cumulating spore numbers is to fit the observed numbers of spores to a nonlinear equation. However, nonlinear equations have been infrequently used in epidemiological research in plant pathology (34). The nonlinear logistic equation used in this study is of the form: $N = K/[1 + \exp(a - r_m t)]$ (35), where N is spore numbers, K is the estimated maximum number of spores, a is a constant of integration defining the position of the curve in relationship to the axis, r_m is the innate capacity of increase, or rate, t is time, and exp is the base of natural logs. The logistic equation is very flexible and as noted by Caughley and Birch (7), "when r_m is below about 0.3 it [the logistic equation] often provides a good empirical fit to the growth of a population whose dynamics are entirely different from those implied by the derivation of the logistic equation. It can, therefore, be justified as a first approximation on pragmatic grounds, as long as a tolerable fit is not misinterpreted to indicate that population processes and logistic assumptions are congruent."

The logistic equation aids in the analysis of data on spore production by estimating the rate of increase in spore numbers and by estimating the maximum number of spores produced in a particular environment.

In the analysis of the spore production data of a *Septoria* spp., it would be useful to have a statistic which would estimate total sporulation throughout the growing season. Area under the sporulation curve is such a statistic since it is an integration of the function describing the change of spore numbers with time. But area under the curve has been used little in studying epidemics of plant pathogens. Van der Plank (63) suggested the use of area under the rust severity curve for studying the relationship between yield loss and disease severity, and area under the disease progress curve has been used to study slow rusting in wheat and barley (29,66).

The disadvantages of area under the curve are: (A) two different epidemics (*e.g.* an epidemic that began early and developed slowly versus one that began late and developed rapidly) may give similar areas under the curve, and (B) area under the curve has been used so little that it may be difficult for many people to interpret the data. Both of these disadvantages may be overcome by reference to appropriate illustrations of the sporulation curves.

The advantages of area under the curve are: (A) it is a single statistic that summarizes the changes in spore populations over the whole growing season, (B) it is very useful in comparing the behavior of a pathogen within and between growing seasons, and (C) because areas can be added, which cannot be done with rates, they can be used to study the cumulative effects of different treatments.

The present study was done to study the population dynamics of *Septoria avenae* f. sp. *triticea, S. nodorum*, and *S. tritici* on spring wheat and barley and on winter wheat and to determine the relative effects of plant parts, plant maturity, and environment on the development of natural epidemics of *Septoria* spp.

Materials and Methods

Experimental Cultivars, Plots, and Design

Natural epidemics of *S. avenae triticea, S. nodorum*, and *S. tritici* were studied at the University of Minnesota Agriculture Experimental Station under routine farming practices. The station is situated at Rosemount, Minnesota, in corn, soybean, and wheat farmland composed of a dark loam soil.

Two spring wheat cultivars (*Triticum aestivum* L.), one spring barley cultivar (*Hordeum vulgare* L.), and one winter wheat cultivar (*T. aestivum* L.) were used. The spring wheats, "Chris" (C.I. 13751), a tall awnless cultivar, and "Era" (C.I. 13986), an awned semidwarf, have been popular in Minnesota during the last 15 years. Both are resistant to the prevalent races of *Puccinia graminis* f. sp. *tritici*, are moderately susceptible to leaf rust, and are moderately susceptible to the three *Septoria* spp. The spring barley, "Larker" (C.I. 10648), a moderately tall, awned, six-row malting cultivar, widely grown in the midwestern U.S., is resistant to stem rust and susceptible to leaf rust and to *S. avenae triticea* and *S. nodorum*. The winter wheat "Cheyenne" (C.I. 8885), widely grown in the U.S. for many years, is susceptible to stem and leaf rust and to *S. avenae triticea* and *S. nodorum*; it is moderately resistant to *S. tritici* in the glasshouse.

Because sporulation of the three *Septoria* spp. was observed on naturally-infected plants, there was no control on the occurrence of a particular species. Thus, the main trends in sporulation of the three species were determined by observing them in replicated plots of the cultivars during 1972, 1973, and 1974.

During the last week in April each year, Chris, Era, and Larker were sown at the rate of 84.1 kg of seed per ha in 2.44 m × 4.88 m plots in a field which had been sown to wheat each year since 1962. The plots were replicated three times in a 3 × 3 completely-randomized design with a 4.88 m border of Era wheat sown between them. In mid-September of 1971 and 1972, Cheyenne winter wheat was sown in a 4.88 m × 42.67 m strip in an area where natural epidemics of the three *Septoria* spp. were known to occur. The center of the strip was divided into three 2.44 m × 4.88 m plots. In 1974, observations were made on plants sampled from Cheyenne planted in border rows around a winter wheat nursery.

All plots and the border rows were fertilized with 70.72 kg per ha of a fertilizer mixture, 10:20:20 (nitrogen:phosphorus:potassium). Two herbicides, Dacthal (dimethyl 2,3,4,6-tetrachloroterephthalate) applied in early May, and 2-4-D (2,4-dichlorophenoxyacetic acid) applied in late May or early June, were used to control weeds.

Sampling and Assessment of Disease and Pathogen

Each sample consisted of the primary tiller from 10 plants selected at random from each plot. Samples, taken at 7 to 10-day intervals throughout the growing season beginning in May, were brought back to the laboratory where the percentage of the leaf area that was necrotic was determined using the scale of James (27), and the number of spores of the *Septoria* spp. was counted. Disease assessment was made only on the primary tillers because of the variability in growth stage, size, and maturity of the other tillers. Unless otherwise stated, disease measurements were expressed on a per-plant basis and refer to the amount of disease on the primary tiller of the plant. Leaf necrosis data were taken only in 1973 and 1974. Similar procedures were used to sample Cheyenne in 1974.

The presence of each *Septoria* spp. was determined by counting pycnidiospores. Before these spores were counted, the organs of the primary tillers were bulked into upper, middle, and lower leaves, stems, and heads. The upper leaves consisted of the flag leaf and the leaf below the flag leaf. The middle leaves consisted of the two middle leaves of the spring cultivars and the four middle leaves of the winter wheat cultivar. The lower leaves consisted of the three lowest leaves of the spring cultivars and the four lowest leaves of the winter wheat cultivar. The plant parts were then soaked for 4 hours, in a known volume of water containing enough Tween 20[R] to make a 0.1

percent solution. The volume of water for soaking the tissues was adjusted according to the bulk of the particular tissue being examined. Lactophenol cotton-blue was added 1 hour after soaking began, to stain spores and to prevent spore germination. Previous experiments had indicated that the maximum number of spores were extruded from pycnidia during the first 4 hours of soaking in water-Tween 20 solution.

At the end of the soaking period, the spore suspensions were shaken by hand to make a uniform suspension of spores, and four subsamples (each 0.02 ml) were removed with the aid of a Hamilton Microliter Syringe[R]. Each subsample was placed on a glass slide and sealed under a 22-mm square coverglass with nailpolish diluted 1:1 by volume with acetone. In each subsample, the spores of each *Septoria* spp. were counted in ten fields of a ×20 flat-field Achromat-objective of a Nikon microscope equipped with ×10 eyepiece. Since spores per microscope field, volume of solution under a field, number of plant parts, and volume of soaking solution were known, the number of spores of each *Septoria* spp. per plant part was calculated. Each mean in the results represents a mean of 12 subsamples (3 replicates × 4 subsamples). The variability associated with this spore counting technique was estimated in a preliminary experiment. The coefficient of variation (standard deviation × 100/grand mean) between subsamples varied between 13.5 and 36.0 percent, with a mean of 22.23 ± 1.14 percent. This estimate of the variation of the spore counting procedure was similar to the variation observed by Johnson and Bowyer (30), for spore counts of *Puccinia striiformis*.

The size, shape, and septation of spores were used to identify the *Septoria* spp. Spores of *S. tritici* were thinnest (1 to 2 μ) and longest (35 to 98 μ) of the three species, where as spores of *S. nodorum* were shortest (15 to 32 μ) (58). Spores of *S. avenae triticea* were intermediate in length (26 to 42 μ) (58) and contained three septa.

Measurement of Plant Growth and Development

In each sample plant development was assessed by measuring the height, growth stage, and the area of the leaves on the tallest tiller. In 1974 the percentage of ground area covered by plants was also estimated. Growth stage was estimated using the Romig scale (Figure 1).

In a preliminary study, leaf area was significantly linearly correlated with the product of leaf length and maximum width. The linear regression coefficients (b_0 and b_1) for the linear relationship between leaf area and length × width were estimated for each cultivar by measuring 100 leaves of different sizes and relating the values of length × width to the measured leaf area of each leaf. The linear regression coefficients are given in Table 1. Therefore, the length and width of each leaf of the primary tiller was measured and leaf areas were then calculated by substituting the product of leaf lengths and widths into linear regression equations of the form:

leaf area = $b_0 + b_1$ (length × width)

where: b_0 and b_1 are linear regression coefficients.

Table 1. Linear regression coefficients (b_0 and b_1), correlation coefficient (r), number of observations (n), and ranges of the independent variable (the product of leaf length and width), and the dependent variable (leaf area) for the linear equations relating the product of leaf length and width to leaf area for four cereal cultivars.

					Range	
					Length × width	
Cultivar[a]	b_0	b_1	r	n	(cm)	Leaf area (cm^2)
Chris	0.27	0.74	0.99	100	2.4 to 30.3	0.9 to 24.0
Era	1.00	0.65	0.92	100	0.3 to 35.6	0.4 to 26.1
Larker	1.18	0.63	0.95	100	0.9 to 44.4	1.1 to 31.2
Cheyenne	0.48	0.75	0.95	100	0.8 to 29.0	0.6 to 23.0

[a]Chris and Era spring wheat, Larker spring barley and Cheyenne winter wheat.

Figure 1. The Romig scale for assessment of the growth stages of cereal plants.

Stage	Description
1	One shoot
2	Beginning of tillering
3	Tillers formed, leaves often twisted spirally. In some varieties of winter wheats, plants may be 'creeping' or prostrate
4	Beginning of the erection of the pseudo-stem, leaf-sheaths beginning to lengthen
5	Pseudo-stem (formed by sheaths of leaves) strongly erected
6	First node of stem visible at base of shoot
7	Second node of stem formed, next-to-last leaf just visible
8	Last leaf visible, but still rolled up; head beginning to swell
9	Ligule of last leaf just visible
10	Boot stage, sheath of last leaf completely grown out, head swollen but not yet visible
11	Awns just showing
12	Heading—¼ of heading process completed
13	Heading—½ of heading process completed
14	Heading—¾ of heading process completed
15	Heading—95 percent of heads out of sheath
16	Beginning of flowering
17	Flowering—complete to top of head
18	Flowering—complete to base of head
19	Kernels near middle of head ⅛ formed
20	Kernels near middle of head ¼ formed
21	Kernels near middle of head ½ formed
22	Kernels near middle of head ¾ formed
23	Kernels fully formed, contents watery
24	Early milk
25	Milk
26	Late milk
27	Early dough
28	Mid-dough—kernel soft but dry
29	Late dough—kernel hard but not ripe
30	Ripe
31	Harvest

Courtesy of Dr. R. W. Romig, Northrup King Co., Minneapolis, MN, unpublished.

Analyses of Data
Moving averages

When a process like sporulation is measured over time, the measurements obtained include a local constant for the underlying process(es) and random fluctuations, *i.e.*

$$N_{mt} = N_{at} + e_t$$

where: N_{mt} = number of spores measured at time 't';
N_{at} = number of spores actually occurring at time 't';
e_t = error term at time 't' with an average value of zero;
$t = 1, 2, ..., n$

The commonly used technique of the 'moving average' or 'running mean' was used to estimate N_{at} (5). A moving average of two was computed by average successive pairs of data to give a new sequence of n-1 observations. The sequence of moving averages of two were then used in further analyses.

Fitting a logistic equation

A logistic equation (35) was fitted to the change in the number of spores of the *Septoria* spp. per plant over time:

$$dN_t/dt = r_m N_t[(K - N_t)/K] \quad [1]$$

where: N_t = number of spores per plant at time 't';
t = sampling time;
r_m = intrinsic rate of increase;
K = upper asymptote or maximal value of N_t in that particular environment (estimated maximum sporulation).

On integration:

$$N_t = K/[1 + \exp(a - r_m t)] \quad [2]$$

where: N_t, r_m and K = as before;
a = a constant of integration defining the position of the curve in relationship to the origin; and
exp = 2.71828 (base of natural logarithms).

The nonlinear regression coefficients of the logistic equation were used to estimate delay of an epidemic. Delay was the number of days from planting to half the estimated maximum sporulation (hereafter ½K). Substituting ½K into equation [2] and rearranging, we have:

$$\exp(a - r_m t_{1/2K}) = (K - \tfrac{1}{2}K)\tfrac{1}{2}K$$

Taking natural logs of both sides and rearranging:

$$t\tfrac{1}{2}K = (a - 1n[(K - \tfrac{1}{2}K)/\tfrac{1}{2}K])/r_m$$

Since

$$1n[(K - \tfrac{1}{2}K)/\tfrac{1}{2}K] = 0,$$

$$t_{1/2K} = a/r_m \quad [3]$$

'Delay' was estimated by equation [3].

The logistic equation was fitted to running means of numbers of spores of each *Septoria* spp. per plant using the FORTRAN IV program NLWOOD, as detailed by Daniel and Wood (12). The program calculates estimates of the coefficients of the nonlinear logistic equation by an iterative technique, utilizing Marquardt's maximum neighborhood method, the Gauss (Taylor Series) method, and the steepest descent method. The program was set for a maximum of 20 iterations; generally the coefficients were estimated within six iterations. The program was tested and found accurate using data in Table 14 of Krebs (35) and in Table 3 of Appendix I of Gause (19).

Calculation of area under the sporulation curve

Area under the curve is given by:

$$\text{Area} = \int_{t_1}^{t_h} f(x)$$

where: t_1 = first sampling date,
t_h = harvest sampling date,
$f(x)$ = some function describing change of spore numbers with time.

