The Effects of *Septoria nodorum* and *Xanthomonas translucens* f. sp. *undulosa* on Photosynthesis and Transpiration of Wheat Flag Leaves

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ABSTRACT

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In photosynthetic studies, either *Xanthomonas translucens* or *Pseudomonas cepacia* was applied in combination with *Septoria nodorum* to flag leaves of wheat at the 50% heading stage. Apparent photosynthetic rate (APR) and transpiration rate of flag leaves did not differ statistically in the *X. translucens* + *S. nodorum* treatment compared with *S. nodorum* alone. An interaction may have occurred when plants were incubated at 24 C; however, at lower incubation temperatures, combined inoculation had no effect compared with inoculation with either organism alone. Flag leaves had higher APR and transpiration rates when *P. cepacia* was applied at the same time as *S. nodorum*. *S. nodorum* may affect photosynthesis by reducing stomatal aperture and concomitantly transpiration. *P. cepacia* appears to be a very effective antagonist when applied at the same time as *S. nodorum*.

Additional key words: black chaff, glume blotch, pathogen interactions, *Triticum aestivum*.

Septoria nodorum (Berk.) Berk., causal organism of glume blotch of wheat (*Triticum aestivum* L.), has been shown to reduce the apparent photosynthetic rate (APR) of wheat flag leaves (11,15–17). The effect of *Xanthomonas translucens* (J. J. & R.) Dows. f. sp. *undulosa* (S. J. & R.) Hagb., incitant of black chaff of wheat, on APR of flag leaves has not been studied, nor has the effect of either pathogen on transpiration. Transpiration rates of several plant species may be increased (1,2,7–9) or reduced (3,4,12,13) by certain pathogens. In some instances, reduced photosynthesis has been correlated with reduced transpiration (5,14).

We attempted to determine if *X. translucens* f. sp. *undulosa* enhanced or hindered *S. nodorum* infection in wheat. *Pseudomonas cepacia* Berk., a known antagonist of *Fusarium oxysporum* f. sp. *cepae* (10), is antagonistic to growth of *S. nodorum* in vitro (J. B. Jones and C. W. Roane, *unpublished*), and its effect on *S. nodorum* in vivo was tested in this study. Because *S. nodorum* reduces APR of flag leaves, APR was used to determine the effect of the two bacteria on the ability of *S. nodorum* to infect and colonize the flag leaf of wheat. If *P. cepacia* is antagonistic to *S. nodorum* in vivo, then the effect of *S. nodorum* on APR of flag leaves should be reduced in the presence of *P. cepacia*. Transpiration was measured to determine its relationship to changes in photosynthesis.

MATERIALS AND METHODS

The spring wheat cultivar Olaf was grown in the greenhouse to the 50% heading stage. Plants were grown in Lodi loam soil limed to pH 6.5 and amended with 10-10-10 fertilizer. When four to five tillers had formed, incandescent lights were used to create a 14-hr day. At the 50% heading stage, plants were inoculated with the following organisms: *S. nodorum* only (Sn), *X. translucens* f. sp. *undulosa* only (Xt), *S. nodorum* and *P. cepacia* applied to the same leaf (SN + Pc), *S. nodorum* and *X. translucens* f. sp. *undulosa* applied to the same leaf (Snt + Xt), or none (control; distilled water applied to the leaf).

Production of inoculum. Conidial inoculum of *S. nodorum* was prepared as follows. Culture 76-106, received from A. L. Scharen (USDA, Montana State University, Bozeman), and culture SN 7, isolated from Arthur wheat from Bland County, VA, were grown on yeast malt agar (4 g of sucrose, 4 g of yeast extract, 4 g of malt extract, 15 g of agar, 1,000 ml of water) at 20 C under continuous fluorescent light for 5–7 days. The plates were flooded with distilled water, and the surface was scraped to dislodge the spores. Spore concentration in the suspension was determined with a hemacytometer. The suspension was then diluted to the desired concentration (Table 1) with distilled water. One drop of Tween 20 (polyoxyethylene sorbitan monolaurate) was added per 100 ml of suspension.

X. translucens f. sp. *undulosa* 5523, obtained from W. A. F. Hagborg, and *P. cepacia* culture A4, obtained from G. J. Griffin (Virginia Polytechnic Institute and State University, Blacksburg), were grown on yeast malt agar plates at 25 C for 48 hr in darkness. Plates were flooded with distilled water, and the suspension was diluted and adjusted to 10^8 colony-forming units per milliliter by measuring optical density at 600 and 590 nm for *X. translucens* f. sp. *undulosa* and *P. cepacia*, respectively. One drop of Tween 20 was added per 100 ml of suspension.

