Competition Between *Pyrenophora tritici-repentis* and *Septoria nodorum* in the Wheat Leaf as Measured with de Wit Replacement Series

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ABSTRACT

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Competitive interactions between *Pyrenophora tritici-repentis* and *Septoria nodorum* were studied quantitatively by a modified plant ecology technique known as "de Wit replacement series." *P. tritici-repentis* and *S. nodorum* were inoculated alone and in various proportions together on wheat plants at anthesis. Mature leaves were harvested and incubated in moist chambers, after which fungal sporocarps were counted. For each inoculation mixture, the relative yield of each fungus (ratio of its sporocarp yield in the mixed inoculation to its sporocarp yield in single inoculation) was plotted against the proportion of that fungus in the inoculation mixture. The relationship between inoculation ratios and relative yields was compared statistically to a hypothetical noncompetition model. Measurable competition occurred between *P. tritici-repentis* and *S. nodorum*. *P. tritici-repentis* was the better competitor because its relative yields were less affected by the presence of *S. nodorum* than vice-versa. The de Wit replacement series is a useful tool for quantitatively examining competitive interactions between plant pathogens.

Additional keywords: *Leptosphaeria nodorum*, *Triticum aestivum*.

Competitive interactions, in the broad sense, are basic to the ecology of plant pathogenic fungi (23). These interactions have been studied by a variety of techniques, including tests of inhibition in vitro (6,27), microscopic observations of hyphal interactions (6,7,17,27,28), and germ tube inhibition tests (5,9,20).

The outcome of competition can be assessed, also; for example, the biomass of the interacting fungi can be measured. However, methods for hyphal biomass measurement are tedious and, in most cases, nonspecific with regard to the fungus measured (12,18). In this study, the "de Wit replacement series" technique was used to investigate the outcome of competitive interactions between two plant pathogens in a host. The technique was developed originally by plant-population ecologists to study competitive interactions between herbaceous plant species (8,13,26). In plant experiments, seeds of two species are sown together in varied proportions, with total plant density held constant to avoid confounding interspecific competitive effects with crowding effects. The relative yield for each species (its yield in mixture divided by its yield in pure stand at the same total plant density) is plotted against the input proportion (Fig. 1). If inter- and intraspecific competition are equal in intensity, the yield of each species is directly proportional to its proportion in the starting mixture. At each input ratio of the two species, the sum of their relative yields gives the relative yield total (RYT); the shape of the RYT line reflects the interaction between the two species in the mixture. Thus, an RYT line that is concave downward (Fig. 1) indicates stronger interspecific than intraspecific competition,

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that is, antagonism, whereas an RYT line that remains at 1.0 results when the species mixture is yielding in proportion to the input.

There are few techniques to statistically analyze data from replacement series experiments. Generally, data simply are examined subjectively, or the RYT of a particular input ratio may be compared statistically with a value of 1.0 (2). In this report, we compare observed relative yields (solid lines in Fig. 1) with a null-hypothesis model in which inter- and intraspecific competition are equal (Fig. 1, dotted lines).

For our experiments, we chose two plant pathogens that commonly occur in leaf-spotting complexes on wheat (*Triticum aestivum* L.): *Pyrenophora tritici-repentis* (Died.) Drechs. (anamorph, *Drechslera tritici-repentis* (Died.) Shoem.), causal agent of tan spot of wheat (15), and *Septoria nodorum* (Berk.) Berk. (teleomorph, *Leptosphaeria nodorum* Müller), causal agent of glume blotch of wheat (11,16,24,25). The two fungi have similar life cycles. Both infect wheat leaves and stems; after death of the host, they survive saprophytically in infested debris where they produce fruiting structures (15,21,24).

The goal of our research was to quantitatively analyze interactions between *P. tritici-repentis* and *S. nodorum* in the wheat leaf by means of the replacement series method. A preliminary report has been published (1).

MATERIALS AND METHODS

Fungal cultures. Virulent isolates of *P. tritici-repentis* (isolates 6R180, MCR-II, Pt-lc) and *S. nodorum* (isolate 2T121A), obtained from diseased wheat in Kansas, were used throughout this study. Stock cultures were maintained on slants of clarified carrot juice agar (CJA) (15 g of agar, filtered juice from 175 g of carrots autoclaved for 20 min and made up to 1 L) at 4 C and were reisolated from diseased plant tissue approximately every 6 mo.