Since f(x) is often not known and, if known, cannot often be integrated, area under the sporulation curve was estimated by summing weighted datum observations to effect an area integration. This was done using the FORTRAN IV subroutine AREA and the associated subroutine INTEG given in Bevington (3). The matrices were inverted using the subroutine INVERT of Davies (13). Accuracy of INVERT was tested using the program TEST of Cooley and Lohnes (11). The AREA subroutine is very flexible; it utilizes observations at unequal time intervals and has the option of fitting linear and higher degree polynomials to the data. Details on how subroutine AREA calculates area under a set of data points, is given in Bevington (3).

A first order polynomial fit between successive data pairs was found to give satisfactory approximation to various sporulation curves found in this study. The accuracy of the program, using first order polynomials between successive data points, was tested using functions of known area. Area of the test examples estimated by the program was within 8 percent, and in most cases within 3 percent, of the calculated area.

Calculation of relative expansion rate of leaves.

The relative expansion rate (RER) of leaves was used as a measure of plant development. The relative expansion rate involves factors affecting the supply of new materials (physiological activity) as well as internal correlation mechanisms, meristematic activity and the mechanisms involved in the origin of new organs and leaf extension (15). The relative expansion during the growing season can be divided into a constant phase in the early stages of plant development, when the supply of new material predominates, and a declining phase, when there is a decrease in the new dry matter that can be converted to new leaf area as the plant architecture becomes more complex (15). The relative expansion rate of leaves was calculated using the formula given in Evans (15).

$$RER = (1n\ LA_{n+1} - 1n\ LA_n)/(t_{n+1} - t_n)$$

where: RER = relative expansion rate,
LA = leaf area at sampling dates n and n+1,
t_n = time of the nth sampling,
t_{n+1} = time of the (n+1)th sampling,
1n = natural logs

Linear correlation analysis

Matrices of simple correlation coefficients between variables, paired in all combinations, were calculated using the computer program BMD 03D (14).

In multiple correlation analysis, multiple and partial correlation coefficients were calculated using the

computer program BMD 03R (14). The square of the multiple correlation coefficient (the coefficient of determination) is the proportion of the variation in one variable (Y) that is accounted by the variation of several independent variables (X_1 to X_3). The partial correlation coefficient is a measure of the association between Y and a single variable, when the other variables are held constant (*e.g.*, between Y and X_1, with X_2 and X_3 held constant) (60). For correlation analysis the numbers of spores of each of the three *Septoria* spp. per leaf were transformed by the $\sqrt{x + \frac{1}{2}}$ transformation (60), and temperature was weighted for its effect on fungal development. The method for calculating weighted temperature is given later.

Analysis of variance

Where appropriate, the significance of differences between main effects (cultivars, plant parts, *Septoria* spp., and years) was determined by the least squares factorial analysis of variance using the computer program BMC 08V (14). Data for the spring wheat and barley cultivars were analyzed separately from those for the winter wheat cultivar. The estimated coefficients of the logistic equation for the two spring wheat and the spring barley cultivars were analyzed in a 3 (cultivars) × 2 (*Septoria* spp.) × 3 (years) factorial analysis of variance, while areas under the sporulation curves were analyzed in a 3 (cultivars) × 2 (*Septoria* spp.) × 5 (plant parts) × 3 (years) factorial analysis of variance. Since the data for the winter wheat cultivar in 1974 were collected from border rows, they were not included in the analysis of variance. The estimated coefficients of the logistic equation for the winter wheat cultivar were analyzed in a 3 (*Septoria* spp.) × 2 (years) factorial analysis of variance. Areas under the sporulation curves were analyzed in a 3 (*Septoria* spp.) × 5 (plant parts) × 2 (years) factorial analysis of variance.

Measurement of rainfall and temperature

Rainfall and temperature information was recorded at the office of the Agricultural Experiment Station at Rosemount located a mile north of the experimental plots.

Linearization of the temperature response curve

Winter wheat is exposed to sub-optimal temperatures for the growth and development of plant and pathogen during the long, cold winters of Minnesota. This cold period must be taken into consideration when studying sporulation of *Septoria* spp. on winter wheat. Thus, it would be useful to weight temperature according to its effect on fungal growth.

Figure 2a shows the temperature responses of *S. nodorum and S. tritici*; no data were available on the effect of temperature on *S. avenae* f. sp. *triticea*. The data for the figure were taken from several different sources in the literature where information is given on the effect of temperature on infection, germination, and growth. Because of the diversity of the data, response to temperature was expressed relative to the maximum relative response observed in the particular study so that in all cases the maximum relative response was one, and the minimum relative response was zero. The correlation coefficient of the third degree polynomial fitted to the data, and representing the temperature response curve, was highly significant ($P \leq 0.01$, $n = 103$). The fitted temperature response curve was typically bell shaped, but skewed towards lower temperatures (Figure 2a).

As can be seen from Fig. 2a, the response of a *Septoria* spp. to a particular temperature range (say 5° C) was proportional to the area under the temperature response curve. That is, the response was proportional to the integral of the fitted third degree polynomial:

$$\int_{t}^{t+5} 0.1348 - 0.0335x + 0.0062x^2 - 0.0001x^3$$

for a 5° C temperature range. Areas under the fitted polynomial, for the 5° C temperature range from 0 to 40°C, are given in Table 2. These areas were used to weight temperature according to its effect on fungal growth.

Weights were calculated by expressing each area under the temperature response curve as a proportion of the area under the optimal 5° C temperature range and are given in Table 2. Thus the temperatures in the optimal 5° C range were not weighted, while temperatures in the suboptimal 5° C ranges were weighted proportional to their effect on fungal growth. The relative response plotted against weighted temperature (temperature in a particular 5° C range multiplied by the weight for that particular temperature range) is given in Figure 2b. The relative response was significantly ($P \leq 0.01$, $n = 102$) linearly related to weighted temperature. The scatter of points about the linear regression line would be considerably less if the data had not been taken from such diverse sources, or if the weights were calculated for temperature ranges less than 5° C.

In this study daily average temperature was weighted by the appropriate weight (*i.e.* weighted temperature = average temperature in 5° C temperature range 'i' × weight for 5° C range 'i') using a program written in FORTRAN IV. The weighted temperatures were cumulated from day of planting to harvest. If the cumulative weighted temperature is di-

Table 2. Area under the temperature response curve shown in Fig. 2a and the weights for the 5°C temperature ranges indicated.[a]

5°C Temperature range	Area under the temperature Response curve	Weight
less than 0	0	0
0 to 5	0.4911	0.1214
5 to 10	0.8788	0.2173
10 to 15	1.9751	0.4884
15 to 20	3.2178	0.7957
20 to 25	4.0441	1
25 to 30	3.8918	0.9623
30 to 35	2.1981	0.5435
35 to 40	0	0

[a]Area under the temperature response curve and the weight are in arbitrary units.

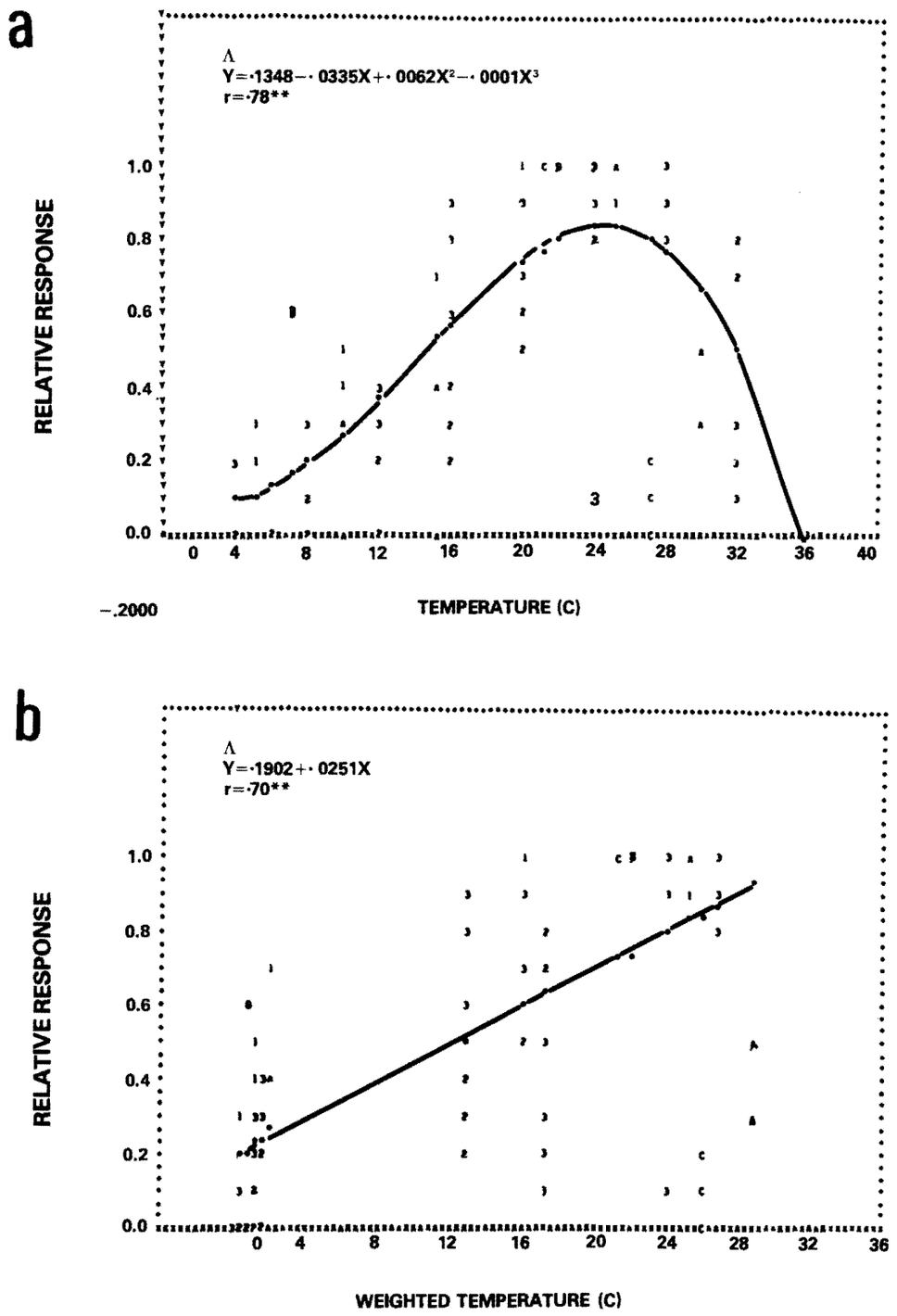
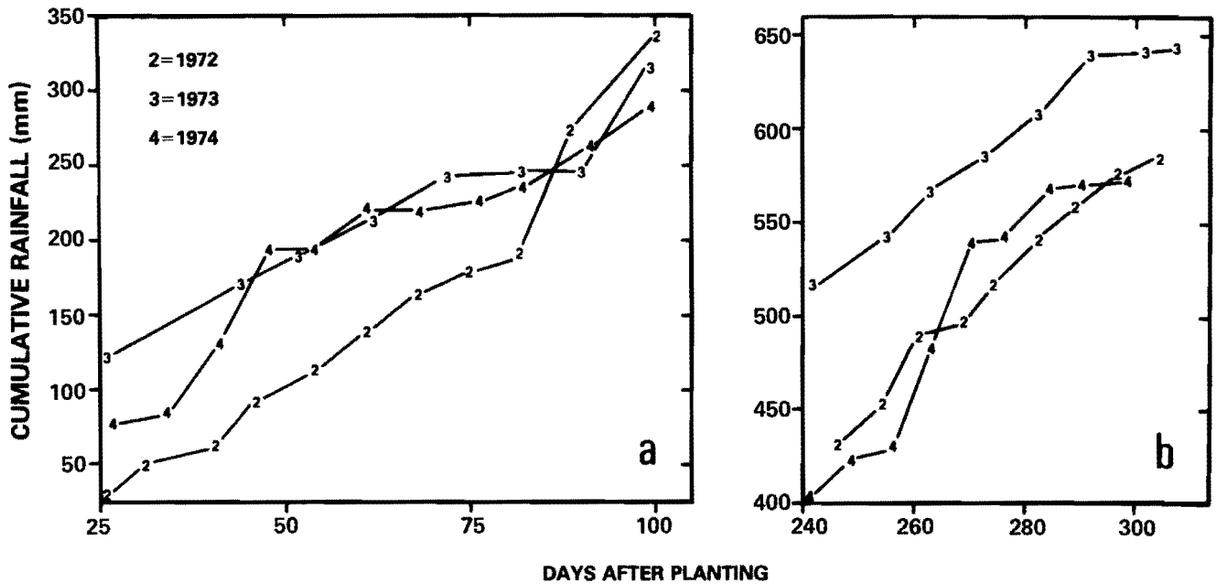


Figure 2ab. A plot of data from the literature, expressed on a relative scale from zero to one, of (A) the repsonse of *Septoria nodorum* and *S. tritici* to temperature in centigrade and (B) the relative response versus weighted temperature. Meaning of symbols: 1—latent period of *S. nodorum* (49), 2—germ tube growth of spores of *S. nodorum* (62), 3—growth of *S. nodorum* on agar (62), A—growth of *S. tritici* on agar (1), B—infection of *S. tritici* on leaves (17), and C—infection of *S. tritici* on leaves (36). Not all points are plotted. Where more than one point coincides, only one symbol is plotted. The full line indicates values of relative response fitted to the data.

Figure 3ab. Cumulative rainfall (in mm) for the sampling days for (A) the spring wheat and barley cultivars and (B) the winter wheat cultivar. See Tables 5 and 6 for growth stage of the cultivars on the days after planting.



vided by the number of days over which it was cumulated, one has weighted temperature degree-days.

Linearization of the growth stage curve

When the growth stages through which a plant passes as it matures are plotted, a typical sigmoid curve is formed and it conforms to the logistic equation. The maximum value for plant growth in this study was 31, or harvest, (Figure 1). Therefore,

$$GS_t = 31/[1 + \exp(a - r_m t)]$$

where: GS_t = the growth stage at sample time t
r_m = growth rate coefficient
a = a constant of integration defining the position of the curve in relationship to the origin.
exp = 2.71828 (base of natural logarithms)

Since it is easier to work with a linear function, the equation was rearranged to:

$$\ln[(31 - GS_t)/GS_t] = a - r_m t$$

which is analogous to the general form of linear regression equation:

$$Y = b_0 - b_1 t.$$

Using linear regression of $\ln[(31 - GS_t)/GS_t]$ against time, t, estimates of a and rate were obtained. Linear correlation coefficients for the linearized growth stage curves for the four cultivars and the three years, varied between .975 and .999. The estimated time to any particular growth stage was calculated using the linearized growth stage curve.

