

Effect of Residue Management on Wetness Duration and Ascocarp Production by *Pyrenophora tritici-repentis* in Wheat Residue

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ABSTRACT

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No-till, mowed, and disked residue treatments were applied to wheat residue infested with *Pyrenophora tritici-repentis* in fields near Manhattan, KS, in 1988 and 1989. Ascocarp production by *P. tritici-repentis* and straw-wetness duration were studied in relation to these treatments and four straw positions relative to the soil surface (above-soil and near-soil; upper part and lower part of standing stubble). Ascocarp production, estimated by counting ascocarps on sampled straw, was significantly affected by straw position and tillage treatment. The number of ascocarps per gram of straw in near-soil straw was only 32 and 42% of that found in the above-soil straw in mowed and no-till treatments, respectively. The difference in the disked treatment was significant only in 1989. In

the standing stubble of no-till plots, the number of ascocarps in the lower part of the stubble was only 12% of that found in the upper part. The number of ascocarps per square meter of field area was reduced by 91% in disked and by 69% in mowed treatments compared with the no-till treatment. Straw wetness was monitored by connecting electrodes to individual straws in the field. The number of straw-wetness hours occurring in wetness periods longer than 12 h (long-period wetness hours) varied with straw position. There were higher numbers of long-period wetness hours in near-soil straw than in above-soil straw in all three tillage treatments. A negative correlation was found between ascocarp production and long-period wetness events in the mowed and no-till treatments.

Pyrenophora tritici-repentis (Died.) Drechs. (anamorph: *Drechslera tritici-repentis* (Died.) Shoem.) is a residue-borne pathogen that causes tan spot, a foliar disease of wheat (*Triticum aestivum* L.) in several regions of the world, including the Central Plains of North America (6,7). An increased occurrence of tan spot has been associated with retention of wheat straw on the soil surface in conservation-tillage farming (7,13,22). If the straw is infested with *P. tritici-repentis*, the pathogen forms ascocarps, which later produce, under favorable conditions, ascospores (primary inoculum for tan spot epidemics). Tan spot severity has been correlated with levels of primary inoculum in the field (1,23), suggesting that reduction of residue-borne primary inoculum could decrease epidemic development and crop damage.

Production of ascospores is dependent on saprophytic growth, overwintering, and ascocarp formation by *P. tritici-repentis* in the residue; these processes are affected by environmental conditions. A previous laboratory study (10) showed that in dead wheat leaves *P. tritici-repentis* grows maximally at a water potential of -0.5 MPa, but that it can grow at a water potential as low as -8.5 MPa. Ascocarp production is minimal at -2.4 MPa and increases as water potential increases. This conducive-ness of high moisture to *P. tritici-repentis* may be reversed under natural conditions, however. In a field study, Pfender and Wootke (12) found that *P. tritici-repentis* survives poorly in straw that

is buried or placed directly on the soil surface. In contrast, it survives well in straw that is slightly above the soil surface, as in standing stubble or within a mulch layer. A field study in Australia (19) reported a similar finding. Pfender and Wootke (12) suggested that residue in close contact with the soil is moist more often and remains moist longer than straw above the soil surface. This high-moisture environment could result in more intense microbial activity and competitive interactions detrimental to survival and inoculum production by *P. tritici-repentis*. In support of this idea, suppression of *P. tritici-repentis* by *Limonomyces roseipellis* Stalpers & Loerakker under laboratory conditions was greater in straw that remained wet for extended periods (9). Under high-moisture conditions, more fungi suppressed saprophytic growth and ascocarp formation than under low-moisture conditions (11). Another laboratory study (20) also showed that moist conditions reduce viability of *P. tritici-repentis* in straw exposed to soil. Thus, data concerning the correlation of ascocarp production to moisture conditions in wheat straw in the field may be useful in understanding survival and inoculum production of *P. tritici-repentis* under natural conditions.

The influence of water potential on survival and inoculum production of *P. tritici-repentis* in wheat straw has not been studied under field conditions, largely because continuous water-potential measurement of wheat residue in the field is technically very difficult. Straw wetness is an alternative but related moisture parameter that can be monitored more easily in the field. Moisture on plant materials, especially leaves, has been measured with

various wetness sensors. Some sensors are used as surrogate leaves (3,5,15,21) and detect free water on their surfaces; others (8,21) detect free surface water using the leaf itself as part of the sensor circuit. In a recent study from Canada (4), an electrical impedance sensor was used to monitor moisture conditions of wheat residue in the field, and ascospore maturation of *P. tritici-repentis* was correlated with accumulated hours of straw water potential ≥ -2.5 MPa. Here we report a 2-yr field experiment on ascocarp production by *P. tritici-repentis* and its correlation with wetness duration of wheat straw under reduced tillage. A preliminary report has been made (24).