To produce inoculum, *P. tritici-repentis* was transferred to CJA dishes and maintained 10 cm beneath 40-W cool-white fluorescent lights with a 12-hr photoperiod at 16 C. Conidial production was stimulated by first flattening the hyphae with a sterile glass rod, then incubating the cultures under continuous light for 24 hr, followed by 12 hr of darkness at 16 C.

Conidia of *S. nodorum* were induced by spreading a concentrated conidial suspension evenly across a CJA dish with a sterile glass rod. Dishes were incubated at 16 C beneath 40-W cool-white fluorescent lights with a 12-hr daylength until pycnidia with cirri were produced (approximately 7–10 days).

Plants. TAM 105, a winter wheat cultivar susceptible to *P. tritici-repentis* and *S. nodorum*, was used for all inoculations. One-week-old seedlings were vernalized for 40 days at 4 C, thinned to one plant per pot, then grown to maturity in a greenhouse (21–25 C). Plants at anthesis (growth stage 10.5.2 Feekes' scale [19]) were used for these experiments.

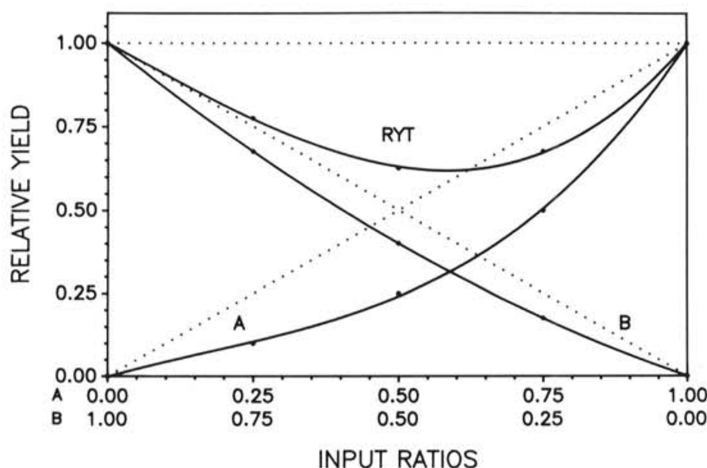

Fig. 1. Example data of replacement series between hypothetical species A and B. Dotted lines indicate equivalence of inter- and intraspecific competition, and solid lines represent interspecific competition between the two species. RYT = relative yield total.

Inoculations. Conidia of *P. tritici-repentis* or *S. nodorum* were collected in sterile water containing 0.05% Tween 20 (Sigma Chemical Company, St. Louis, MO). Conidia were quantified microscopically and adjusted to the concentrations shown in Table 1. For *P. tritici-repentis*, conidial suspensions were collected from dishes of the three isolates, then combined before quantifying and adjusting the inoculum concentration. In preliminary experiments (S. Adee, *unpublished*), single-pathogen inoculations at the listed maximum spore concentrations of *P. tritici-repentis* or *S. nodorum* gave approximately equal numbers of lesions for the two pathogens (approximately 30–35 per leaf). These lesion numbers are similar to the highest number observed in the field for *P. tritici-repentis* (E. Adee and W. Pfender, *unpublished*).

DeVilbiss atomizers (The DeVilbiss Company, Somerset, PA) were used to spray spore suspensions onto wheat leaves. Before inoculations, five atomizers with similar output (0.32 ± 0.03 ml/sec) were selected, one for each treatment. Atomizers were attached to an air pump (Gast Manufacturing Corp., Benton Harbor, MI), and spore suspensions were sprayed on leaves at approximately 80 kPa. The top three leaves (flag leaf and the two leaves below it [flag-1 and flag-2]) of two tillers per pot were sprayed, each leaf for 2 sec. The design of each experiment was a randomized complete block with two replicates (pots) per treatment. Data were collected from tillers according to leaf position, and the data from the two tillers per pot were averaged to produce each replicate value used in the statistical analysis.