Variation in Rainfall

Spring wheat and barley growing season

Cumulative rainfall, recorded from early May to early August of 1972, 1973, and 1974, is given in Figure 3a. The amount of rain which fell from early to mid-May varied with the year; the least amount fell during 1972, the most during 1973. An intermediate amount fell in 1974. During early June to mid-July, or 40 to 80 days after planting, the cumulative rainfall in 1973 and 1974 was about the same, but it was about 70 mm less in 1972. At the end of each of the growing seasons, total rainfall was similar; the difference between the two extreme years (1972 and 1974) was only 51 mm.

The distribution of rain within a given season varied greatly from year to year (Figures 3a and 4). In 1972 there were frequent showers in May and June with about 14 ± 4 mm of rain per shower; in July the showers were also frequent but they averaged about 38 ± 6 mm per shower (Figures 3a and 4).

The pattern of consistent rain throughout 1972 is also seen in the monthly distribution of the number of rainy days and the number of hours that rain fell (Table 3).

In 1973 the greatest amount of rain fell early in the growing season (Figure 3a). Cumulative rainfall increased steadily until early July, 72 days after planting, when spring wheat kernels were just beginning to form and spring barley kernels were in the early dough growth stage. There was a dry period in mid-July, followed by heavy showers towards the end of July (Figure 4).

Winter wheat growing season

Cumulative rainfall, from mid-September to mid-July of 1971-1972, 1972-1973, and 1973-1974, is given in Figure 3b. The greatest amount of rain, not including snow melt, was in 1972-1973. The rainfall in 1972-1973 and 1973-1974 was about 65 mm less than that for 1972-1973.

Table 3. The number of days and hours during which rain fell in each month of 1971-1972, 1972-1973, and 1973-1974.

Month	1971-1972 Days	1971-1972 Hours	1972-1973 Days	1972-1973 Hours	1973-1974 Days	1973-1974 Hours
September	5	30	5	25	8	22
October	12	73	12	49	6	17
November	10	107	5	20	6	35
December	13	35	9	57	14	42
January	7	15	4	22	6	10
February	5	22	5	31	8	52
March	7	60	7	26	9	29
April	16	65	13	70	9	33
May	11	38	14	67	12	59
June	10	29	13	33	10	43
July	20	65	10	19	8	13
August[a]	4	9	1	4	3	20
Mean	10±1	46±8	8±1	35±6	8±1	31±4

[a]First week of August only.

In 1971-1972 there was relatively continuous rain to support the development of *Septoria* spp. all season (Figure 3b). In 1972-1973, there was enough rain to support the *Septoria* spp. from mid-May to the beginning of July, the time when winter wheat was in early dough. There was little rain after early July, 1973 (Figures 3b and 4). Even though cumulative rainfall at the end of 1973-1974 was similar to that in 1971-1972, the distribution of rainfall throughout the two seasons differed greatly (Figure 3b). In comparison to the 1971-1972 season when rain fell more or less continuously throughout the season, heavy showers fell in the 1973-1974 season between the end of May to the end of June, when the kernels were just beginning to form in the heads. Little rain fell after the end of June, 1974 (Figures 3b and 4).

Variation in Temperature

Spring wheat and barley growing season

Cumulative weighted temperature at different sampling dates after planting is given in Figure 5a. The 1972 season was the warmest, and 1973 the coolest. At the beginning of each season cumulative weighted temperature differed greatly, but at the end of the seasons it was about the same each year.

Winter wheat growing season

The 1971-1972 season was the warmest and the 1972-1973 season the coolest (Figure 5b).

Plant Growth Between Years

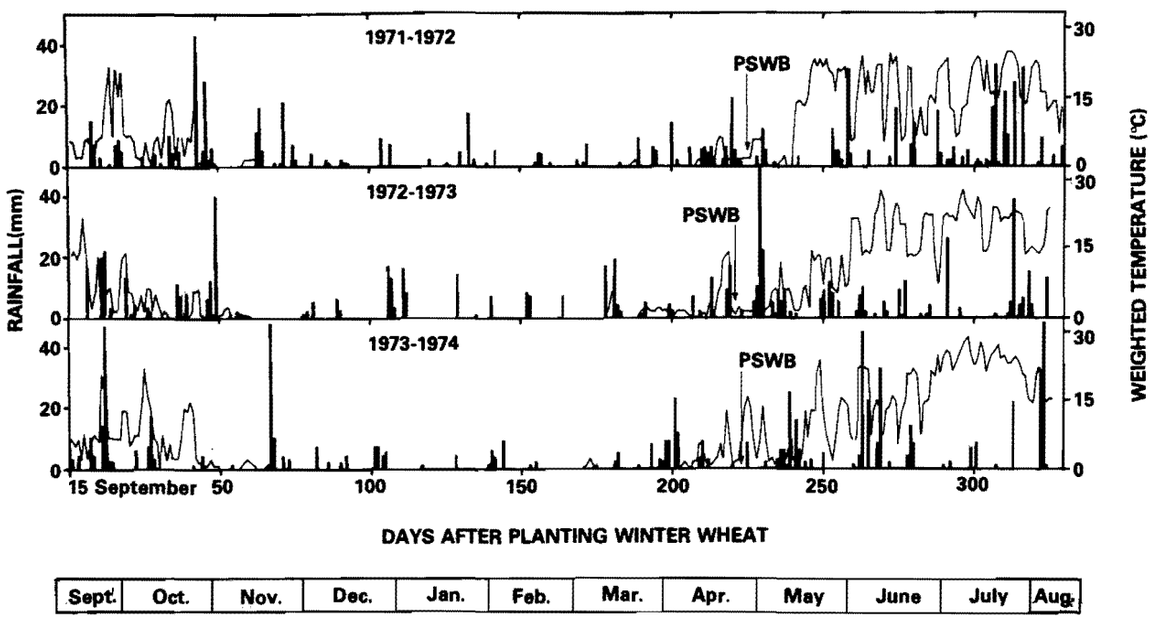
The period of plant growth in days from planting to the boot or beginning of flowering growth stages is presented in Table 4. These growth stages were chosen because infection by the *Septoria* spp. during this period greatly affects grain development (56). In 1972 the growth stages occurred seven days earlier than in

Table 4. Days from planting to boot or beginning of flowering growth stages for the four cultivars in three years.

Cultivar[a]	1972 Boot	1972 Flower	1973 Boot	1973 Flower	1974 Boot	1974 Flower
Chris	50	61	60	68	53	63
Era	52	61	58	66	55	66
Larker	43	53	48	57	49	58
Cheyenne	256	265	264	273	260	272

[a]Chris and Era spring wheat, Larker spring barley, and Cheyenne winter wheat.

Figure 4. Daily fluctuations in rainfall in mm (bars) and weighted temperature in °C (continuous line) for the 1971-1972, 1972-1973, and 1973-1974 growing seasons at Rosemount, Minnesota. PSWB indicates planting of spring wheat and barley.



1973 and about five days earlier than in 1974, because 1972 was the warmest of the three seasons (Figure 5). The growth stages at each of the sampling dates in 1972, 1973, and 1974 are given in Tables 5 and 6.

Results

Sporulation of Septoria spp. on Spring Wheat and Barley

Septoria avenae f. sp. *triticea* and *S. nodorum* were observed on spring wheat and barley each year of the 3 years of study, but *S. tritici* was not seen. Each *Septoria* spp. was found on winter wheat each year of the study. The annual trends in sporulation of the *Septoria* spp. on spring wheat and barley are graphically summarized in Figure 6. Growth stage data are summarized in Table 5.

Septoria avenae triticea was first seen on both Chris and Era spring wheats between 40 and 60 days after planting (Figure 6). Rapid increase in sporulation occurred 75 to 85 days after planting when the plants were approximately at the late milk growth stage. Total sporulation of *S. avenae triticea* on Chris was greatest in 1974 and least and about equal in 1972 and 1973, respectively (Figure 6). In contrast to this, total sporulation on Era was greatest in 1973 and 1974, and least in 1972 (Figure 6).

Sporulation of *S. avenae triticea* on Larker barley was similar to that on spring wheats. It was first seen between 40 and 70 days after planting and then it

Table 5. Growth stage (according to the Romig scale) of Chris and Era spring wheat and Larker spring barley at certain dates and days after planting.

			Growth stage		
Year	Date	Days after planting	Chris	Era	Larker
1972	May 21	26	2	1	2
	May 27	32	3	2	4
	June 4	40	5	4	7
	June 10	46	8	8	13
	June 18	54	12	12	21
	June 24	60	18	18	25
	July 2	68	22	22	26
	July 8	74	24	24	27
	July 15	81	26	26	28
	July 22	88	28	28	29
	August 3	100	29	30	30
1973	June 3	42	2	3	5
	June 13	52	6	7	12
	June 23	62	10	12	22
	July 3	72	20	20	27
	July 13	82	26	26	28
	July 21	90	28	28	29
	July 30	99	30	30	30
1974	May 20	26	2	2	2
	May 28	34	4	4	4
	June 4	41	6	5	6
	June 11	48	7	6	8
	June 17	54	8	8	10
	June 25	62	10	9	16
	July 1	68	17	15	23
	July 9	76	23	22	27
	July 15	82	26	24	28
	July 24	91	28	28	30
	August 2	100	30	30	31

Figure 5ab. Cumulative weighted temperature (in °C) for the sampling days for: (A) the spring wheat and barley cultivars and (B) the winter wheat cultivar. See Tables 5 and 6 for the growth stages of the cultivars on the days after planting.

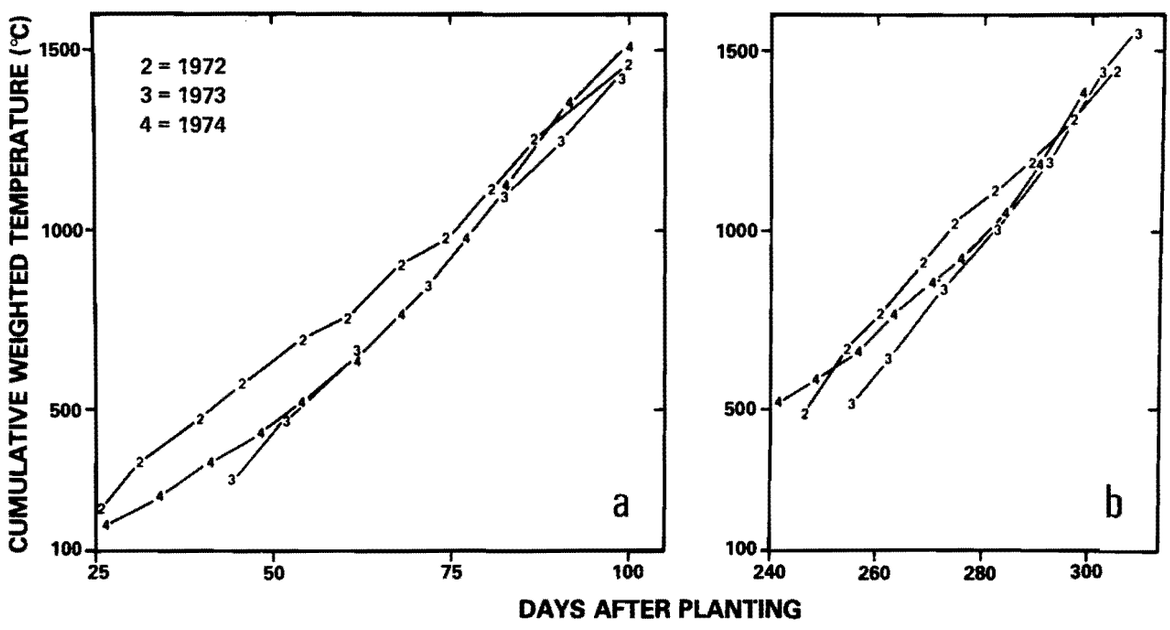


Table 6. Growth stage (according to the Romig scale) of Cheyenne winter wheat on certain dates and days after planting.

Year	Date	Days after planting	Growth Stage
1972	May 17	246	6
	May 25	254	8
	May 31	260	11
	June 8	268	16
	June 14	274	24
	June 22	282	27
	June 28	288	28
	July 6	296	29
	July 14	304	30
1973	May 24	252	6
	June 3	262	8
	June 13	272	12
	June 23	282	20
	July 3	292	27
	July 13	302	29
	July 19	308	30
1974	May 12	240	5
	May 20	248	6
	May 28	256	8
	June 4	263	9
	June 11	270	12
	June 17	276	17
	June 25	284	21
	July 1	290	24
	July 9	298	28

increased rapidly about 25 days later (Figure 6). In contrast to sporulation of *S. avenae triticea* on spring wheats, the highest level of sporulation on barley occurred in 1972 and the least in 1974.

The difference in sporulation of *S. avenae triticea* on barley and wheat in different years probably was due to the fact that in 1972 barley was severely infected with *Puccinia hordei* Otth., but there was very little leaf rust in 1973 and 1974. Barley plants infected with *P. hordei* are more susceptible to *S. avenae triticea* than are rust-free plants (53).

Spores of *S. nodorum* were first detected on Chris and Era spring wheats 40 days after planting in both 1972 and 1973, when the first node was just visible (Figure 6, Table 5). Sporulation increased rapidly after the boot growth stage, about 40 days after planting. In 1974 spores were first observed 50 days after planting and the rapid increase in sporulation did not occur until about 25 days later, when the kernels were fully formed and their contents watery. Sporulation of *S. nodorum* on Chris and Era was greatest in 1973 and least in 1974; sporulation was intermediate in 1972 (Figure 6).

Sporulation on Larker barley each growing season followed the same trends as that on spring wheats. However, it was less in 1974 than in the other two years and less than on the spring wheats (Figure 6). It was greatest in 1972, probably because of the presence of leaf rust (64).

Sporulation of Septoria spp. on Winter Wheat

The annual trends in sporulation of the *Septoria* spp. on Cheyenne winter wheat are graphically summarized in Figure 7. Growth stage data are summarized in Table 6.