MATERIALS AND METHODS

Field experiments were conducted near Manhattan, KS. Winter wheat (cv. TAM105) was planted during October of 1987 and 1988 to provide residue for experiments in 1988 and 1989, respectively. After seedling emergence, oat kernels (50 g/m²) infested with *P. tritici-repentis* were spread in the field to ensure the occurrence of tan spot of wheat in the spring. Epidemic development was enhanced by overhead irrigation. Virtually all plants had tan spot lesions on the flag and lower leaves by late May in both 1988 and 1989. Wheat was harvested with a combine on 16 June and 26 June in 1988 and 1989, respectively, leaving standing stubble approximately 35–40 cm tall. After harvest, one of three types of residue management (no-till, mowed, or disked) was immediately applied to the wheat residue. In the no-till treatment, the threshed straw was raked and uniformly redispersed among rows of stubble to provide a relatively uniform layer of straw, with the lowermost of the threshed straws in close contact with the soil. The stubble and threshed straw in the remaining two treatments were mowed with a rotary mower set at a height of 5 cm. The mowed treatment received no further tillage; the disked treatment was chiseled once and then disked once. Plots were 6.1 × 1.5 m in 1988 and 3.1 × 1.2 m in 1989. Throughout the two field experiments, glyphosate (Roundup, 45 g a.i./ha) was applied uniformly to all plots as needed for weed control.

Measurement of ascocarp production in wheat residue.

Estimates of ascocarp production in the plots were made from randomly chosen straw samples taken during November of 1988 and February of 1990. Six sampling sites (each having an area of 28 cm² in the mowed and no-till plots and 78 cm² in the disked plots) were chosen randomly from the threshed or standing-stubble straw position in each plot. Straw from the six sites was thoroughly mixed to produce one bulk sample. To estimate the number of ascocarps in each sample, the straw was air-dried, weighed, and visually sorted into three categories of ascocarp density (high, medium, and low). Then a random subsample (approximately 0.05, 0.05, and 0.15 g per subsample in the three respective categories, representing at least 10% of the sample) was taken from each category. The subsample was examined with a dissecting microscope at a magnification of 25× to determine the number of ascocarps of *P. tritici-repentis* present. Finally, the number of ascocarps per unit weight of straw was calculated for each threshed-straw or standing-stubble position.

Threshed straw was sampled from two straw positions (above-soil and near-soil). Straw in the above-soil straw layer position was approximately 1–4 cm above the soil surface. Near-soil straw was beneath the above-soil straw layer in close contact with the soil. In the no-till treatment, in addition to above-soil and near-soil straw positions, straw from two straw positions in the standing stubble was sampled viz. the upper (top 10 cm) and the lower (bottom 10 cm) standing stubble. In sum, two positions were sampled in the mowed and disked treatments; four positions were sampled in the no-till treatment. There were four replicate plots for each residue treatment. The plots were arranged in randomized complete blocks in the 1988 experiment and were completely randomized in the 1989 experiment.

The effect of threshed-straw position on the number of ascocarps per gram of stubble straw was analyzed as a split-plot design, with residue treatments as main plots and straw positions as subplots in both the 1988 and 1989 experiments. Because standing

stubble was present only in the no-till treatment, the number of ascocarps per gram of straw was analyzed separately but presented in the same table as the threshed-straw positions of all three residue treatments. Total ascocarp production and surface-borne residue for each residue treatment were obtained by summing over the two threshed-straw positions for the disked and mowed treatments and summing over all four straw positions for the no-till treatment. The total number of ascocarps per gram of straw or per unit area (inoculum density) and the amount of wheat straw per unit area in three residue treatments were analyzed as a randomized complete-block design in 1988 and as a completely randomized design in 1989.

Straw-wetness measurement. Straw-wetness measurements were collected to illustrate the moisture conditions of wheat residue in the three types of residue management. Although this is only one of many physical and biological factors affecting the microenvironments of wheat residue in which *P. tritici-repentis* survives saprophytically and overwinters, we assumed that moisture's effects may be important enough to be correlated with ascocarp production. Therefore, we examined straw-wetness data to find any attributes correlated with the observed effect of straw position on ascocarp production.