Two methods of inoculation were used. In the first method (coinoculation), conidia of both *P. tritici-repentis* and *S. nodorum* were applied simultaneously at their respective concentrations. Initial experiments indicated that, when both fungi were applied simultaneously, *S. nodorum* did not compete as well as *P. tritici-repentis*. To determine whether prior access to the leaf by *S. nodorum* would give it a competitive advantage, a second method of inoculation (time lag) also was used. For this method, plants first were inoculated with respective concentrations of *S. nodorum* and 4 days later with the appropriate concentrations of *P. tritici-repentis*. In two of the three experiments reported here, both types of inoculations were performed in the same experiment.

After inoculation, leaves were allowed to air dry, and then plants were placed in a mist chamber in a greenhouse at 21–25 C to favor infection (14,22). DeVilbiss humidifiers in the chamber were used to keep a thin layer of moisture on the leaves. After 48 hr, plants were returned to the greenhouse bench.

When seed had reached ripeness (growth stage 11.4 Feekes' scale [19]), tillers were cut and left to dry for 1–2 days on the greenhouse bench. The top three leaves from each tiller were collected for experiments.

Fungal yield. Sporocarp development was induced by putting leaves in glass petri dishes (100 × 20 mm) containing damp, sterile

TABLE 1. Spore concentrations of *Pyrenophora tritici-repentis* and *Septoria nodorum* used for leaf inoculations

	Coinoculation		Time-lag inoculation	
			Day 0	Day 4
Treatment[a]	Ptr[b]	Sn[c]	Sn[c]	Ptr[b]
1	2.50	0	0[d]	2.50
2	1.75	0.5	0.5	1.75
3	1.25	1.0	1.0	1.25
4	0.62	1.5	1.5	0.62
5	0	2.0	2.0	0[d]

[a]Treatments 1–5 designate, respectively, the following input ratios of resultant lesions of *P. tritici-repentis* to lesions of *S. nodorum*: 1:0, 0.75:0.25, 0.5:0.5, 0.25:0.75, and 0:1.

[b]Ptr = conidia and conidiophores of *P. tritici-repentis* per milliliter (× 10^3).

[c]Sn = conidia of *S. nodorum* per milliliter (× 10^6).

[d]On day 0 and day 4, a 0.05% Tween 20 solution was sprayed on uninoculated plants.

vermiculite covered with sterile plastic embroidery screen. Wheat leaves (one per dish) were cut into 3–4 pieces and placed on the screen. Dishes were placed approximately 30 cm below 40-W cool-white fluorescent lights with a 12-hr photoperiod at room temperature (23–25 C) for 3 wk. Leaves then were removed from the dishes, placed in test tubes containing sterile distilled water containing 0.05% Tween 20 (Sigma Chemical Company), and agitated by means of a vortex mixer for 2 min; this treatment removed conidia of *P. tritici-repentis* and spores of contaminating fungi and softened the leaves. Leaves then were mounted in the water-Tween solution between two microscope slides.

Microscopic observations were made at ×22. Pycnidia of *S. nodorum* and ascocarps of *P. tritici-repentis* on each leaf were counted. Because ascocarp sizes varied greatly, total ascocarp volume per leaf was estimated. Ascocarps were categorized as small (150–300 μm), medium (300–500 μm), or large (500–800 μm). The mean volume of an ascocarp in each class (calculated as a sphere having a diameter equal to the mean of the class value) was multiplied by the total number in each class, and these volumes were summed. Because pycnidial sizes of *S. nodorum* did not vary significantly, total numbers were recorded. Fruiting body production for each fungus was divided by the area of the leaf (average width × length) to produce values of fungal yield per unit leaf area.

Relative yield values (0–1.0) of *P. tritici-repentis* and *S. nodorum* were calculated by dividing their average yield in mixture by their average single-inoculation yield. The relative yield for *P. tritici-repentis* was calculated from ascocarp volume per unit leaf area; the relative yield of *S. nodorum* was calculated from number of pycnidia per unit leaf area. Relative yield totals were calculated by adding the relative yields of *P. tritici-repentis* and *S. nodorum* for each treatment.