In each year of the study *S. avenae triticea* was first seen on Cheyenne about 260 days after planting when plants were in the early-boot growth stage (Figure 7). Sporulation did not increase until after heading, 275 to 280 days after planting. Sporulation of *S. avenae triticea* was greatest in 1973 and least in 1972.

Sporulation of *S. nodorum* on Cheyenne varied considerably from year to year (Figure 7). In 1973 it decreased between 252 and 272 days from planting when the plants were elongating, and increased thereafter. In 1974 sporulation began about 250 days after planting but did not rapidly increase until after flowering, 275 days after planting. Very little sporulation of *S. nodorum* was observed in 1972.

Sporulation of *S. tritici* on Cheyenne differed greatly from that observed for the other two species of *Septoria*. In 1972 and 1974 sporulation of *S. tritici* was greatest early in the season, when plants were beginning to elongate and the flag leaf and leaf below the flag leaf were developing, about 250 days after planting, but it generally decreased thereafter (Figure 7). The pattern of sporulation of *S. tritici* observed in 1973 differed greatly from that in 1972 and 1974. Sporulation increased to a maximum between 270 and 290 days after planting, when the plants were at the heading to early dough growth stage, but it decreased thereafter.

Quantitative Differences in Estimated Maximum Sporulation

The maximum number of spores of the *Septoria* spp. produced per primary tiller each year was estimated by the K coefficient of the logistic equation (Table 7). Analysis of variance indicated that the differ-

Table 7. Estimated maximum number of spores of *Septoria avenae* f. sp. *triticea*, *S. nodorum*, and *S. tritici* on the primary tillers of four cereal cultivars in 1972, 1973, and 1974.

Septoria spp.	Year	Cultivar[a]			
		Chris	Era	Larker	Cheyenne
S. avenae triticea	1972	41±27[b]	16± 6	87± 38	116± 48
	1973	149± 4	377±20	356±182	601±452
	1974	50± 4	32± 7	22± 4	59[c]
	Mean[d]	80±19	142±59	155± 74	316±199
S. nodorum	1972	86±16	66±31	21± 1	105± 42
	1973	190±36	240±56	110± 73	651± 17
	1974	64± 7	33± 8	9± 3	885
	Mean	113±23	113±37	47± 26	450±127
S. tritici[e]	1972				664± 420
	1973				196± 20
	1974				700
	Mean				468±186

[a]Chris and Era spring wheat, Larker spring barley and Cheyenne winter wheat.

[b]Data are K values for a logistic equation fitted to sporulation curves of each *Septoria* spp. Each value is the mean ± standard error of the mean of three replicates ($\times 10^3$).

[c]Measurements of sporulation made on one replicate.

[d]Mean ± standard error of the mean of three replicates in each of three years ($\times 10^3$).

[e]*S. tritici* was not observed on the spring cultivars.

Figure 6. Number of spores of *Septoria avenae triticea* and *S. nodorum* per primary tiller of Chris and Era spring wheats and of Larker spring barley in 1972, 1973, and 1974. See Table 5 for exact growth stages.

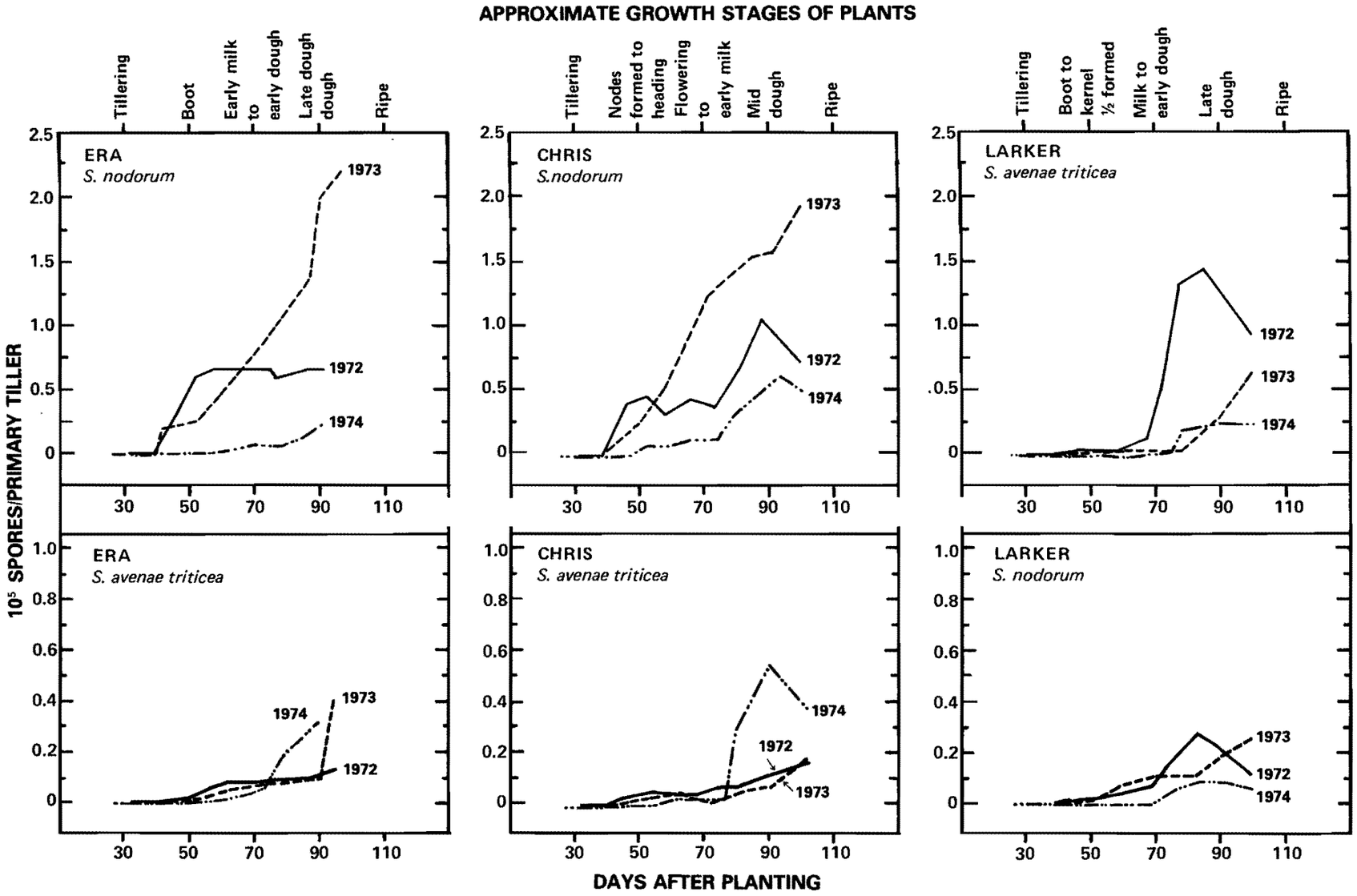
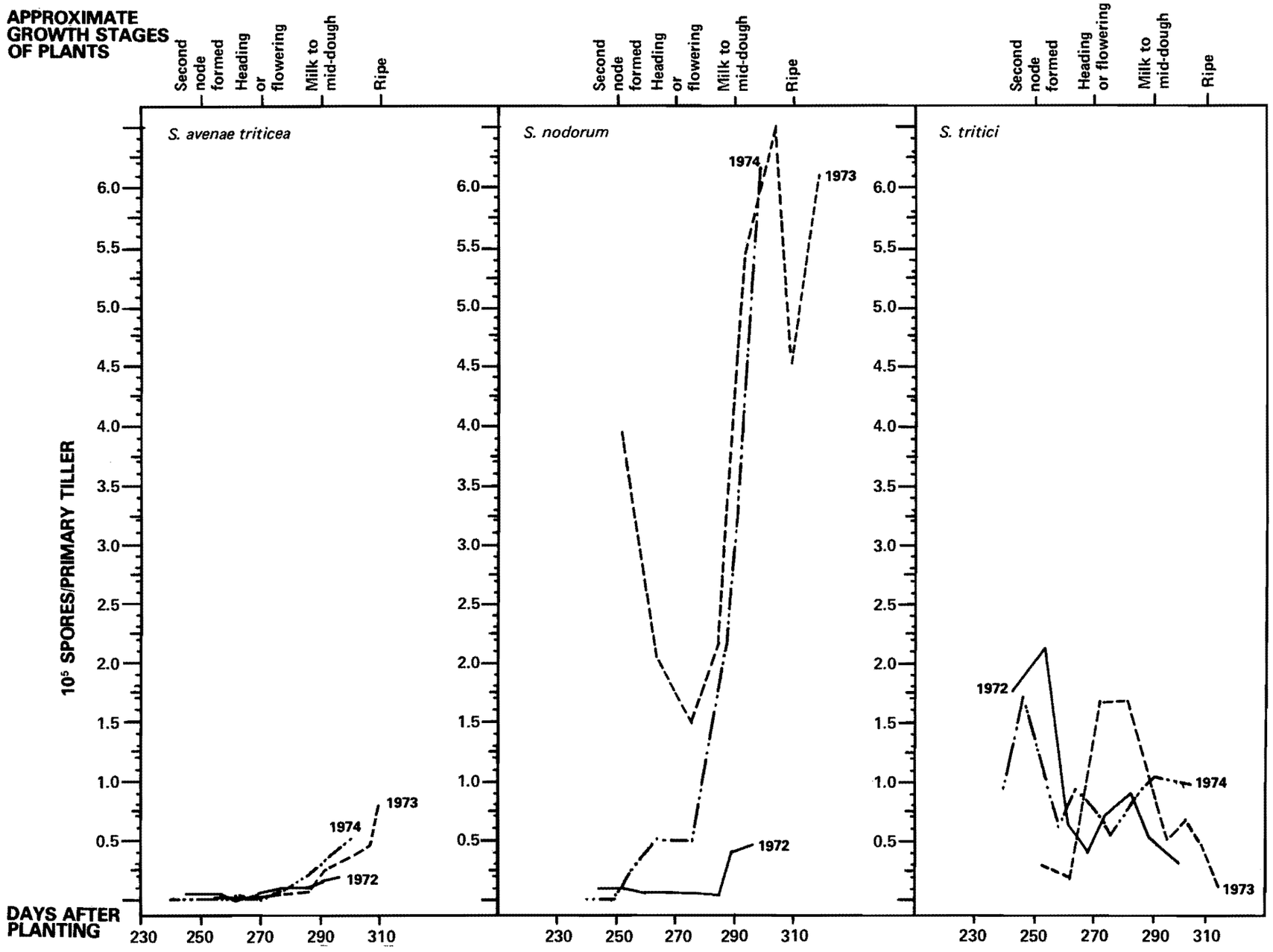


Figure 7. Number of spores of *Septoria avenae* f. sp. *triticea, S. nodorum* and *S. tritici* per primary tiller of Cheyenne winter wheat in 1972 , 1973, and 1974 . See Table 6 for exact growth stages.



ences in estimated maximum sporulation of *S. avenae triticea* and *S. nodorum* were significant on the spring wheats and barley ($P \leq 0.01$) between years, but not between cultivars and *Septoria* spp. On the winter wheat cultivar Cheyenne, the differences in maximum sporulation were not significant between years or *Septoria* spp.

On the spring wheats, the estimated maximum sporulation of *S. avenae triticea* was greatest in 1973 (Table 7). There were no consistent differences in maximum sporulation on spring wheat and barley. Maximum sporulation on Cheyenne winter wheat was consistently greater than on the spring wheats.

The estimated maximum sporulation of *S. nodorum* was greatest in 1973, on both spring wheat cultivars. Sporulation was consistently less on Larker barley than on the spring wheats (Table 7). The estimated maximum sporulation of *S. nodorum* was consistently greater on winter wheat than on the spring wheats and barley.

No *S. tritici* was observed on the spring wheat cultivars. On winter wheat, the least amount of sporulation of *S. tritici* was observed in 1973, which is in contrast to the sporulation of *S. avenae triticea* and *S. nodorum*.

Quantitative Differences in Estimated Intrinsic Rate of Sporulation

Analysis of variance indicated that the intrinsic rate of sporulation (Table 8) varied significantly between years ($P \leq 0.01$), but not between cultivars or *Septoria* spp.

The mean intrinsic rate of sporulation of *S. avenae triticea* and *S. nodorum* was least in 1973 and greatest in 1974. There were no consistent trends in the rate on the spring wheat and barely cultivars, but on winter wheat it was about half that observed on the spring cultivars (Table 8).

In contrast to the rates of sporulation by *S. avenae* and *S. nodorum,* which were positive, the rates of sporulation by *S. tritici* were all negative (Table 8), a reflection of the decrease in sporulation of this species as the season progressed (Figure 7).

Quantitative Differences in Estimated Delay of Sporulation

The delay in sporulation, defined as the period from planting to half the estimated maximum sporulation, indicates when in the growing season the greatest increase in sporulation occurred (Table 9). Because sporulation of *S. tritici* declined as the growing season progressed (Figure 7), delays were not calculated for this species.

Analysis of variance indicated that the difference in delay between years and *Septoria* spp. were significant ($P \leq 0.01$) in spring cultivars, but not in the winter wheat cultivar.

Delay in sporulation by *S. avenae triticea* on all cultivars was greatest in 1973 (Table 9). On Larker barley, the delay was about nine days less than on spring wheats, and each year on all cultivars it occurred after flowering.

Table 8. Mean estimated rates of increase per day of *Septoria avenae* f. sp. *triticea*, *S. nodorum* and *S. tritici* on four cereal cultivars in 1972, 1973, and 1974.

Septoria spp.	Year	Cultivar[a] Chris	Era	Larker	Cheyenne
S. avenae triticea	1972	.330±.231[b]	.071±.014	.271±.046	.071±.003
	1973	.070±.006	.110±.012	.160±.025	.104±.016
	1974	.196±.009	.550±.243	.332±.075	.195[c]
	Mean[d]	.198±.077	.244±.104	.254±.036	.103±.018
S. nodorum	1972	.423±.311	.369±.042	.252±.033	.097±.032
	1973	.170±.054	.133±.019	.131±.068	.104±.014
	1974	.186±.022	.186±.024	.331±.117	.151
	Mean	.260±.100	.229±.039	.238±.050	.108±.015
S. tritici[e]	1972				−.068±.012
	1973				−.149±.002
	1974				−.011
	Mean				−.094±.021

[a]Chris and Era spring wheat, Larker spring barley, and Cheyenne winter wheat.