Inoculation procedure. Spore suspensions of *S. nodorum* were sprayed on to both sides of flag leaves and entire plants until runoff. *X. translucens* f. sp. *undulosa* was applied in two ways. In the first method, 600-mesh Carborundum was applied to the flag leaf, the bacterial suspension was sprayed onto the plants, and the leaves were rubbed gently with a sterile cotton swab. Distilled water was substituted for the bacterial suspension in the controls. In the second method, the leaves were pricked with pins bearing drops of bacterial suspension. The inoculation tool was made from a #4 cork stopper with 10 pins spaced evenly at the base, as described by Hagborg (6). Control plants were pricked with pins carrying distilled water. *P. cepacia* was applied by spraying the plants until runoff. In all instances, the bacterial suspension was applied before the fungal spore suspension.

Four experiments were done to determine if spore concentration and incubation temperature influenced the interaction between *S. nodorum* and *X. translucens*. Table 1 lists spore densities and

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incubation temperatures for the experiments. In all experiments, plants were incubated in polyethylene bags for 72 hr after inoculation.

Leaf area. For experiments 1 and 3, flag leaves were removed from plants when photosynthetic and transpiration readings were completed. Leaf area was determined with the type AAM-2, Hayashi Derko Co., area meter.

For experiments 2 and 4, flag leaves were left on the plants through maturity. At the end of the experiment, leaf area was determined by measuring the length of the blade and the width at the median of the leaf. Leaf areas were calculated from a regression equation determined by plotting actual area of nine leaves (cm^2) against leaf length (cm) × leaf width (cm). Leaf areas were then estimated by finding the point on the actual area axis corresponding to the point on the regression line for the leaf width × leaf length area.

Yield parameters. Plants from experiments 2 and 4 were grown to maturity, when grain was harvested by hand. Grain number, grain weight per head, and weight per grain were measured.

TABLE 1. Treatments, *Septoria nodorum* spore concentrations, and incubation temperatures used in photosynthesis studies

Experiment Treatment	Concentration of *S. nodorum* (spores/ml)	Incubation temperature (C)
Experiment 1		
Septoria nodorum (Sn)	1×10^6	24
Xanthomonas translucens (Xt)		
S. nodorum + *X. translucens* (Sn+Xt)		
S. nodorum + *P. cepacia* (Sn+Pc)		
Control		
Experiment 2		
S. nodorum (Sn)	3×10^6	24 day, 21 night
X. translucens (Xt)		
S. nodorum + *X. translucens* (Sn+Xt)		
P. cepacia (24 hr) + *S. nodorum* (24Pc + Sn)[a]		
S. nodorum + *P. cepacia* (Sn+Pc)		
Control		
Experiment 3		
S. nodorum (Sn)	5×10^6	24
X. translucens (Xt)		
S. nodorum + *X. translucens* (Sn+Xt)		
S. nodorum + *P. cepacia* (Sn+Pc)		
Control		
Experiment 4		
S. nodorum (Sn)	5×10^6	21
X. translucens (Xt)		
S. nodorum + *X. translucens* (Sn+Xt)		
S. nodorum + *P. cepacia* (Sn+Pc)		
Control		

[a] *P. cepacia* applied 24 hr before *S. nodorum*.

Measurement of transpiration and photosynthesis. Plants were placed in fumigation chambers lighted with sodium lamps before and during measurements of transpiration and photosynthesis. The light level at the leaf surface was 28,000 lux. Air temperature ranged from 25 to 28 C, and relative humidity was 40%. Plants were allowed to equilibrate in chambers under the lights for 1 hr before photosynthetic and transpiration readings were taken.

The procedures for measuring photosynthesis and respiration were described by Wolf et al (20). The flag leaf was placed in a glass single-leaf chamber through which air flowed across the leaf at 300 cm/sec, and a reference air line was connected to an empty chamber. Water vapor flux from the leaf was obtained by passing reference air at 1 L/min and sample air at 2.6 L/min through a Beckman infrared analyzer (model IR-215) that was adapted for water vapor measurements. The CO_2 flux was obtained by passing the reference and sample air at identical flow rates through the analyzer. Equipment was calibrated according to the methods described by Stauffer (18).