To test the effect of competition on conidial production of *P. tritici-repentis*, conidia on the leaves of treatments 1 and 4 (Table 1) were counted after sporocarp data were taken. To count conidia, each leaf first was cut into 0.5-cm pieces and ground in a blender for 30 sec in 0.05% Tween solution. Dilutions of this suspension were placed in a counting dish, and conidia were counted at ×40 magnification with the use of a microscope. Conidia of *P. tritici-repentis* that previously had been removed from the leaf with the aid of the vortex mixer were similarly counted; the two estimates were summed for total conidia per leaf.

Statistical analysis. Statistical analysis of data consisted of three parts. For each fungus, observed relative yield lines were compared statistically with the reference lines for equality of inter- and intraspecific competition (Fig. 1) by a lack-of-fit regression test (10). Secondly, a pairwise *t*-test for treatments 2, 3, and 4 deter-

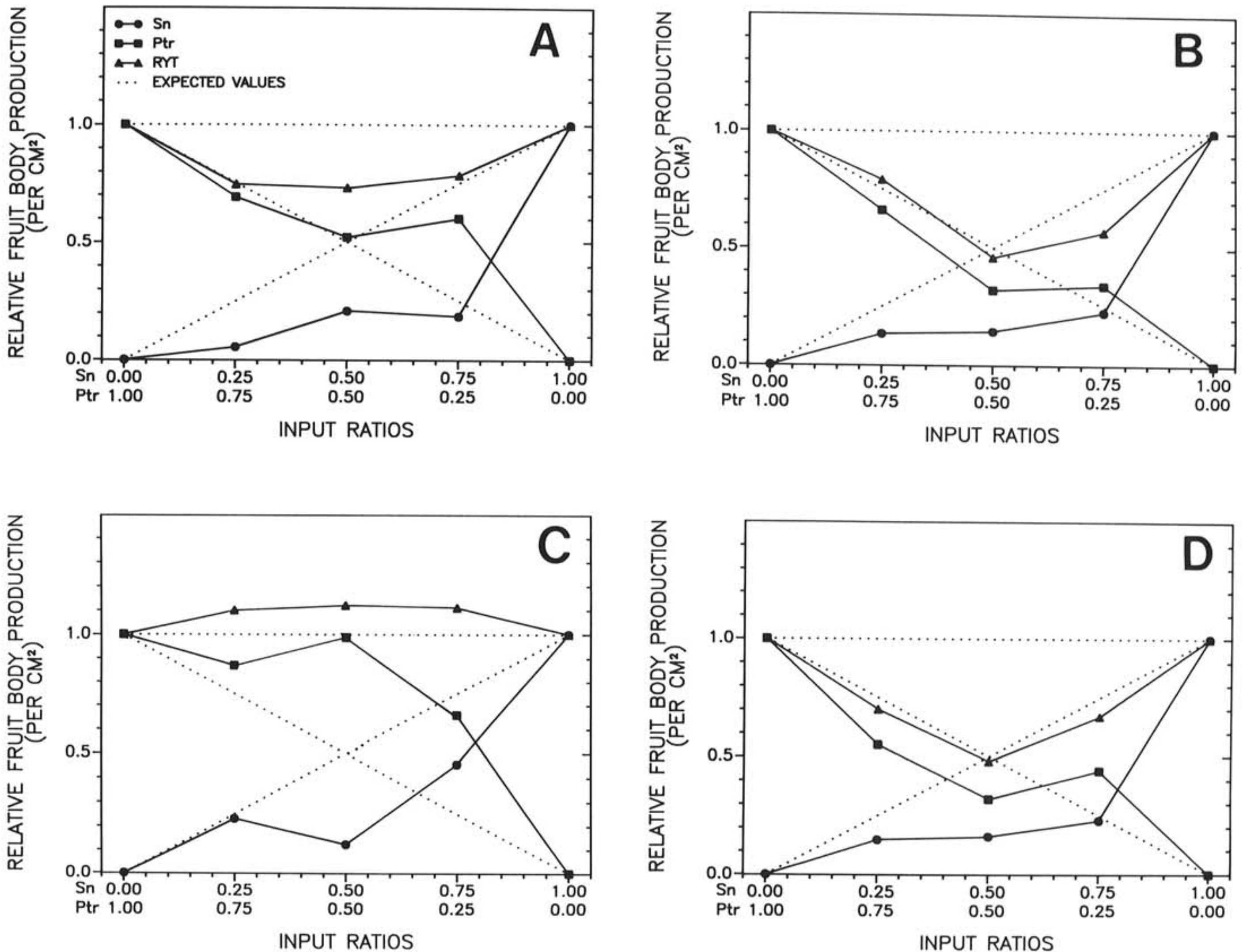

Fig. 2. Relative sporocarp production for *Pyrenophora tritici-repentis* and *Septoria nodorum* resulting from varied conidial input ratios. **A,** Sporocarp production on flag leaf coinoculated with both fungi. **B,** Sporocarp production on flag leaf that was inoculated first with *S. nodorum*, followed 4 days later by *P. tritici-repentis* (time-lag inoculation). **C,** Coinoculation, and **D,** time-lag inoculation of flag-1 leaf. Data points are the means of two replicates from one experiment (experiment 2). Experiment was repeated with similar results. Sn = yield of pycnidia of *S. nodorum*; Ptr = yield of ascocarp of *P. tritici-repentis*; and RYT = relative yield total. Expected values (dotted lines) are reference values indicating equal inter- and intraspecific competition.

mined which observed means differed significantly from the respective points on the reference line. (Although equivalence of inter- and intraspecific competition is not typical in nature, the reference lines were used for testing this equivalence as a null hypothesis for either or both fungi.) Finally, observed RYTs were compared by a nonparametric sign test, with a reference line having a value of 1.0. For this comparison, observations of RYT for each of the treatments 2, 3, and 4 were categorized as greater than (+) or less than (−) a reference value (1.0); the probability that the observed distribution of categories (+ or −) was attributable to chance was tested (4).

RESULTS