Weather data records (2) showed that 1988 was an extremely dry year in Manhattan, KS. The total annual precipitation in 1988 was 513 mm (322 mm below the normal average precipitation of 1951–1980); the total precipitation during the 2-mo period of October and November was only 40 mm (71 mm below the normal average for the same period during 1951–1980). Although the annual total precipitation in 1989 (823 mm) was very close to the normal average precipitation (1951–1980), the cumulative precipitation during the period of August–December (545 mm) was 229 mm above the normal average. Snowfall occurred during December of 1988, February of 1989, and January–March of 1990. The highest mean temperatures of the 2-yr period (26.9 and 26.8 °C) occurred in August of 1988 and July of 1989, respectively.

To monitor the occurrence and duration of moisture in the straw, a wetness sensor was constructed. The straw-wetness sensor consists of a pair of electrodes (plated steel alligator clips; Newark Corp., Chicago, IL) clamped onto the wheat straw. The tips of the electrodes are bent to form semicircles, so they fit tightly over the straw; the distance between the two electrodes of each sensor on the straw is approximately 0.5 cm. The electrodes are soldered to 22-gauge wires approximately 12 m long and connected to a micrologger (model 21X, Campbell Scientific, Logan, UT) in the field. When current is applied to the circuit, it must move through the straw between the electrode contact points; the electrical impedance depends on the moisture in the straw. A reference resistor, 100 kohms, is incorporated in the circuit to form an AC half-bridge circuit, and the micrologger is programmed to output half-bridge measurements that indicate the electrical impedance of the straw. The micrologger output is a ratio of measured sensor voltage to applied excitation voltage, and the wetness reading is this dimensionless number multiplied by -10^3 . When the straw is dry and impedance is high, the wetness reading remains low. When the straw becomes wet, the wetness reading increases, indicating a lower impedance in the straw.

To determine the relationship between straw wetness and water potential, wetness sensors were attached to field straws in a controlled misting environment in the greenhouse. Straws were wetted with mist for several hours while wetness data were recorded. At various times during wetting and subsequent drying, wetness readings of randomly selected straws were recorded, and these straws were immediately detached from the sensor clips for water potential measurement. Each time at least four straws were sampled randomly from 10 or more sensors and placed individually in closed 0.5-ml microcentrifuge tubes. Each of these microcentrifuge tubes was then inserted into a polystyrene board in a polystyrene box, to keep the straw under isothermal conditions and to avoid condensation in the tube, and then transported to the laboratory. Preliminary experiments showed that prolonged storage of moistened straw in the microcentrifuge tube (up to

48 h) did not change straw water potential significantly. In the laboratory, water potential of the straw was measured by using a thermocouple psychrometer (Decagon, Logan, UT). Five similar experiments were performed to determine the relationship of water potential to wetness reading of wheat straw. The relationship between straw wetness and water potential was used to choose a threshold value of straw wetness at which the corresponding water potential was so low that *P. tritici-repentis* would not be expected to grow (approximately -10 MPa [10]). This threshold subsequently was used to calculate wetness duration of each wetting event in the field. A straw-wetness reading above the threshold value indicated a wetting event.

To monitor straw wetness in the field, wetness sensors were attached to straws at above- and near-soil straw positions in disked and mowed treatments and at two additional positions (upper and lower stubble) in the no-till treatment (in the same field plots as described earlier). Sensors (one per position per plot) were placed in three replicate plots for each residue treatment in the 1988 experiment and in four replicate plots in the 1989 experiment. Straw-wetness readings were recorded every half-hour from 4 October through 23 November 1988 and from 3 August to 4 December 1989. A PASCAL computer program was written to process the recorded wetness data by using the threshold wetness reading determined earlier. Data were initially processed by categorizing each wetting period as: 0-2, 2-6, 6-12, 12-24, 24-48, 48-72, 72-96 h, or longer than 96 h in duration. Preliminary analysis indicated that the number of cumulative wetness hours occurring in wetness periods longer than 12 h was greatly affected by the degree of residue management and straw positions. Therefore, straw-wetness data are presented here as the number of cumulative wetness hours from wetness periods of two categories: those shorter than 12 h (short-period wetness events) and those longer than 12 h (long-period wetness events).

The effect of the threshed-straw position on the number of cumulative wetness hours, from wetness periods shorter than 12 h (short-period wetness events) or longer than 12 h (long-period wetness events), was analyzed as a split-plot design with residue treatments as main plots and straw positions as subplots in both the 1988 and 1989 experiments. The number of short-period or long-period wetness hours in the standing-stubble positions was analyzed separately but is presented in the same figure as threshed straw.

In addition, a regression analysis between the number of ascocarps per gram of straw and the number of short-period or long-period wetness hours in each residue treatment was performed. All statistical analyses in this study were performed separately for the 2 yr of experiments.