[b]Data are K values for a logistic equation fitted to sporulation curves of each *Septoria* spp. Each value is the mean ± standard error of the mean of three replicates ($\times 10^3$).

[c]Measurements of sporulation made on one replicate.

[d]Mean ± standard error of the mean of three replicates in each of three years ($\times 10^3$).

[e]*S. tritici* was not observed on the spring cultivars.

Table 9. Estimated mean delay in sporulation (days from planting to half the estimated maximum sporulation) of *Septoria avenae* f. sp. *triticea* and *S. nodorum* on four cereal cultivars in 1972, 1973, and 1974.

Septoria spp.[b]	Year	Cultivar[a] Chris	Era	Larker	Cheyenne
S. avenae triticea	1972	83±23	80±12	75± 1	315±12
	1973	133± 3	121± 3	106± 8	324±14
	1974	82± 3	81± 1	80±0.1	289[c]
	Mean[d]	100±11	94± 8	87± 5	315± 8
S. nodorum	1972	60± 9	47± 3	71± 1	305± 20
	1973	72± 7	76± 4	104± 24	283±0.3
	1974	83± 1	82± 2	77± 2	293
	Mean	71± 5	68± 6	84± 9	294± 9

[a]Chris and Era spring wheat, Larker spring barley, and Cheyenne winter wheat.

[b]Data are K values for a logistic equation fitted to sporulation curves of each *Septoria* spp. Each value is the mean ± standard error of the mean of three replicates ($\times 10^3$).

[c]Measurements of sporulation made on one replicate.

[d]Mean ± standard error of the mean of three replicates in each of three years ($\times 10^3$).

Delay in sporulation by *S. nodorum* on all cultivars was 2 to 41 days less than that for *S. avenae triticea* (Table 9). On the spring wheats, the delay was greatest in 1974, when it occurred after the plants were in the milk growth stage, and least in 1972, when it occurred after the plants were in the boot growth stage. On barley the delay was about 15 days greater than for spring wheat. The delay was greatest in 1973 and least in 1972, and it occurred after the plants were in the dough growth stage each year.

Development of the Septoria spp. on Plant Parts

To understand in greater detail the development of the three *Septoria* spp. within a growing season, the

relationship between leaf necrosis and sporulation by the *Septoria* spp. was determined on lower, middle and upper leaves, and on stems and heads. Data were collected on all cultivars in each year of the study, but since conclusions were similar for all cultivars each year, only data for Era, Larker, and Cheyenne for 1973 are illustrated in Figures 8 to 10.

General trends in changes in the percentage of the leaf area that was necrotic in 1973 are given in Figure 8.

For both Era wheat and Larker barley, the lowest increase in the percentage of necrotic tissue was on the lowest leaves and greatest on the upper leaves; necrosis increased from 20 to 100 percent in about 35 days on the lowest leaves, but the same change in the percentage of necrosis occurred in only 15 days on the upper leaves (Figure 8). Leaves were 100 percent necrotic 10 days earlier on Larker barley than on Era wheat.

At the commencement of sampling of Cheyenne winter wheat in 1973, the lowest leaf layer was nearly dead (Figure 8). Leaf necrosis increased more rapidly on the upper leaves of winter wheat than on the middle leaves.

The curves, representing the trends in sporulation on the leaves, stems and heads, given in Figures 9 and 10, are cumulative curves for sporulation on successive plant parts, so that the final curve represents the change of sporulation per plant, with time. The spaces under the curves indicate the effect of the plant parts on the sporulation of the *Septoria* spp.

On both Era wheat and Larker barley, sporulation of *S. avenae triticea* on the lowest leaves increased until about 75 days after planting, by which time the leaves were completely necrotic (Figure 8), but decreased thereafter (Figure 9). Sporulation of *S. avenae triticea* increased on the middle leaves of spring wheat about 20 days earlier than on barley. Sporulation of *S. avenae triticea* on the middle leaves of spring wheat increased until the leaf area was about 50 percent necrotic, with little change thereafter. On the upper leaves, the greatest increase in sporulation of *S. avenae triticea* occurred after the 85th day from planting, when about 20 percent of the leaf area was necrotic and when spring wheat and barley were at the milk and mid-dough growth stages, respectively. For both spring wheat and barley, the rapid increase in sporulation of *S. avenae triticea* late in the season (Figure 6) was due to sporulation on the upper leaves and stems (Figure 9).

On Cheyenne winter wheat, there was little sporulation of *S. avenae triticea* on the lowest leaves (Figure 10). Sporulation on the middle leaves increased until 305 days from planting, by which time the leaves were dead, but decreased thereafter. On the upper leaves the greatest increase in sporulation occurred after about 280 days from planting, when plants had completed flowering. The rapid increase in sporulation of *S. avenae triticea* late in the season (Figure 7) occurred primarily on the upper leaves (Figure 10).

The sporulation of *S. nodorum* differed greatly from that observed for *S. avenae triticea* on Era wheat and Larker barley (Figure 9). Most of the sporulation of *S. nodorum* was on the lower and middle leaves, whereas most of the sporulation of *S. avenae triticea* was on upper leaves. Sporulation of *S. avenae triticea* was on upper leaves. Sporulation of *S. nodorum* on the lower and middle leaves increased until the leaves were dead; then it decreased (Figures 8 and 9). The decline of sporulation of *S. nodorum* on dead leaves was most pronounced on spring wheat.

Figure 8. Percentage of leaf area that was necrotic on the lower (L), middle (M), and upper (U) leaves of primary tillers of Era spring wheat, Larker spring barley, and Cheyenne winter wheat in 1973. See Tables 5 and 6 for exact growth stages.

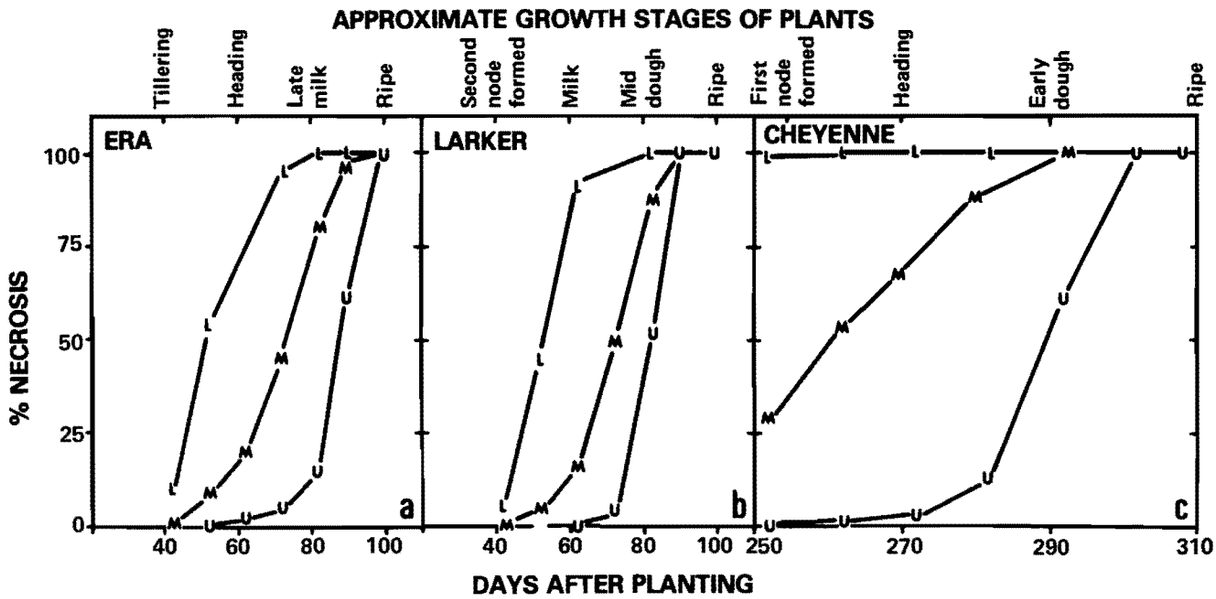


Figure 9. Cumulative number of spores of *Septoria avenae* f. sp. *triticea* and *S. nodorum* on the lower (L), middle (M), and upper (U) leaves, stem (S) and head (H) of primary tillers of Era spring wheat and Larker spring barley in 1973. Cumulative sporulation is indicated by: 1=L, 2=L+M, 3 + L+M+U, 4= L+M+U+S, and 5= L+M+U+S+H. See Table 5 for exact growth stages.

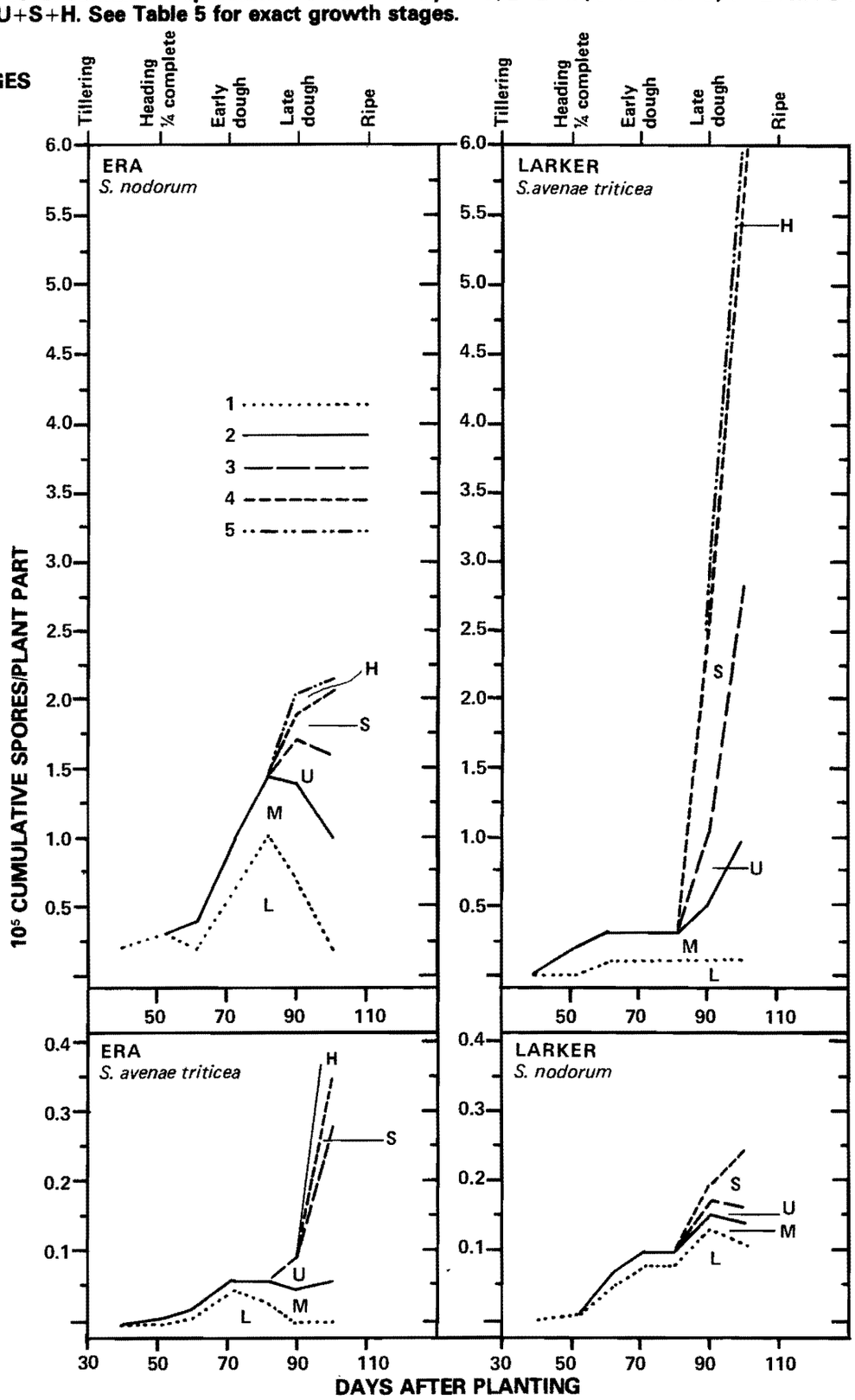
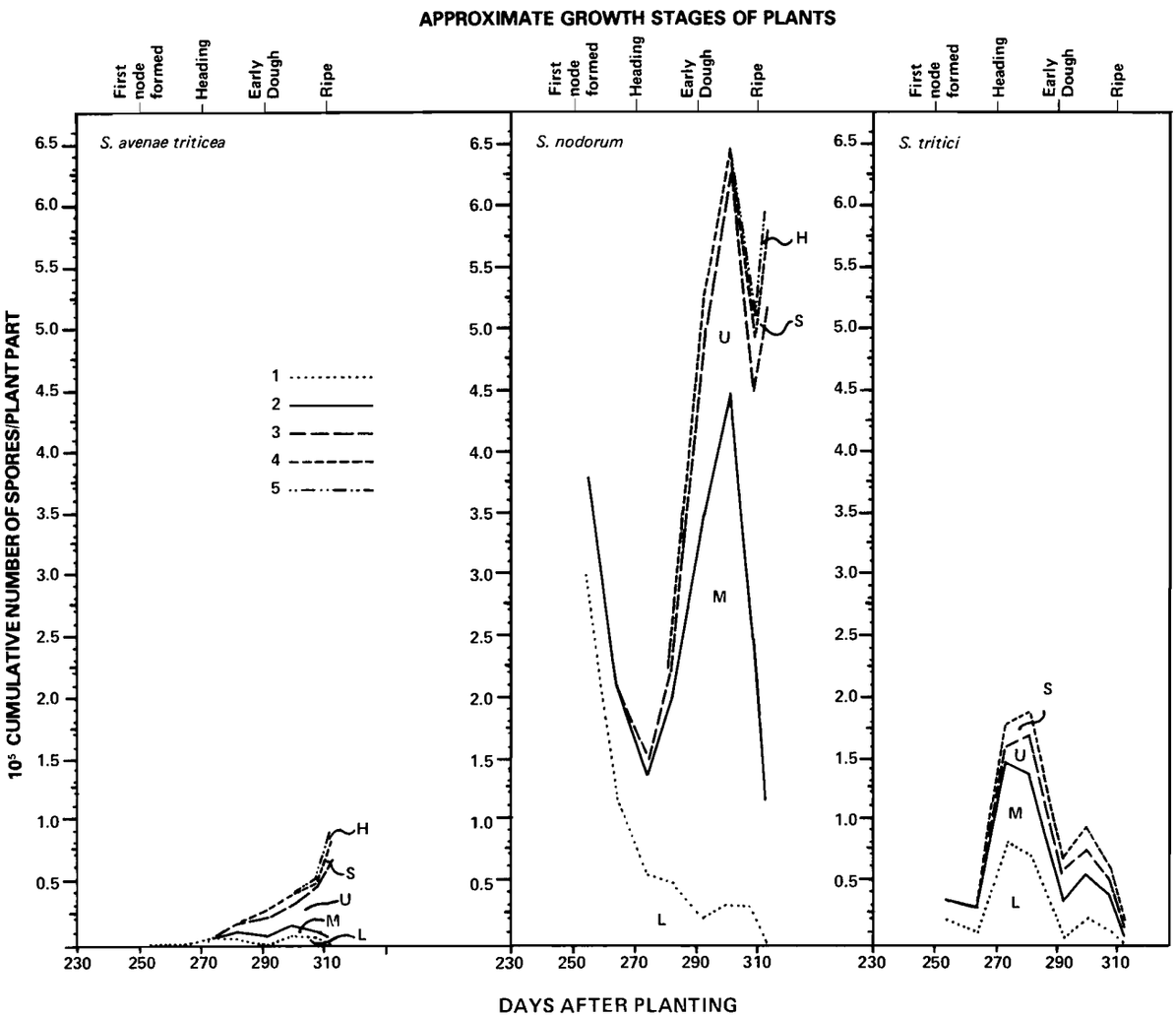