Fungal sporulation. Size of ascocarps of *P. tritici-repentis* ranged from approximately 150 to 800 μm. There was no significant effect of treatment, leaf position, or method of inoculation on ascocarp size. Medium-sized ascocarps contributed the most (approximately 85%) to the total ascocarp volume (data not shown).

Generally, sporocarps of the two fungi tended to occur in separate clusters, rather than being randomly interspersed on leaves. Number of pycnidia and total ascocarp volume were variable among experiments, as reflected by significant time-of-experiment effect; therefore, experiments were not analyzed across time, but individually. No significant differences between treatments 1 and 4 or between leaf positions were found for numbers of conidia of *P. tritici-repentis*.

Interpretation of model. Relative yields of *P. tritici-repentis* and *S. nodorum* were plotted against their input proportions in mixture and compared with reference lines denoting equal inter- and intraspecific competition. For each treatment (input ratio), the yield of each fungus is expressed in relative terms, where yield of the fungus in its single-inoculation treatment equals 1.0.

The relative yield values of *P. tritici-repentis* were more similar to the hypothetical model than were the relative yield values of *S. nodorum*, as observed in experiment 2 (Fig. 2), for example. The sharp reduction of the relative yield of *S. nodorum* on the right side of the figure caused the intersection between the relative yield lines for the two fungi to shift to right of center. The RYT line from coinoculation data indicated some variability, but the RYT lines from time-lag experiments consistently were lower than 1.0.

When the observed responses and hypothetical reference lines were compared by lack-of-fit and *t*-tests (Table 2), the lack-of-fit tests indicated that relative yield lines of *P. tritici-repentis* from both coinoculation and time-lag experiments usually fit the hypothetical model (straight lines). In the coinoculation experiments, *t*-tests indicated that data points for *P. tritici-repentis* were generally equal to or greater than the model reference values. The *t*-tests for time-lag experiments indicated that most of the observed points for *P. tritici-repentis* were equal to or less than the model values.

For *S. nodorum*, the lack-of-fit test (Table 2) indicated that relative yield lines tended not to fit the reference line for coinoculation experiments; in the time-lag experiments, *S. nodorum* fit in 50% of the trials. In experiments for which *t*-tests indicated statistical significance, the points for *S. nodorum* consistently fell below the reference value for both coinoculation and time-lag experiments.