RESULTS

Relationship between wetness measurement and water potential. Figure 1 illustrates the relationship between wetness measurement

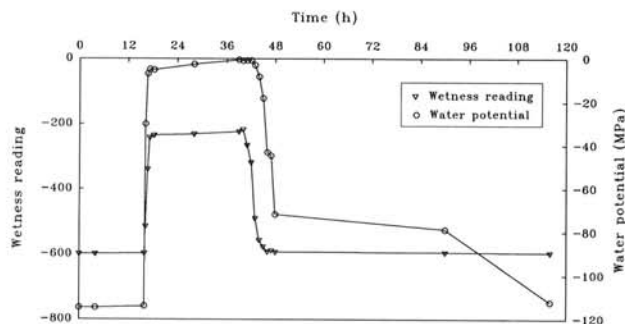


Fig. 1. Relationship of wetness measurement to water potential of wheat straw. Individual straw pieces attached to wetness-sensing circuits were placed in a greenhouse. Intermittent mist was applied to straw, beginning at 16 h; misting was discontinued at 40 h. Straws were removed periodically for water-potential measurement.

ment and water potential of wheat straw during and after wetting treatment in the greenhouse. Unwetted straw had a wetness reading of approximately -600 to -620, corresponding to a low water potential in the range of -80 to -120 MPa. Within 1 to 2 h of the onset of intermittent misting, wetness readings and water potential of the wheat straw changed dramatically: Wetness readings increased above -300, and water potential increased to over -10 MPa. Over the next 24 h, while the straw-wetness reading remained relatively stable, straw water potential continued to increase slowly to the highest level of about -1 MPa. After misting stopped, the straw-wetness reading started to decrease immediately, and the straw water potential began to decrease gradually as the straw dried. There was a time lag between decrease in the straw-wetness reading and decrease in the water potential, because straw water potential did not begin to decrease until approximately 3 h after the misting treatment stopped. At that time, straw water potential showed a drastic change paralleling the one observed in wetness reading 3 h previously.

From data such as those in Figure 1, a wetness reading of -550 was chosen as the threshold value used to calculate the number and duration of wetting periods for straw in field experiments. Readings below this threshold straw-wetness reading indicated straw water potential lower than -10 MPa. A wetness reading above -550 indicated straw water potential higher (wetter) than -8 to -10 MPa. Previous studies have shown that *P. tritici-repentis* does not grow at a water potential below -10.5 MPa in nonsterilized, infested wheat leaves (10).

Ascocarp production by *P. tritici-repentis*. Ascocarp production by *P. tritici-repentis* was greatly affected by straw position and residue treatment. In the mowed and no-till treatments, the number of ascocarps per gram of straw was significantly higher (at $\alpha = 0.10$ or smaller) in above-soil straw than in near-soil straw (Table 1). For near-soil straw, ascocarp production was only 24-30% and 37-43% of that found in the above-soil straw in mowed and no-till treatments, respectively. In the disked treatment, the difference in the number of ascocarps between above-soil and near-soil straw was significant in 1989 but not in 1988 (at $\alpha = 0.10$). For standing-stubble positions in no-till plots, the upper part had 3- to 19-fold more ascocarps than did the lower part.

Ascocarp production, measured per gram of straw, differed among the three residue treatments in 1988 but not in 1989 (Table 2). Averaged over all straw positions, the number of ascocarps per gram of straw was higher (at $\alpha = 0.05$) in the no-till than in the disked and mowed treatments in 1988. In 1989, it was similar in all three treatments.

The amount of surface-borne straw per unit area in the field was greatly affected by residue management (Table 2). In the

TABLE 1. Number of ascocarps of *Pyrenophora tritici-repentis* per gram of straw as affected by straw position in three residue treatments during 1988 and 1989

| Straw type and position | Residue treatment and year | | | | | |
|-------------------------|----------------------------|------|-------|------|-----------------|------|
| | Disked | | Mowed | | No-till | |
| | 1988 | 1989 | 1988 | 1989 | 1988 | 1989 |
| Threshed | | | | | | |
| Near-soil | 465 | 402 | 269 | 298 | 1,042 | 237 |
| Above-soil | 690 | 837 | 889 | 866 | 2,426 | 637 |
| | NS ^a | * | (*) | ** | ** | * |
| Stubble | | | | | | |
| Lower | ... | ... | ... | ... | 105 | 195 |
| Upper | ... | ... | ... | ... | 2,025 | 573 |
| | ... | ... | ... | ... | ** ^b | ** |

^a Effect of threshed-straw position on number of ascocarps was analyzed as a split-plot design with residue treatments as main plots and straw positions as subplots in both 1988 and 1989 experiments. The two values in the same column are not different (NS), or different at the 0.10 (**), 0.05 (*), or 0.01 (***) level of probability.