Figure 10. Cumulative number of spores of *Septoria avenae* f. sp. *triticea*, *S. nodorum*, and *S. tritici* on the lower (L), middle (M) and upper (U) leaves, stem (S) and head (H) of primary tillers of Cheyenne winter wheat in 1973. Cumulative sporulation is indicated by: 1 = L, 2 = L+M, 3 = *LMU*, 4 = *LMUS*, and 5 = L+M+U+S+H. See Table 6 for exact growth stages.



On the lowest leaves of Cheyenne winter wheat, sporulation of *S. nodorum* was greatest very early in the 1973 growing season, but decreased with each successive sampling until the end of the growing season (Figure 10); the lowest leaves were dead during this time (Figure 8). On the middle leaves, sporulation decreased initially (Figure 10) and then increased until about the 300th day from planting, and then rapidly decreased, when the middle leaves were dead (Figure 8). Sporulation of *S. nodorum* on the upper leaves increased until after 300 days from planting and decreased thereafter (Figure 10), when the leaves were dead (Figure 8). The increase in sporulation of *S. nodorum* between the 270th and 300th day from planting (Figure 7), was due to sporulation on middle and upper leaves (Figure 10).

Sporulation of *S. tritici* increased on all leaves of Cheyenne winter wheat in 1973, and was maximum about 270 days after planting (Figure 10). Maximum sporulation was 20 to 30 days earlier than that of the other two species (Figure 10). Sporulation of *S. tritici* decreased on all leaves beginning on about the 280th day after planting until the end of the growing season (Figure 10), during which time nearly all leaves were dead (Figure 8).

Quantitative Differences in the Sporulation of the Septoria spp. on Different Plant Parts

The area under the sporulation curve was used to quantitatively compare total sporulation of the Septoria spp. on the different plant parts (Tables 10 to 13).

For spring cultivars, analysis of variance indicated that the differences between years, *Septoria* spp., cultivars, and plant parts were highly significant ($P \leq 0.01$). On partitioning differences between spring cultivars, there were no significant differences between the

spring wheats, but the difference between them and the spring barley cultivar was significant ($P \leq 0.01$). For the winter wheat cultivar, differences between years, *Septoria* spp., and plant parts were significant ($P \leq 0.01$).

Most of the sporulation of *S. avenae triticea* on Chris and Era spring wheats occurred on the leaves, with little or none occurring on stems or heads (Tables 10 and 11). Most of the sporulation was on the middle or upper leaves, with only 16 percent occurring on the lower leaves.

Much of the sporulation of *S. avenae triticea* on Larker spring barley occurred on the upper and middle leaves, with most of it being on the upper leaf layer in 1972 and 1973 (Table 12). Sporulation of *S. avenae triticea* on the lower leaves was less than that on

Table 10. Area under the sporulation curves of *Septoria avenae* f. sp. *triticea* and *S. nodorum* on the plant parts of the spring wheat cultivar Chris in 1972, 1973, and 1974.

Plant part	1972	1973	1974	Mean[b]
S. avenae triticea				
Lower leaves	66± 24[a]	76± 21	45± 18	62± 12
Middle leaves	68± 10	79± 6	394±104	180± 61
Upper leaves	159± 64	53± 5	466± 45	226± 66
Stem	20± 8	8	0	9± 4
Head	25± 12	0	0	8± 5
S. nodorum				
Lower leaves	733±242	2942±733	163± 48	1280± 479
Middle leaves	1264±281	1574±173	600± 16	1146± 172
Upper leaves	1139± 93	698±330	377± 57	738± 149
Stem	95± 17	241± 52	0	112± 38
Head	55± 8	0	0	18± 9

[a]Each value is the mean area (in arbitrary units) ± standard error of the mean of three replicates ($\times 10^3$).
[b]Mean ± standard error of the mean of three replicates in each of three years ($\times 10^3$).

Table 11. Area under the sporulation curves of *Septoria avenae* f. sp. *triticea* and *S. nodorum* on the plant parts of the spring wheat cultivar Era in 1972, 1973, and 1974.

Plant part	1972	1973	1974	Mean[b]
S. avenae triticea				
Lower leaves	55± 17[a]	73± 44	73± 23	67± 16
Middle leaves	110± 22	110± 28	144± 29	122± 14
Upper leaves	114± 10	145± 7	97± 11	122± 8
Stem	14± 5	34± 13	0	16± 6
Head	21± 5	5	0	9± 4
S. nodorum				
Lower leaves	1315±381	2423±337	77± 23	1272± 369
Middle leaves	1259±756	1824±289	173± 38	1085± 337
Upper leaves	616±308	624±165	71± 21	437± 136
Stem	131± 36	432±113	0	188± 73
Head	62± 25	6± 6	0	23± 12

[a]Each value is the mean area (in arbitrary units) ± standard error of the mean of three replicates ($\times 10^3$).
[b]Mean ± standard error of the mean of three replicates in each of three years ($\times 10^3$).

Table 12. Area under the sporulation curves of *Septoria avenae* f. sp. *triticea* and *S. nodorum* on plant parts of the spring barley cultivar Larker in 1972, 1973, and 1974.

Plant part	1972	1973	1974	Mean[b]
S. avenae triticea				
Lower leaves	65± 12[a]	64± 16	15± 2	48± 10
Middle leaves	786±219	100± 12	252± 32	379± 122
Upper leaves	1561±209	126± 47	63± 34	583± 252
Stem	612±252	270± 17	93± 15	325± 105
Head	230± 70	7± 4	0	79± 43
S. nodorum				
Lower leaves	51± 5	376± 86	12± 7	147± 63
Middle leaves	133± 4	57± 19	169± 55	120± 24
Upper leaves	300± 34	18± 14	5± 4	108± 49
Stem	118± 16	51± 16	27± 27	65± 17
Head	20± 6	0	0	7± 4

[a]Each value is the mean area (in arbitrary units) ± standard error of the mean of three replicates ($\times 10^3$).
[b]Mean ± standard error of the mean of three replicates in each of three years ($\times 10^3$).

Table 13. Area under the sporulation curves of *Septoria avenae* f. sp. *triticea*, *S. nodorum*, and *S. tritici* on plant parts of the winter wheat cultivar Cheyenne in 1972, 1973, and 1974.

Plant Part	1972	1973	1974[b]	Mean[c]
S. avenae triticea				
Lower leaves	47± 5[a]	44± 12	0	39± 8
Middle leaves	41± 7	174± 28	350	142± 44
Upper leaves	226± 11	673± 45	242	420± 91
Stem	19± 2	128± 33	0	63± 26
Head	2± 0	3± 1	0	2± 1
S. nodorum				
Lower leaves	422± 27	4139±246	516	2028± 752
Middle leaves	370±106	12475±298	6026	6366±2292
Upper leaves	314± 27	4966±118	690	2362± 923
Stem	166± 32	1112±110	0	548± 205
Head	4± 1	12± 2	0	7± 2
S. Tritici				
Lower leaves	2635± 58	1992±141	2923	2400± 160
Middle leaves	1232±242	2457±154	2123	1884± 259
Upper leaves	869± 16	538± 14	655	696± 63
Stem	210± 58	175± 37	0	165± 38
Head	4± 2	0	0	2± 1

[a]Each value is the mean area (in arbitrary units) ±standard error of the mean of three replicates ($\times 10^3$).

[b]Measurements of sporulation made on one replicate.

[c]Mean ± standard error of the mean of three replicates in each of two years and the one observation in 1974 ($\times 10^3$).

stems, which was the opposite to that observed on spring wheats (Tables 10 to 12). As on spring wheats, the least amount of sporulation occurred on the heads.

As on spring wheats and barley, most of the sporulation of *S. avenae triticea* occurrred on the middle and upper leaves of Cheyenne (Table 13). There was no consistent difference between sporulation of *S. avenae triticea* on the lower leaves and stems; the least sporulation was on the heads.

Sporulation of *S. nodorum* on Era and Chris wheat was about 10 times that observed for *S. avenae triticea* (Tables 10 and 11). Most of the sporulation of *S. nodorum* occurred on the leaves, with the least on stems and heads. Unlike *S. avenae triticea*, most of the sporulation of *S. nodorum* tended to occur on the lower and middle leaves (Tables 10 and 11).

Sporulation of *S. nodorum* on Larker spring barley was about three times less than that for *S. avenae triticea*, with most of the sporulation occurring on the leaves (Table 12). The sporulation was least on heads; on stems it was intermediate.

Sporulation of *S. nodorum* on Cheyenne winter wheat was greater than that of *S. avenae triticea* (Table 13), as on spring wheat. Most of the sporulation of *S. nodorum* occurred on leaves of Cheyenne winter wheat, with the least amount on the heads, and an intermediate amount on the stems.

Septoria tritici was observed only on the winter wheat Cheyenne. The amount of sporulation was greatest on the lower and middle leaves and least on heads (Table 13).

Interaction Between Environment, Plant Growth, and Sporulation of the Septoria spp.

Simple linear correlation coefficients for the relationship between sporulation by the *Septoria* spp. and plant growth and climatological variables are given in Tables 14 to 16. The data for the three years of the study were pooled for the correlation analysis.

All of the simple linear correlation coefficients for the relationship between sporulation of *S. avenae triticea* and *S. nodorum* on Chris and Era spring wheats, and the plant growth and climatological variables (Table 14) were highly significant ($P \leq 0.01$). The data for Chris and Era spring wheats were pooled because there was no significant difference in sporulation of *S. avenae triticea* and *S. nodorum* on these two cultivars. The correlation coefficients for the relationship between sporulation of *S. avenae triticea* and *S. nodorum* and the relative expansion rate of leaves were negative because the relative expansion rate decreased as the season progressed (Figure 11). On the spring wheat cultivars the greatest correlation coefficients were for the relationship between sporulation of *S. avenae triticea* and necrosis and temperature, and between sporulation of *S. nodorum* and growth stage and temperature.

The simple linear correlation coefficients for the relationship between sporulation of *S. avenae triticea* and *S. nodorum* on Larker spring barley (Table 15) were all significant ($P \leq 0.05$). The greatest correlation coefficients were between sporulation of either species and necrosis, temperature and growth stage, as was the case for the spring wheat cultivars.

Simple correlation coefficients for the relationship between sporulation of the three *Septoria* species on Cheyenne winter wheat and plant growth and climatological variables are given in Table 16. All the correlation coefficients for the relationship between sporulation of *S. avenae triticea* and plant growth, rainfall, temperature, and necrosis were highly significant ($P \leq 0.01$) with the coefficients for the relationship between sporulation of *S. avenae triticea* and necrosis, temperature and growth stage being the greatest. The correlation coefficients for the relationship between

Figure 11. Relationship between percentage of ground area covered by plant parts (■), plant height (●), leaf relative expansion rate (RER) in cm² per day (▲), and sporulation of *Septoria avenae* f. sp. *triticea* (○), *S. nodorum* (□), and *S. tritici* (△) on Era spring wheat, Larker spring barley, and Cheyenne winter wheat in 1974. Data on percentage of ground area covered by plant parts were not taken for Cheyenne. See Tables 5 and 6 for exact growth of stages.