Multivariate analysis of variance was used on the photosynthetic and transpiration data. A profile analysis was run because there were two or more groups (treatments) versus time. In this way, the average photosynthetic rate was determined in each treatment for days 0–14. Differences among treatments for each day were analyzed.

RESULTS

Experiment 1—photosynthesis. Photosynthetic data are summarized in Table 2 and illustrated in Fig. 1. Leaves in the control treatment had low APR values toward the end of the experiment. Rates for the Sn treatment were statistically lower than for the control treatment on day 4, while the Sn+Xt treatment had significantly lower rates than the control on days 4, 6–9, and 11. The Sn treatment was significantly lower than the Xt treatment on days 4, 6–9, 11, and 14. Leaves from the Sn+Pc treatment had a significantly higher APR than those from the Sn treatment on days 11 and 13, whereas they were higher than those of the Sn + Xt treatment on days 6–9, 11, and 14.

The average APRs of leaves from the Sn and Sn+Xt treatments were significantly lower than those from the Xt and Sn+Pc treatments (Table 2). Leaves from the control treatment deteriorated throughout the experiment, and APR did not differ significantly from that of any other treatment.

Transpiration. Transpiration data from experiment 1 are summarized in Table 2 and illustrated in Fig. 2. Transpiration rates of leaves in the Sn and Sn+Xt treatments were not significantly lower than the control treatment throughout the experiment. Rates in the Sn treatment were significantly lower than in the Xt treatment on days 7, 9, 11, and 13, while rates in the Sn+Xt treatment were lower than in the Xt treatment on days 7, 9, 11, and 14. Rates in the Sn+Pc treatment were not significantly different from those in the Sn + Xt or Sn treatments throughout the experiment.

The average transpiration rates were highest for leaves in the Xt treatment, followed by those in the Sn+Pc treatment (Table 2). The control treatment leaves deteriorated throughout the

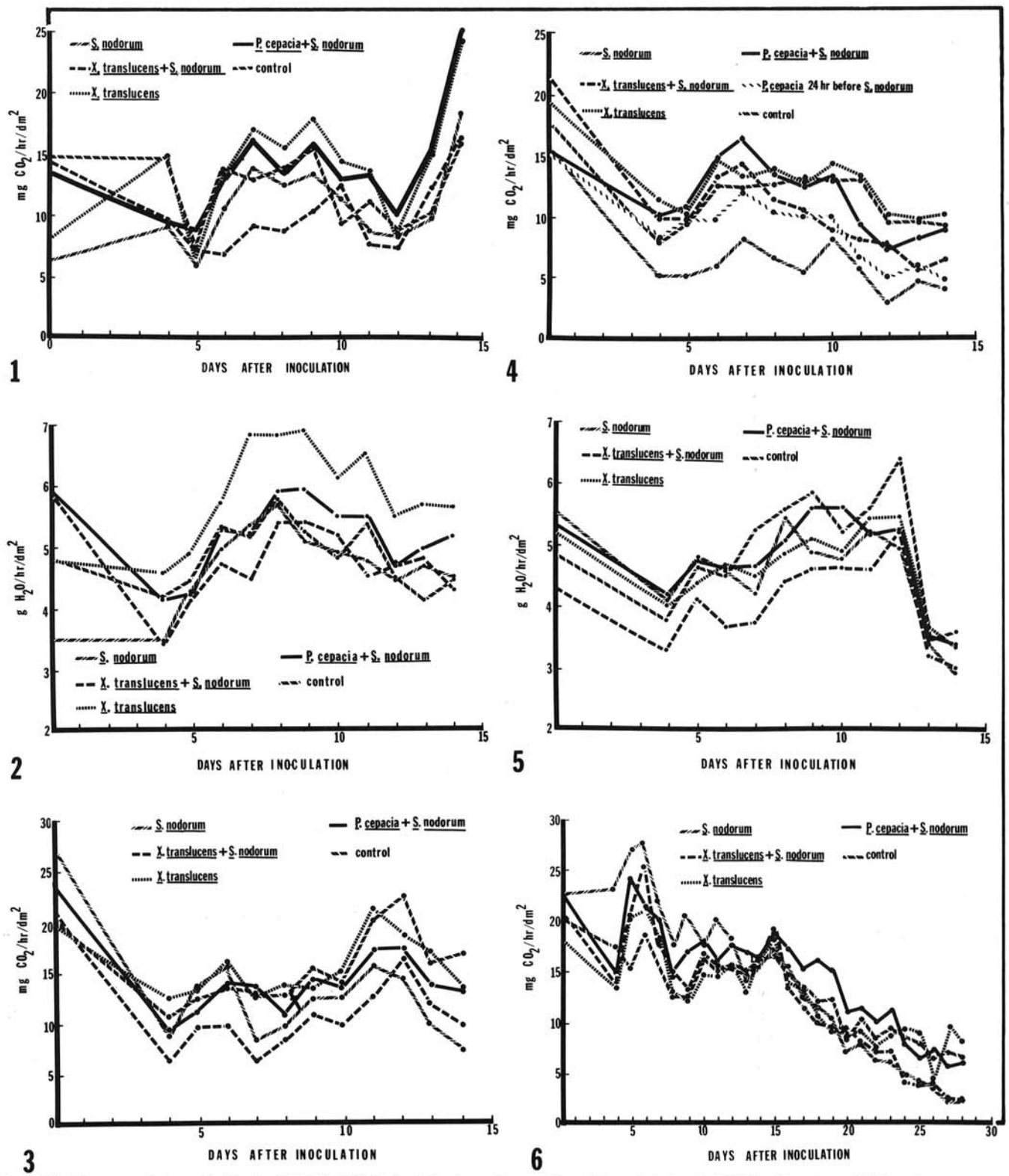
TABLE 2. Average photosynthetic and transpiration rates of flag leaves in experiment 1