^b Standing-stubble position was analyzed separately as a randomized complete-block design. The two values in the same column are not different (NS), or different at the 0.01 (***) level of probability.

TABLE 2. Amount of wheat straw and straw-borne ascocarps of *Pyrenophora tritici-repentis* in relation to three residue treatments in 1988 and 1989

| Residue treatment | 1988 | | | 1989 | | |
|-------------------|------------------------------------|---------------------------|------------------------------|-----------------------|---------------------------|------------------------------|
| | Ascocarps per g straw ^a | Straw (g/m ²) | Ascocarps per m ² | Ascocarps per g straw | Straw (g/m ²) | Ascocarps per m ² |
| Disked | 602 a ^b | 64 a | 36,000 a | 521 a | 100 a | 51,000 a |
| Mowed | 640 a | 224 b | 136,000 a | 487 a | 330 b | 156,000 b |
| No-till | 1,198 b | 492 c | 596,000 b | 483 a | 491 c | 224,000 c |

^aThe numbers are weighted-average number of ascocarps of two straw positions in disked and mowed treatments, and four straw positions in the no-till treatment.

^bDifferent letters in the same column indicate that the values are significantly different according to Duncan's multiple range test ($\alpha = 0.05$).

disked treatment, the amount of straw in the field was only 12–18% (1988 and 1989) of that found in the no-till treatment. The amount of straw residue in the disked treatment was only 29–30% of that found in the mowed treatment. Similarly, there was significantly (at $\alpha = 0.05$) less (42–59%) surface-borne residue in the mowed treatment than the no-till treatment. In no-till plots, the standing stubble provided a larger share of the total amount of residue than did the threshed straw in 1988 but not in 1989 (data not shown).

The number of ascocarps per gram of straw multiplied by the amount of straw per square meter allowed estimates of the inoculum density (ascocarps per square meter). The inoculum density was affected by residue management. More ascocarps per square meter were found in the no-till than in the disked treatment (Table 2). Averaged over the 2 yr, the inoculum density in disked plots was only 9.2% of that found in no-till plots. The no-till treatment also had a higher inoculum density than the mowed treatment. More ascocarps per square meter were found in mowed plots than in disked plots in 1989. In 1988, estimated ascocarp production in the disked treatment was only 26% of that found in the mowed treatment, although the difference was not significant (at $\alpha = 0.05$). Within the no-till treatment, stubble straw contributed more to ascocarp production per square meter than did the threshed straw in 1988 but not in 1989 (data not shown).

Wetness duration of wheat residue in the field. Cumulative straw-wetness hours occurring in short-period wetness events are illustrated in Figure 2 (A and C). For threshed straw, above-soil straw had significantly more short-period wetness hours than did near-soil straw in all three residue treatments in 1989 but not in 1988. In no-till stubble, the difference was not significant (at $\alpha = 0.10$) between the upper part and the lower part in either year.

The number of straw-wetness hours occurring in long-wetness periods was greatly affected by residue management and straw position (Fig. 2B and D). In a comparison of the two straw positions, more long-period wetness hours were recorded in near-soil than in above-soil straw in all residue treatments, except the disked treatment in 1988 (at $\alpha = 0.10$ or smaller) (Fig. 2B). Similarly, in stubble-straw positions of no-till treatment, there were more long-period wetness hours in the lower parts than in the upper parts in 1988 (at $\alpha = 0.10$) but not in 1989. Averaged across the two threshed-straw positions, there were more long-period wetness hours in mowed and no-till than in disked plots in 1988; the reverse was true in 1989 when the disked treatment had a higher number of long-period wetness hours than either no-till or mowed plots (data not shown).

Regression analysis of ascocarp production. It is important to emphasize that the purpose of the regression analysis was not to test the effect of wetness on ascocarp production but rather to look for correlations that would suggest a relationship between ascocarp production and straw wetness—one of many environmental factors. Ascocarp production by *P. tritici-repentis* and straw-wetness measurement were correlated by trying several regression models. Preliminary analyses showed that the best linear regressions were achieved when both the number of ascocarps per gram of straw and the number of long-period wetness hours were logarithmically transformed.