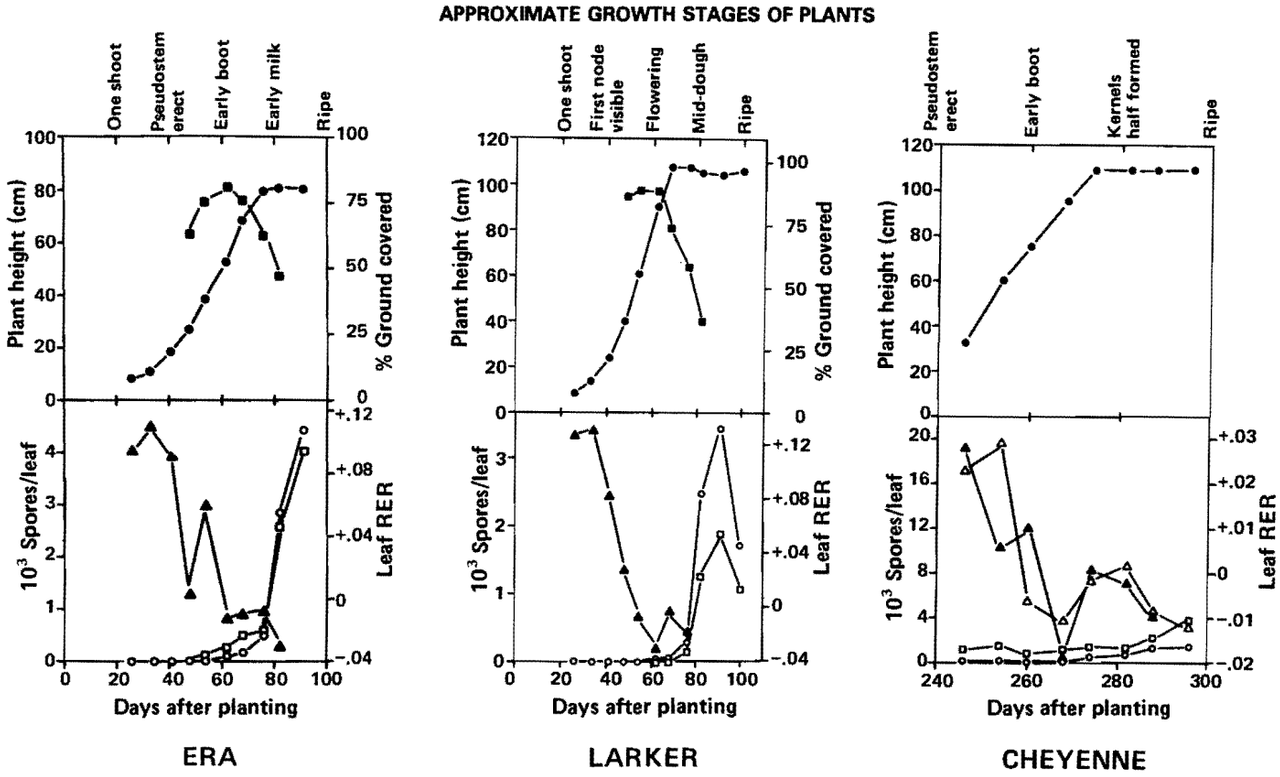


Table 14. Simple correlation coefficients for the linear relationship between sporulation of *Septoria avenae* f. sp. *triticea* and *S. nodorum* on Chris and Era spring wheat and variables indicated.

Variable	Spores of *S. avenae triticea* per leaf	Spores of *S. nodorum* per leaf
Leaf relative expansion rate in cm² per day[a]	−0.64[d]	−0.61
Plant height[b]	0.72	0.72
Growth stage[b]	0.81	0.80
Cumulative rainfall after planting (mm)[b]	0.65	0.64
Cumulative weighted temperature after planting (°C)[b]	0.86	0.80
Percentage necrotic leaf area[c]	0.82	0.73
Number of spores of *S. avenae triticea* per leaf[b]	1	0.65

[a] n = 46.

[b] n = 57.

[c] n = 35.

[d] All correlation coefficients are significant at $P \leq 0.01$.

Table 15. Simple correlation coefficients for the linear relationship between sporulation of *Septoria avenae* f. sp. *triticea* and *S. nodorum* on Larker spring barley and the variables indicated.

Variable	Spores of *S. avenae triticea* per leaf	Spores of *S. nodorum* per leaf
Leaf relative expansion rate in cm^2 per day	−0.42*	−0.48*
Plant height[b]	0.43*	0.59**
Growth stage[b]	0.68**	0.84**
Cumulative rainfall after planting (mm)[b]	0.48*	0.63**
Cumulative weighted temperature after planting (°C)[b]	0.74**	0.88**
Percentage necrotic leaf area[c]	0.88**	0.95**
Number of spores of *S. avenae triticea* per leaf[b]	1	0.88**

**Indicates significance at $P \leq 0.01$.

*Indicates significance at $P \leq 0.05$.

[a]n = 22.

[b]n = 27.

[c]n = 17.

Table 16. Simple correlation coefficients for linear relationships between sporulation of *Septoria avenae* f. sp. *triticea, S. nodorum,* and *S. tritici* on Cheyenne winter wheat with the variables indicated.

Variable	Spores of *S. avenae triticea* per leaf	Spores of *S. Nodorum* per leaf	Spores of *S. tritici* per leaf
Leaf relative expansion rate in cm^2 per day[a]	−0.53**	−0.33	0.31
Plant height[b]	0.68**	0.40	−0.37
Growth stage[b]	0.81**	0.52**	−0.37
Cumulative rainfall after planting (mm)[b]	0.67**	0.74**	−0.46*
Cumulative weighted temperature after planting (°C)[b]	0.87**	0.62**	−0.29
Percentage necrotic leaf area[c]	0.94**	0.84**	−0.19
Number of spores of *S. avenae triticea* per leaf[b]	1	0.79**	−0.11
Number of spores of *S. nodorum* per leaf[b]		1	−0.01

**Indicates significance at $P \leq 0.01$.

*Indicates significance at $P \leq 0.05$, while numbers not followed by an asterisk indicate $P > 0.05$.

[a]n=18.

[b]n=24.

[c]n=16.

sporulation of *S. nodorum* and growth stage, rainfall, temperature, necrosis, and sporulation of *S. avenae triticea* were highly significant ($P \leq 0.01$), with the coefficients for the relationship between sporulation of *S. nodorum* and rainfall, necrosis, and sporulation of *S. avenae triticea* being the greatest. Sporulation of *S. tritici* was significant only for the relationship with rainfall. The coefficients for the relationship between sporulation of *S. tritici* and all the variables except leaf relative expansion rate, were negative because sporulation of *S. tritici* declined on Cheyenne winter wheat as the growing season progressed.

Relationship Between Percentage of Necrotic Leaf Area and Sporulation of the Septoria spp.

The results of multiple correlation analysis between the percentage of the leaf area that was necrotic and sporulation of the three *Septoria* species are presented in Table 17. In all cases the multiple correlation coefficients were highly significant ($P \leq 0.01$). With the exception of Larker data in 1974, the partial correlation coefficients for *S. nodorum* were consistently positive and significant, and, with the exception of Larker data in 1974 and Cheyenne data in 1973, were greater than those for *S. avenae triticea* and *S. tritici*. The only significant partial correlation coefficients for *S. avenae triticea* were for the Cheyenne data in 1973. The *S. avenae triticea* partial correlation coefficients were negative for the 1974 data of Chris and Era spring wheats and Cheyenne winter wheat, but they were positive for the other cultivars and years. The *S. tritici* partial correlation coefficients were positive for the Cheyenne winter wheat data in 1973, and negative and significant for the data in 1974.

Table 17. Partial correlation coefficients, sample size, and the multiple correlation coefficients for multiple correlation analysis between percentage of the leaf area that was necrotic and the number of spores of *Septoria avenae* f. sp. *triticea*, *S. nodorum*, and *S. tritici* per leaf of the cultivars.

Cultivar[a]	Year	Partial correlation coefficients			Sample size	Multiple correlation coefficients
		S. avenae triticea	*S. nodorum*	*S. tritici*[c]		
		$r_{y1.23}$[b]	$r_{y2.13}$	$r_{y3.12}$	no.	R
Chris and Era	1973	0.29	0.91**	–	14	0.98**
	1974	−0.40	0.61**	–	21	0.90**
Larker	1973	0.07	0.89**	–	7	0.96**
	1974	0.63	−0.46	–	10	0.95**
Cheyenne	1973	0.96**	0.94*	0.74	7	0.99**
	1974	−0.40	0.89**	−0.86*	9	0.99**

**Indicates significance at $P \leq 0.01$.

*Indicates significance at $P \leq 0.05$; numbers not followed by an asterik indicate $P > 0.05$.

[a]Chris and era spring wheat, Larker spring barley and Cheyenne winter wheat.

[b]Denotes the partial correlation of Y on X_1 for fixed values of the other variables.

[c]*Septoria tritici* was not observed on the spring cultivars.

Table 18. Partial correlation coefficients, sample size, and the multiple correlation coefficients for the multiple correlation analysis between the number of spores of *Septoria avenae* f. sp. *triticea*, *S. nodorum*, and *S. tritici*, per plant and temperature, growth stage, and rainfall.

cultivar[a]	Partial correlation coefficients			Sample size	Multiple correlation coefficients
	Temperature[c]	Growth stage[d]	Rainfall[e]		
	$r_{y1.23}$	$r_{y2.13}$	$r_{y3.12}$	No.	R
S. avenae triticea					
Chris and Era	0.56**	−0.27*	−0.24	57	0.88**
Larker	0.48*	−0.09	−0.27	27	0.77**
Cheyenne	0.52*	−0.18	−0.03	24	0.87**
S. nodorum					
Chris and Era	0.12	0.16	−0.04	57	0.80**
Larker	0.53**	0.07	−0.25	27	0.89**
Cheyenne	0.46*	−0.46*	0.55*	24	0.80**
S. tritici					
Cheyenne	0.44*	−0.42	−0.45*	24	0.61*

**Indicates significance at $P \leq 0.01$.

*Indicates significance at $P \leq 0.05$; numbers not followed by an asterisk indicate $P > 0.05$.

[a]Chris and Era spring wheat, Larker spring barley and Cheyenne winter wheat.

[b]Denotes the partial correlation of Y on X_1 for fixed values of the other variable.

[c]Cumulative weighted temperature in °C after planting.

[d]Growth stage according to scale in Figure 1.

[e]Cumulative rainfall in mm after planting.

Sporulation in Relation to Host Development

The relationship between plant development and sporulation of the *Septoria* spp. is graphically summarized in Figure 11. Since conclusions for all cultivars were similar, only data for Era and Larker for 1974, and Cheyenne for 1972 are illustrated in Figure 11. While leaves of the spring cultivars were rapidly expanding, there was little sporulation of *S. avenae triticea* or of *S. nodorum* (Figure 11). Sporulation did not increase until the relative expansion rate of leaves had decreased considerably, after the boot growth stage when the percentage of ground covered by plants began to decrease as stems elongated.

The relationship between sporulation of *S. avenae triticea* and *S. nodorum* and plant development for the winter wheat cultivar Cheyenne (Figure 11), was similar to that described for the spring cultivars. However, sporulation of *S. tritici* decreased as leaf relative expansion rate decreased.

Sporulation in Relation to Plant Growth Stage, Rainfall, and Temperature

The results of multiple correlation analysis between numbers of spores of the *Septoria* spp. per leaf and cumulative weighted temperature after planting, plant growth stage, and cumulative weighted rainfall after planting are given in Table 18. Simple correlation coefficients for the linear relationship between the variables used in the multiple correlation analysis are given in Tables 14 to 16. The correlation analysis was done on data for each crop pooled for the three years of the study. In all cases the multiple correlation coefficients were significant ($P \leq 0.05$). The partial correla-

Table 19. Coefficients of determination for the multiple correlation anaysis between sporulation of *Septoria avenae* f. sp. *triticea*, *S. nodorum*, and *S. tritici* and various combinations of temperature, growth stage, and rainfall.

Cultivar[a]	Model	*S. avenae triticea*	*S. nodorum*	*S. tritici*[e]
Chris and Era	TEMP[b]+GS[c]+RAIN[d]	0.76	0.65	
	TEMP+GS	0.75	0.65	
	TEMP+RAIN	0.75	0.64	
	GS+RAIN	0.66	0.64	
	TEMP	0.74	0.64	
Larker	TEMP+GS+RAIN	0.59	0.80	
	TEMP+GS	0.56	0.78	
	TEMP+RAIN	0.59	0.80	
	GS+RAIN	0.47	0.72	
	TEMP	0.55	0.77	
Cheyenne	TEMP+GS+RAIN	0.76	0.64	0.37
	TEMP+GS	0.76	0.49	0.21
	TEMP+RAIN	0.75	0.55	0.23
	GS+RAIN	0.75	0.54	0.21
	TEMP	0.76	0.38	0.08

[a]Chris and Era spring wheat, Larker spring barley and Cheyenne winter wheat.
[b]TEMP=Cumulative weighted temperature after planting (in °C).
[c]GS=Growth stage according to the scale in Figure 1.
[d]RAIN=Cumulative rainfall after planting (in mm).
[e]*Septoria tritici* was not observed on the spring cultivars.

tion coefficients for temperature were consistently positive and, with the exception of sporulation of *S. nodorum* on spring wheat, were significant.

For sporulation of *S. avenae triticea* on all cultivars, the partial correlation coefficients for temperature were consistently significant and greater than those for growth stage and rainfall. The partial correlation coefficients for growth stage were negative for sporulation of *S. avenae triticea* on all the cultivars, positive for sporulation of *S. nodorum* on the spring wheat and barley cultivars, and negative for sporulation of *S. nodorum* and *S. tritici* on winter wheat. With the exception for *S. nodorum* on Cheyenne winter wheat, the partial correlation coefficients for rainfall were negative.

Table 19 gives the coefficients of determination for the relationship between sporulation of the *Septoria* spp. and various combinations of the environmental variables. For sporulation of *S. avenae triticea* on all cultivars, and sporulation of *S. nodorum* on Larker spring barley, deletion of temperature from the model resulted in the greatest reduction in the coefficient of determination. For sporulation of *S. nodorum* on Cheyenne winter wheat, deletion of rainfall from the model resulted in the greatest reduction in the coefficient of determination. For sporulation of *S. nodorum* on spring wheat and for *S. tritici* on Cheyenne winter wheat, the deletion of temperature, growth stage, or rainfall resulted in about equal reduction in the coefficient of determination.

Discussion

During the three years of the study natural infection of spring wheat by *Septoria tritici* was not observed. This is in agreement with survey data which suggests that *S. tritici* rarely occurs on spring wheat in the upper midwestern United States. In Minnesota *S. tritici* was found in only three of 66 spring wheat fields surveyed in 1969 and 1970 (50). Hosford *et al.* (25) did not find the fungus on spring wheat in surveys in North Dakota in 1967, and Sprague and Fischer (59) found it to be "virtually absent" in this area of the midwestern U.S. *Septoria avenae* f. sp. *triticea* and *S. nodorum* were observed on spring wheat each year. All three species of *Septoria* were observed on winter wheat. This information suggests that the life cycle of *S. tritici* is basically different from that of *S. avenae triticea* and *S. nodorum* and an analysis of the differences in the winter and spring wheat growing seasons may give clues as to the reasons that *S. tritici* is so seldom observed on spring wheat.