Treatment	Average apparent photosynthesis rate (mg CO_2/hr/dm^2)[z]	Percentage of control	Average transpiration rate (g H_2O/hr/dm^2)[z]
Control	13.1 abc	100	4.8 ab
Xanthomonas translucens (Xt)	14.8 a	113	5.8 a
Septoria nodorum (Sn)	11.3 c	86	4.6 b
S. nodorum + *X. translucens* (Sn + Xt)	9.8 c	75	4.7 ab
S. nodorum + *Pseudomonas cepacia* (Sn+Pc)	14.1 ab	108	5.2 ab

[z] Numbers within a column followed by the same letter are not significantly different at the 0.05 level. Statistical analysis was done on average photosynthesis and transpiration data for 14 days after inoculation.

experiment and had a low average transpiration rate. Leaves from the Sn and Sn + Xt treatments had the lowest average transpiration rates. Leaves from the Sn treatment were the only ones with an average transpiration rate significantly below that of the Xt treatment.

Experiment 2—photosynthesis. The effect of the treatments on the APR over a 14-day period are shown in Fig. 4, and data are summarized in Table 3. The APR of the leaves of the Sn treatment was significantly lower than that of the control treatment on days 5, 6, and 8–14, whereas the APR of the Sn + Xt treatment was statistically lower than that of the control treatment on days 10 and 11. The APR of leaves in the Sn + Pc treatment was significantly



Figs. 1–6. 1, Apparent photosynthetic rates (APRs) of Olaf wheat flag leaves in experiment 1 inoculated at the 50% heading stage with *Pseudomonas cepacia* + *Septoria nodorum, S. nodorum* + *Xanthomonas translucens, S. nodorum* alone, *X. translucens* alone, or no organism (control). **2,** Transpiration rates of Olaf wheat flag leaves in experiment 1. **3,** APRs of Olaf wheat flag leaves in experiment 3 inoculated at the 50% heading stage with the same organisms as in experiment 1. **4,** APRs of Olaf wheat flag leaves in experiment 2 inoculated at the 50% heading stage with *P. cepacia* + *S. nodorum, S. nodorum* + *X. translucens, S. nodorum* alone, *X. translucens* alone, *P. cepacia* 24 hr before *S. nodorum*, or no organism (control). **5,** Transpiration rates of Olaf wheat flag leaves in experiment 3. **6,** APRs of Olaf wheat flag leaves in experiment 4 inoculated at the 50% heading stage with the same organisms as in experiment 1.

higher than that of the Sn treatment on days 5–10, 12, and 14. The APR in the 24Pc + Sn treatment was significantly higher than the APR in the Sn treatment on days 5 and 9.

Average APR of the Sn and Sn + Xt treatments was reduced 42.8 and 8.5%, respectively, compared with the control. The leaves of the Sn + Pc treatment had an average APR equal to 101.7% of that of the control treatment. The Sn treatment had the only average APR that was significantly below the average APR of the control.