Figure 3 illustrates the regression analysis of ascocarp production by *P. tritici-repentis* in the three types of residue management. In the mowed (Fig. 3B and E) and no-till treatments (Fig. 3C

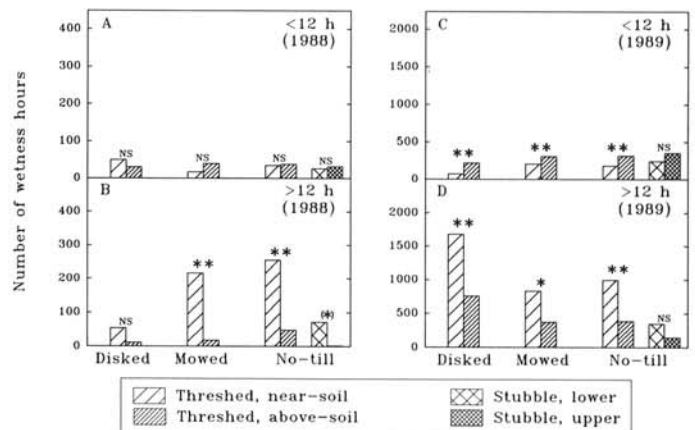


Fig. 2. Total number of wetness hours occurring in short-period (<12 h) (A and C) and long-period (>12 h) (B and D) wetness events as affected by straw position and residue management treatment in 1988 (A and B) and 1989 (C and D), respectively. Effect of threshed-straw position on number of short-period or long-period wetness hours was analyzed as a split-plot design with residue treatments as main plots and straw positions as subplots in both 1988 and 1989 experiments. Standing-stubble position was analyzed separately as a randomized complete-block design. All statistical analyses were done separately for the 2 yr of experiments. The symbols indicate whether the two adjacent bars from each residue treatment were not different (NS) or different at the 0.10 (*), 0.05 (*), or 0.01 (***) level of probability. The scales differ for the 2 yrs' data.

and F), there was a negative linear relationship between logarithmic ascocarp production and long-period wetness hours (at $\alpha = 0.10$ or smaller), indicated by R^2 values ranging from 0.62 to 0.90. In the disked treatment (Fig. 3A and D), however, there was no linear relationship between ascocarp production and straw wetness ($R^2 = 0.30$ and 0.14 in 1988 and 1989, respectively). Regression of the number of ascocarps with the number of short-period wetness hours was not significant in most of the residue treatments (analysis not shown).

DISCUSSION

The effect of straw moisture on saprophytic growth and ascocarp formation by *P. tritici-repentis* in wheat straw has not been studied under field conditions. In a recent study, Fernandes et al (4) used an impedance sensor to monitor straw wetness in the field, and the wetness readings were correlated with the water content and water potential of wheat residue. The wetness sensor used in our study was not intended to quantify the relationship between straw wetness and water potential but simply to estimate the number of hours within which growth or development of *P. tritici-repentis* and associated microorganisms (11,12) occur. In our study, the effect of weathering and decomposition of wheat straw on straw-moisture characteristics was not investigated. Other investigators (4,17) have determined that weathering and decomposition of straw affects the water content and water potential relationship, particularly at intermediate to dry water-potential levels (≤ -2.5 MPa). In the current study, the duration of this level of straw moisture within each wetness

period generally was short, however, so the error in computing the length of wetness periods should be minimal.

The dates of wetness-data collection differed between the 2 yr of experiments, and wetness data reported in this study were not from the entire fall and winter due to technical problems. The data, therefore, represent a sample of wetness conditions, rather than the entire wetness history in the field. Ascocarp formation on straw in Kansas has been observed in the field as early as August and appears to be essentially complete by December (W. F. Pfender and A. Nus, unpublished data). Therefore, wetness data collected 1–5 mo after harvest provide useful information on field moisture conditions and the underlying relationship between straw moisture and ascocarp production.

Residue-borne ascocarps of *P. tritici-repentis* are the inoculum source for primary infections in tan spot epidemics (1,13,14,22,23). Thus, the number of ascocarps per gram of straw not only provides a useful measure of saprophytic survival of the pathogen in the field but also indicates the effectiveness of various control measures (such as cultural or biological controls) in reducing primary inoculum level. In the present study, the influence of straw placement in the field on survival and ascocarp production by *P. tritici-repentis* was evident; above-soil straw had a much higher number of ascocarps per gram of straw than near-soil straw. As a result, the increased proximity of wheat straw to soil reduces ascocarp production. These data support the previous hypothesis (12) that the survival of *P. tritici-repentis* in the field declines in wheat straw that is in contact with soil.