The semidwarf wheats have been thought to be more susceptible than tall wheats to *Septoria* spp. (61). We saw no significant difference in the sporulation of *S. avenae triticea* and *S. nodorum* on the two spring wheat cultivars, Chris and Era. This suggests that, under Minnesota conditions, the tall stature of Chris, and the semi-dwarf stature of Era, had little effect on the sporulation of the two fungi.

Sporulation of *S. avenae triticea* and *S. nodorum* on Larker spring barley was significantly different from that on the spring wheats. Sporulation of *S. avenae triticea* was greater on barley than on spring wheat, even in years when the barley was not infected with leaf rust (*Puccinia hordei*). Sporulation of *S. avenae triticea* on rusted barley plants may be greater than on rust-free plants (53). The differences in *S. avenae triticea* sporulation on the two crops may be due to differences in susceptibility; in glasshouse tests Larker barley was more susceptible than Era wheat. Differences in the maturity of two crops may also have been important. In the field *S. avenae triticea* develops best on senescing tissue (31).

Sporulation of *S. nodorum* was less on barley than on spring wheat. This may have been because barley is probably less susceptible than spring wheat and because the plots were in a field that had been sown to wheat since 1962, which means that the *S. nodorum* present consisted of isolates adapted to wheat. Isolates of *S. nodorum* from wheat infect barley less readily than wheat (48).

Sporulation of all three *Septoria* spp. was greater on the winter wheat cultivar than the spring cultivars. Some factors that may have contributed to this include: A) the greater length of the winter wheat growing season than the spring growing season (300 days compared to 100 for winter and spring growing seasons, respectively), or B) the cool, wet conditions that occurred in March, April, and early May in Minnesota (Figure 4), when the winter wheat was tillering. Because *S. avenae triticea* and *S. nodorum* seem to develop best on senescing tissue, the earlier maturity

of the winter wheat, as compared to that of the spring cultivars (Tables 5 and 6), may also have been important.

Most of the sporulation of the three *Septoria* spp. occurred on leaves with little or none on heads. Sporulation on stems was intermediate between that on leaves and heads. In Minnesota head infection by the three *Septoria* spp. has rarely been observed. Symptoms of *S. avenae triticea* infection have been observed on barley heads at Crookston, Minnesota, during wet years. Occasionally symptoms of head infection by *S. nodorum* may be found in late maturing or in late planted seed-increase plots. In Minnesota heading begins in mid to late June (Table 5) so that the environmental conditions of late June and early July may be generally unfavorable for head infection by the three *Septoria* spp. That the amount of rain in July may be important is supported by the observation that the greatest amount of head infection was seen on the spring cultivars in 1972 (Tables 10 to 12), when the July weather was wetter than in the other two years of the study (Figure 4). In England, Hewett (21) concluded that the severity of seed-borne infection by *S. nodorum* was determined by the amount of rainfall in July.

Head infection by the *Septoria* spp. is probably of minor importance in Minnesota. Thus, in Minnesota the survival of the *Septoria* spp. on infected seed is probably not as important as survival on infected crop debris and wild grasses.

On spring wheat, the sporulation of *S. avenae triticea* was greatest after flowering due to the sporulation on the upper leaves. We have also noted a greater number of fields infected with *S. avenae triticea* when surveys were conducted after the plants had headed (50). Because this fungus increases so late in the growing season, it probably has little effect on yield, as suggested by Johnson (31). Sporulation by *S. nodorum* tended to increase earlier than that for *S. avenae triticea* and most of the sporulation occurred on the lower and middle leaves.

On spring barley the trends in sporulation by *S. avenae triticea* were similar to those observed on spring wheat. However, in contrast to wheat, sporulation by *S. nodorum* on barley tended to occur later than that for *S. avenae triticea*. As already noted, *S. nodorum* infects barley less readily than wheat. Because *S. avenae triticea* and *S. nodorum* occur so late in the season, they probably cause little yield reduction of barley in Minnesota.

On winter wheat the pattern of sporulation of *S. avenae triticea* and *S. nodorum* was similar to that observed for spring wheat. Whereas the greatest increase in sporulation by these two fungi was observed late in the season, the greatest sporulation of *S. tritici* occurred early in the season, and most of the sporulation of *S. tritici* was on the lowest leaves. Jenkins and Morgan (28) also observed an early increase of *S. tritici* followed by an increase of *S. nodorum* followed by an increase of *S. nodorum* later in the season, on naturally infected winter wheat in England.

On Cheyenne winter wheat sporulation of *S. tritici* tended to decline as the growing season progressed. This decline was because the sporulation occurred on the lower leaves with little occurring on the upper leaves. Thus, as the lower leaves died and decomposed, the removal of spores was greater than replacement from the upper leaf layer. This decline in sporulation of *S. tritici* on winter wheat should be checked on other winter wheat cultivars.

It has been suggested that the differences in the development of *S. nodorum* and *S. tritici* on winter wheat may be due to differences in moisture requirements for infection (23) or to the presence of different amounts of inoculum of each of the species early in the season (33). However, our observations on sporulation of the three *Septoria* spp. on the different leaves suggest that the explanation is not so simple. We suggest the following factors: (A) host resistance, (B) nutritional differences, (C) interaction with organisms in the phyllosphere, and (D) environmental differences.

Host resistance may be an important factor affecting infection and sporulation of *S. avenae triticea*. This species is considered to be a weak pathogen and has a marked tendency to develop on senescing leaves and sheaths (31). Thus its striking increase in sporulation late in the season may be associated with declining host resistance as the plant matures. The rapid rate of senescence of the upper leaves as compared to the lower leaves (Figure 9) may indicate a change in host resistance that affects sporulation of *S. avenae triticea*. The poor sporulation of *S. avenae triticea* on the lower leaves may be due to the presence of specific inhibitors in young leaves that influence growth of the *Septoria* spp. Pelletier and Comeau (39) found a water-soluble inhibitor in young oat leaves that reduced growth and sporulation of *S. avenae* Frank.

We saw no apparent change in host resistance associated with increasing plant age and the development of *S. nodorum* and *S. tritici* (32,56). However, Cooke and Fozzard (10) attributed the development of *S. nodorum* at the milky ripe stage of plant growth to an increase in plant susceptibility that occurred at flowering time. In glasshouse tests we noted that Cheyenne may be moderately resistant to *S. tritici*. Thus the decline in sporulation of *S. tritici* observed on Cheyenne may have been due to some degree of resistance in this cultivar.

Changes in the available nutrients in the leaves may also influence the sporulation of the three *Septoria* spp. As plants change from the vegetative to the reproductive stage of development, mineral salts, sugars, and amino acids are translocated from the leaves and stems to the developing seeds (42). In glasshouse studies we have noted that "green islands" often form around lesions due to infection by *S. tritici* (22,65), but these have not been observed around lesions by *S. avenae triticea* or *S. nodorum*. This may indicate a greater nutritional requirement for sporulation in leaf tissue for *S. tritici* than for the other two fungi. "Green island" formation may indicate the translocation of nitrogen and sugars to the lesion from the surrounding tissue (6). Also pycnidia of *S. tritici* that form in dead tissue are smaller than those that form in living tissue. Thus the relocation of nutrients out of leaves to the

developing head may stimulate sporulation of *S. avenae* and *S. nodorum*, but inhibit sporulation of *S. tritici*. A critical study is needed on the relative nutritional requirements of the three *Septoria* species.

Sporulation of *S. avenae triticea* and *S. nodorum* increased on leaves as they became senescent, but it tended to decline once the leaf was dead. Depletion of nutrients in the dead leaf tissue by leaching with rain and utilization by saprophytic organisms may have contributed to the decline in sporulation of *S. avenae triticea* and *S. nodorum* on dead tissue.

Sporulation of the *Septoria* spp. may have been affected by other microorganisms in the phyllosphere. The presence of pollen (18) and *Sporobolomyces roseus* (1) in the phyllosphere have been found to stimulate *S. nodorum* and we have observed the stimulation of sporulation of *S. avenae triticea* on agar by the presence of a white yeast isolated from wheat leaf washings. The amount of pollen and number of organisms in the phyllosphere increases after heading (18) and this may have influenced the growth and sporulation of the *Septoria* spp. in the later stages of plant development.

Whether or not *S. tritici* interacts with the organisms in the phyllosphere is not known.

Environmental differences in the developing crop may affect the *Septoria* spp. Crop development can be considered in three phases: (A) an open phase during the seedling growth stage; (B) a closed phase when the leaves meet across the rows to form a dense canopy; and (C) an open phase after the boot growth stage, when the plants are elongating. The greatest increase in sporulation of *S. avenae triticea* and *S. nodorum* occurred during the open phase after the plants passed the boot growth stage (Figure 13). An open crop has been reported to facilitate disease development of *S. nodorum* (24,37), possibly by allowing for greater dispersal of pycnidiospores. The open nature of the crop after the boot growth stage may lead to greater fluctuations in moisture than would occur in the middle, or closed phase, and favor the *Septoria* species with the shortest moisture requirements for infection and sporulation. Holmes and Colhoun (23) suggest that, because *S. tritici* requires longer periods of moisture for infection that does *S. nodorum*, it would be at a greater selective disadvantage than *S. nodorum* under conditions of fluctuating moisture. Unfortunately, leaf wetness measurements were not made in this study, nor have they been made in any study reported to date on the development of the *Septoria* spp. Since the *Septoria* spp. are dependent on moisture for dispersal, infection, and sporulation, a careful and critical study is needed of the relationship of leaf wetness on the different leaf layers and the pattern of development of the *Septoria* spp. on them.

Multiple correlation analyses indicated that temperature may be more important than growth stage and rainfall in explaining the variation in sporulation of the three *Septoria* spp. Unfortunately there are no reported studies on the relative effect of temperature on infection and sporulation of the three *Septoria* spp.

It is possible that temperature and the duration of leaf wetness would better explain the variation in sporulation than would temperature and rainfall because *S. avenae triticea* and *S. nodorum* need free water on the leaf surface for pycnidia to form (49,50). The occurrence of rain determines whether or not pycnidia form, but the formation of pycnidia and spores probably depends on temperature and the period of time that the leaf surface remains wet. There is a critical need for leaf wetness records to be kept when studying epidemics of the *Septoria* spp.

Interpretation of the relationship between environmental factors and sporulation of the *Septoria* spp. in the field is hampered by the lack of information on factors affecting sporulation in leaf tissue. Studies of the factors affecting sporulation of the *Septoria* spp. are confounded by the fact that spore formation is dependent on pycnidium formation. Laboratory studies on the *Septoria* spp. on wheat suggest that the relationship between numbers of spores and the numbers of pycnidia is a complex due to differences in the size and maturity of the pycnidia and due to the presence of empty pycnidia. Periods of wetting and drying are also important (16,20). Also the factors favoring spore formation differ from those favoring pycnidium formation (8), as observed for reproduction of *S. nodorum* on agar (40,47). Because there is so little knowledge of pycnidium and spore formation by the *Septoria* spp., and because such information should aid in understanding and predicting epidemics, work on this topic should be done, especially in plant tissue growing in the field.

Differences in the mode of dispersal between the *Septoria* spp. may affect the pattern of sporulation on the various leaves. *Septoria avenae triticea* forms perithecia in infected plant parts and showers of ascospores may occur after rain (54). Perithecia of *S. nodorum* and *S. tritici* have not been reported in Minnesota. As ascospores are air-borne, they would tend to be trapped on the upper leaf layers of the developing crop, rather than in the lower leaf layers.

The relative importance of the three *Septoria* spp. as the cause of leaf necrosis of wheat in Minnesota changes with the pattern of their sporulation on the different leaves. On winter wheat *S. tritici* probably caused most of the necrosis on the lower and middle leaves early in the season. As the season progressed, *S. nodorum* appeared to be a major cause of the necrosis on the middle leaves, and late in the season both *S. avenae triticea* and *S. nodorum* probably caused most of the necrosis on the upper leaf layer. On spring wheat *S. tritici* was not present. Multiple correlation analysis indicated that *S. nodorum* probably caused most of the necrosis of all the leaf layers of spring wheat. *Septoria avenae triticea* was probably a cause of most of the necrosis of the upper leaves of spring wheat late in the season. While these conclusions appear to be sound, the relationship between leaf necrosis and sporulation by the three *Septoria* spp. is a two-way relationship because necrosis may stimulate sporulation. Necrosis may also be caused by pathogens other than *Septoria*.

Only inferences about the relative importance of the three *Septoria* spp. on yield can be derived from the data presented. Johnson (31) suggested that, because *S. avenae triticea* develops so late in the season, it probably has little effect on yield. Observations on the development of *S. avenae triticea* in this study tend to support his conclusion. *Septoria nodorum* may be more important than *S. avenae triticea* in causing yield loss of wheat because sporulation of *S. nodorum* was greater than that of *S. avenae triticea* and *S. nodorum* probably caused much of the necrosis on all of the leaves. *Septoria tritici* was found only on winter wheat and it was probably of minor importance in causing yield loss because it was found primarily on the lower and middle leaves. Sporulation of *S. tritici* was not significantly correlated with leaf necrosis.

While it is concluded that *S. nodorum* is probably the most important *Septoria* spp. on wheat in Minnesota, *S. avenae triticea* and *S. tritici* have the potential of being a serious threat to wheat culture in this state. *Septoria* spp. on wheat have a history of changing from what was thought to be a "minor" pathogen to being a destructive threat to wheat production. For example, the release of the susceptible cultivar Fortuna in Montana resulted in a striking increase in *S. nodorum* with considerable yield loss (45). The rapid increase in *S. nodorum* led to the recall of Fortuna and to the testing of all commercial cultivars for resistance to this pathogen before they are released in Montana. In North Africa, with the introduction of the semi-dwarf wheats and the associated changes in cultural practices, *S. tritici* developed from the status of being a pathogen of minor importance to one of being a major threat to wheat production in the area (61). Within Minnesota, infected winter wheat, spring wheat, and barley, and wild grasses are reservoirs of inoculum for the initiation of epidemics. Thus with a change of cultivars or of cultural practices (*e.g.* the larger wheat acreage and shorter rotations associated with increase in the demand for wheat in the last few years), conditions may become more favorable for the occurrence of severe epidemics of the *Septoria* spp. on wheat in Minnesota. Therefore, it would be prudent to continually monitor the changes in the *Septoria* spp. from season to season, and where practically feasible, incorporate known sources of resistance into the commercial cultivars.

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