In disease severity ratings of the flag leaves, no necrosis was observed in the control and Xt treatments (Table 3). Leaves from Sn, Sn + Xt, Sn + Pc, and 24Pc + Sn treatments had necrosis ratings of 18.9, 22.0, 4.1, and 16.3%, respectively. Grain weight per head was lowest in the control, Sn + Xt, and Sn treatments and highest in the 24Pc + Sn treatment (Table 3). Weight per grain in the 24PC + Sn treatment was slightly less than that in the Sn + Xt and Sn treatments. Plants in the Sn + Pc treatment had a slightly higher weight per grain, while plants in the Xt and control treatments had the greatest weight per grain.

Experiment 3—photosynthesis. The APRs of all treatments in experiment 3 over a 14-day period are shown in Fig. 3 and summarized in Table 4. The Sn + Xt treatment caused significantly lower APR values than the control on days 4, 7, 11, 12, and 14. The APR of leaves in the Sn treatment was significantly below that of the control from day 12 through the end of the experiment, but the APR of leaves in the Sn + Pc treatment was not significantly lower than that of the control on any day during the experiment. That of the Sn + Pc treatment was statistically higher than that of the Sn + Xt treatment on day 7 and higher than that of the Sn treatment on day 14. The APR of the Sn + Pc treatment was consistently higher than that of the Sn treatment from day 7 to day 14 and higher than that of the Sn + Xt treatment throughout the experiment.

The average APRs of the Sn + Xt and Sn treatments were 71 and 83%, respectively, of that of the control treatment. The average APR of the Sn + Xt treatment over the 14-day period was significantly lower than that of all other treatments except Sn. When average APRs were determined for days 11–14, those in the Sn treatment were lowest and were significantly less than those of the control and Xt treatments.

Transpiration. Transpiration data from experiment 3 are summarized in Table 4 and illustrated in Fig. 5. The transpiration rates of the Sn + Xt treatment were significantly lower than those of the control treatment on days 6–9, 11, and 12. On day 6, transpiration rates of the Sn + Xt treatment were significantly below those of the Sn treatment. The rates of the Sn treatment were significantly lower than those of the control on days 7, 9, and 12. The transpiration rates of Sn + Pc differed significantly from those of the control only on day 12. In Sn + Pc, rates were significantly higher than in Sn + Xt on days 6, 7, 9, and 10 and were not significantly higher than in Sn throughout the experiment. The Xt treatment was significantly different from the control on day 12.

Sn + Xt was the only treatment that reduced average transpiration rates of leaves significantly compared with the control. Average transpiration rates of the Sn and control treatments

TABLE 3. Average photosynthetic rate, yield parameters, and disease severity in experiment 2

Treatment	Average apparent photosynthesis rate (mg CO_2/hr/dm^2)[y]	Percentage of control	Grains per head	Grain weight per head (g)	Weight per grain (g)	Disease severity (percentage of leaf affected)
Control	11.8 ab	100	5.1	0.157	0.031	0
Xanthomonas translucens (Xt)	12.8 a	109	8.6	0.255	0.030	0
Septoria nodorum (Sn)	6.8 c	57	9.1	0.187	0.021	19
S. nodorum + *X. translucens* (Sn + Xt)	10.8 bc	92	7.8	0.162	0.021	22
S. nodorum + *Pseudomonas cepacia* (Sn + Pc)	12.0 ab	102	7.9	0.192	0.024	4
S. nodorum + *P. cepacia* (24Pc + Sn)[z]	9.2 bc	78	0.418	0.020	0.020	16

[y]Numbers followed by the same letter are not significantly different at the 0.05 level. Statistical analysis was done on average photosynthesis data only.
[z]*P. cepacia* applied 24 hr before *S. nodorum*.

TABLE 4. Average photosynthesis and transpiration rates of flag leaves in experiment 3

Treatment	Average apparent photosynthesis rate (mg CO_2/hr/dm^2)[z]	Percentage of control	Average apparent photosynthesis rate for days 11–14 (mg CO_2/hr/dm^2)[z]	Average transpiration rate (g/H_2O/hr/dm^2)[z]
Control	15.7 a	100	18.9 a	4.9 a
Xanthomonas translucens (Xt)	15.7 a	100	17.5 ab	4.6 ab
Septoria nodorum (Sn)	13.0 ab	83	11.9 c	4.6 ab
S. nodorum + *X. translucens* (Sn + Xt)	11.1 b	71	12.6 c	4.1 b
S. nodorum + *Pseudomonas cepacia* (Sn + Pc)	14.3 a	91	15.3 bc	4.8 a

[z]Numbers within a column followed by the same letter are not significantly different at the 0.05 level.