The difference in ascocarp production between straw positions may be related to numerous biotic and abiotic factors in the microenvironment, and moisture is probably a major determinant. In our study of surface-borne wheat residue, the number of straw-wetness hours occurring in wetting periods either longer than or shorter than 12 h varied with straw position. A large number of long-period wetness hours was found in straw having close contact with soil, reinforcing our hypothesis (12) that straw in close contact with soil is wet more often and remains moist longer than straw above the soil surface. Regression analysis further indicated that reduced ascocarp production in the residue is

correlated with this high-moisture condition. A high-moisture level, while favorable to the growth of *P. tritici-repentis* (10,16), is also favorable to many other microorganisms. A previous laboratory study (11) showed that saprophytic growth and ascocarp formation of *P. tritici-repentis* is inhibited by several antagonists under prolonged, constant high moisture (3-wk period). In the microenvironment of above-soil straw, however, prolonged wetness is relatively uncommon, and primary colonizers such as *P. tritici-repentis* may possess a competitive advantage over fungi requiring high moisture for their growth. Because of its ability to grow in low-moisture conditions (as low as -8.5 MPa), *P. tritici-repentis* can apparently take advantage of these short periods of high moisture by initiating growth sooner in the wetting event and maintaining growth longer than potential antagonistic fungi (11,12). The growth of several antagonistic fungi is significantly suppressed or completely stopped at water potentials drier than -0.5 MPa (11). In near-soil straw, however, where long-period wetness durations are frequently observed, the competitive advantage of *P. tritici-repentis* over other fungi is lost, and saprophytic and/or antagonistic secondary colonizers (11) may establish and compete effectively with *P. tritici-repentis* and other primary colonizers. Straw in the moist near-soil environment, initially occupied mainly by a group of pathogens, is gradually colonized by saprophytic organisms (12,20), including potential antagonists. The change in microbial composition induced by long-period wetness duration may further intensify competitive microbial interactions in this microenvironment, consequently reducing survival of the tan spot pathogen in the residue.

In comparison to long-period wetness hours, the influence of straw placement on short-period wetness hours was not as distinct. Only in the 1989 experiment did the two threshed-straw positions differ in the number of short-period wetness hours. This could be attributed in part to the drought conditions. The regression analysis generally did not show a positive relationship between short-period wetness hours and ascocarp production (analysis not shown). This lack of correlation is probably due in part to the overriding influence of long-period wetness hours rather than a failure of short-period wetness hours to foster ascocarp formation, as was discussed earlier. In near-soil straw, the ratio of short-period wetness hours to long-period wetness hours was very small, whereas it was much higher in above-soil straw (Fig. 2); the possible favorable effect of short-period wetness may have been overcome by the negative effect of long-period wetness in the near-soil straw. However, controlled experiments would be required to determine the effect of short-period moisture and its interaction with long-period moisture and ascocarp production in the residue.

In the no-till treatment, there was a great difference between the 2 yr in the number of ascocarps formed on standing stubble. During the fall of 1988 and spring of 1989, a severe drought occurred in Kansas. Tan spot infection did not start until late in the spring, and the subsequent low level of infestation by the pathogen could have contributed to the smaller ascocarp number found in the no-till treatment in the 1989 experiment compared to those found in 1988.

For both years, the difference between the upper and lower portions of standing stubble in the number of ascocarps (Table 1) could also partly be attributed to differing preharvest colonization of *P. tritici-repentis*, although straw moisture and microbial interaction are also important additional factors, as they are for the threshed straw. Standing stubble in the no-till treatment presents a unique situation as compared to threshed straw. Standing stubble originated as the lower portions of wheat plants. Colonization of *P. tritici-repentis* in lower internodes of senesced stems is not as complete as that in the upper stem (18). Redistribution of chopped straw after harvest minimizes the nonuniformity of preharvest fungal colonization in the threshed straw, but redistribution is impossible for standing stubble. Therefore, the difference between preharvest colonization in the lower and upper parts of standing stubble may also contribute to the differing ascocarp production between these straw positions.