TABLE 5. Average photosynthetic rate, yield parameters, and disease severity in experiment 4

Treatment	Average apparent photosynthesis rate (mg CO_2/hr/dm^2)[z]	Percentage of control	Grains per head	Grain weight per head (g)	Weight per grain (g)	Disease severity (percentage of leaf affected)
Control	14.0 a	100	13.3	0.42	0.032	0
Xanthomonas translucens (Xt)	12.9 a	92	15.1	0.44	0.029	0
Septoria nodorum (Sn)	13.8 a	98	11.3	0.37	0.033	44
S. nodorum + *X. translucens* (Sn + Xt)	12.9 a	88	12.3	0.39	0.032	33
S. nodorum + *Pseudomonas cepacia* (Sn + Pc)	14.7 a	105	9.0	0.28	0.031	21

[z]Numbers followed by the same letter are not significantly different at the 0.05 level. Statistical analysis was done on average photosynthesis data only.

did not differ significantly.

Experiment 4—photosynthesis. No significant differences were observed among the treatments in experiment 4 throughout the 28-day experiment. APRs gradually decreased in all treatments from day 0 through day 28 (Fig. 6).

The weight per grain and average APR were essentially unaffected by the treatments (Table 5). Disease on flag leaves was much more severe in the Sn and Sn + Xt treatments, with ratings of 44.4 and 33.1%, respectively, than in the Sn + Pc treatment (20.6%). The Xt and control treatments had disease ratings of zero. No significant differences were found between the control and any other treatment in average APR. The Sn + Xt treatment reduced average APR by 12.0% compared with the control.

DISCUSSION

Previous reports indicated that infection by *S. nodorum* significantly reduced photosynthesis of flag leaves (11,15–17). In this study, at 21 C, *S. nodorum* did not reduce the APR of flag leaves. *X. translucens* f. sp. *undulosa* alone did not affect the APR of flag leaves. When both organisms were applied to the same leaf, APR was not significantly reduced from that of leaves inoculated with the fungus alone. Experiments 1 and 3, in which inoculation with both organisms resulted in a greater reduction of APR, though not significantly lower than *S. nodorum* alone, were the only two cases which may have had an interaction. Thus, *X. translucens* neither enhanced nor hindered the effect of *S. nodorum*.

When inoculated at the same time as *S. nodorum*, *P. cepacia* partially or completely reduced the effect of *S. nodorum* on APR. However, when applied 24 hr before *S. nodorum*, *P. cepacia* had little effect on the reduction of APR caused by *S. nodorum*. Thus, *P. cepacia* may be antagonistic when applied at the same time as *S. nodorum* but appears to lose its effect after 24 hr on the leaf surface.

Incubation temperature appeared to have an important influence on the effect of *S. nodorum* on APR of wheat flag leaves. Thomas (19) found similar disease severity on seedlings inoculated at temperatures between 18 and 30 C. In experiment 4, *S. nodorum* had a less pronounced effect on APR than in experiments 1, 2, and 3, in which higher temperatures during part or all of the incubation period markedly reduced APR. Measuring APR may be a more sensitive measurement of disease severity than rating external symptoms. This effect needs further study.

Transpiration rates of flag leaves were not reduced as extensively as APR by *S. nodorum*. However, a reduction in transpiration did accompany a reduction in APR. Reduced transpiration in infected plants has been observed previously (3,4,12,13). However, in experiment 3, APR decreased markedly in flag leaves receiving the Sn, Sn + Xt, and Sn + Pc treatments from day 11 through day 14 without a large drop in transpiration. A synergistic effect between *X. translucens* f. sp. *undulosa* and *S. nodorum* may have been operating in experiment 3, in which the greatest reduction in transpiration occurred in the dual inoculation. *P. cepacia* with *S. nodorum* had no effect on transpiration.

Based on the results of these four experiments, *X. translucens* and *S. nodorum* probably do not interact significantly in nature. Transpiration, APR, and disease severity were not appreciably affected when *S. nodorum* was applied in combination with *X. translucens* or alone.

Scharen and Krupinsky (16) stated that measuring APR may be a good way to select cultivars with resistance to *S. nodorum*. Because *S. nodorum* was shown in previous studies to reduce APR (11, 15–17), and because *P. cepacia* effectively reduced the effect of *S. nodorum* on flag leaves in experiments 1, 2, and 3, measuring APR may be a useful way to detect antagonists of *S. nodorum*.

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