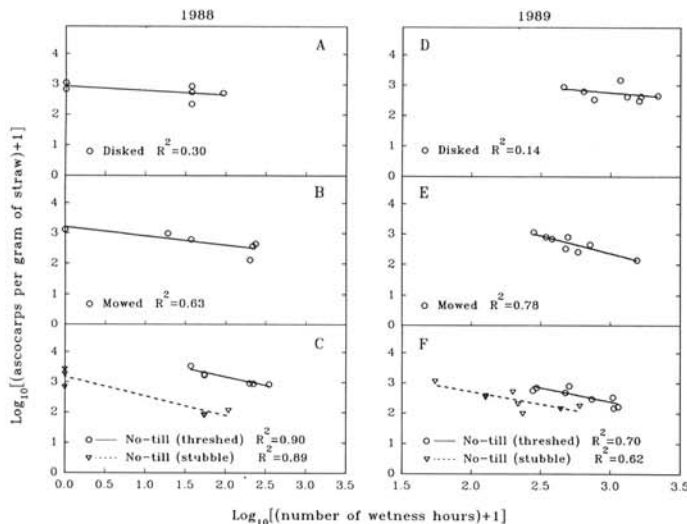


Fig. 3. Number of ascocarps per gram of straw (y), correlated with the number of long-period (>12 h) wetness hours (x) in respective residue treatments. Six wetness sensors were used in each residue treatment in 1988 and eight in 1989. Whereas logarithmic regressions [$Y = (\log_{10}(y + 1)); X = \log_{10}(x + 1)$] were not significant ($\alpha = 0.10$) for threshed straw of the disked treatment in 1988 (A) ($Y = 2.9277 - 0.1462X$) and 1989 (D) ($Y = 3.8590 - 0.3715X$), significant logarithmic regressions were obtained for the other two residue treatments: threshed straw of the mowed treatment in 1988 (B) ($Y = 3.2058 - 0.3044X$) and in 1989 (E) ($Y = 5.8560 - 1.1672X$); threshed straw of the no-till treatment in 1988 (C) ($Y = 4.2931 - 0.5646X$) and in 1989 (F) ($Y = 5.1544 - 0.9281X$); and standing stubble of the no-till treatment in 1988 (C) ($Y = 3.1737 - 0.6436X$) and in 1989 (F) ($Y = 4.3607 - 0.8273X$). The scales differ.

Our observation that *P. tritici-repentis* produces fewer ascocarps in the lower portion of standing stubble than in the upper portion (Table 1) differs from an Australian report (16) suggesting that more ascocarps developed on wheat stubble in direct contact with moist soil than in adjacent upright stubble. Low moisture in the upper stubble was thought to be responsible for the reduced ascocarp formation there. Although the Australian study provided no data to confirm the observation, the discrepancy between that study and ours has several possible explanations. The environmental conditions in Australia and Kansas could be very different, and the exposed position of standing stubble may make its microenvironment especially responsive to the ambient physical conditions at these two locations. In addition, the type of residue management (not described in the Australian study) may also be a factor, because the height of standing stubble and stand density may influence the microenvironment of stubble straw.

In contrast to the mowed and no-till treatments, the disked treatment produced a relatively small difference between the two straw positions in the number of ascocarps per gram of straw. This similarity in ascocarp production between the two positions in the disked treatment probably is related to the fact that the two straw positions are not very different physically. In the disked treatment, the distinction between above-soil and near-soil straw positions was not as conspicuous as in the mowed or no-till treatment, because the mulch layer of straw on the soil surface was not very thick after disking. Straw from both positions in the disked treatment was readily exposed to disturbance by rain and air movement. Often, muddy soil was found on wheat straw at both positions; the increased contact of the above-soil straw with the soil could lead to a microenvironment more similar to that of near-soil straw.

In the present study, disked and mowed treatments significantly reduced inoculum density in the field in both years when compared with no-till treatment. However, the magnitude of reduction was not the same for the 2 yr. In the disked treatment, ascocarp production (ascocarps per square meter) was about 5 and 20% of that found in the no-till treatment in 1988 and 1989, respectively; the respective amount of residue per unit area was about 12 and 18% of that found in the no-till treatment in the 2 yr. The decrease in inoculum density in disked plots in 1988 was a combined result of reductions in the number of ascocarps per gram of straw and the amount of residue in the field. In 1989, however, the decrease in inoculum density was due solely to the reduced retention of surface-borne residue. Similar conclusions can be drawn for the mowed treatment in 1988 and 1989.

The lowest ascocarp production (37×10^3 ascocarps per square meter) found in this study (disked treatment) was higher than an inoculum density of 5,000–25,000 or 12,700–31,200 ascocarps per square meter, which are required to produce moderate to severe disease in Kansas (1) and Canada (23), respectively. It appears that neither the disked nor the mowed treatment used in this study for residue management was effective in reducing primary inoculum level sufficiently to eliminate yield loss. However, it is important to point out that the straw residue in this study came from an extremely heavily infested wheat field. Furthermore, the residue treatments are not standard farming practices for continuous wheat production. As a result, larger-scale trials of tillage treatments in fields with normal levels of the pathogen are needed to demonstrate the utility of tillage in the management of tan spot. The present study also demonstrated that prolonged wetness may be correlated with reduced inoculum production in the field; therefore, management practices that increase straw-wetness duration could reduce inoculum production in the residue by favoring indigenous or applied biocontrol agents.

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