The RYT for flag and flag-1 leaves in coinoculation experiments was significantly below the reference line (RYT = 1.0), except in one case for each leaf, as determined by a nonparametric sign test (Table 3). In time-lag experiments, RYTs for both leaves were consistently below the reference RYT of 1.0 (Table 3).

Data collected from the flag-2 leaf (Fig. 3) were highly variable within and between experiments; therefore, statistical analyses of these data are not presented.

DISCUSSION

Whereas several other investigators have studied fungal competition on host surfaces (5,9,20), our goal was to quantify the competitive interaction between *P. tritici-repentis* and *S. nodorum* during colonization of the wheat leaf. The de Wit replacement series technique was effective for this purpose; the relative yield of *S. nodorum* consistently was reduced in the presence of *P. tritici-repentis* as the wheat leaf was colonized.

Lack-of-fit and *t*-test comparisons of relative yield lines indicated that *P. tritici-repentis* was the better competitor (Table 2). Relative yield lines for *P. tritici-repentis* were either greater than or not significantly different from the reference line, indicating that competitive effects from *S. nodorum* were less than or equivalent to intraspecific competition of *P. tritici-repentis*. In contrast, several of the relative yield lines for *S. nodorum* were less than the reference line, and none of its relative yields were significantly greater than the reference values. This greater sensitivity of *S. nodorum* to competition can be seen in its downwardly concave shape. Further, the rightward displacement of the intersection of relative yield lines for the two fungi (Fig. 2) indicated that *P. tritici-repentis* was capturing nutrients at the expense of *S. nodorum*. Time-lag inoculations resulted

TABLE 2. Results of coinoculation and time-lag experiments comparing reference versus observed relative yield values of individual species

		Pyrenophora tritici-repentis				*Septoria nodorum*			
			t-test[d]				*t*-test		
Experiment[a]	Leaf[b]	Linear[c]	Above	NS	Below	Linear	Above	NS	Below
Coinoculation									
1	1	Yes	···	3	···	No	···	···	3
	2	Yes	···	2	1	No	···	···	3
2	1	Yes	···	3	···	No	···	···	3
	2	No	3	···	···	Yes	···	1	2
3	1	No	2	1	···	Yes	···	2	1
	2	No	2	1	···	No	···	···	3
Time lag									
2	1	Yes	···	2	1	Yes	···	···	3
	2	Yes	···	1	2	Yes	···	1	2
3	1	Yes	···	1	2	No	···	···	3
	2	Yes	1	2	···	No	···	···	3

[a] Experiment 1 consisted only of coinoculations. Experiments 2 and 3 consisted of both coinoculations and time-lag inoculations.

[b] Leaf 1 = flag leaf; leaf 2 = flag-1 leaf.

[c] Linearity tested by lack of fit. "Yes" denotes regression not significantly different ($P = 0.05$) from reference line. "No" denotes significant lack of fit from reference line. Lack-of-fit test for experiment 1 had 7 degrees of freedom, and the tests for experiments 2 and 3 had 8 degrees of freedom.

[d] *t*-test ($P = 0.05$) done for means of treatments 2, 3, and 4, testing the hypothesis that the difference between the observed and reference values = 0. Values are the number of points (out of three) above, not significantly different from (NS), or below the respective reference points.

TABLE 3. Analysis of relative yield totals (RYT) for coinoculation and time-lag experiments

Experiment	Leaf[a]	RYT observations compared with reference[b]		
		Less than	Equal to	Greater than
Coinoculation				
1	1	5*	1	...
	2	6*	...	...
2	1	6*	...	...
	2	2	...	4
3	1	3	1	2
	2	6*	...	...
Time lag				
2	1	6*	...	...
	2	6*	...	...
3	1	6*	...	...
	2	6*	...	...

[a] Leaf 1 = flag leaf; leaf 2 = flag-1 leaf.
[b] Number of RYT observations (out of six) that were less than, equal to, or greater than 1.0 for each experiment and leaf position. Nonparametric sign test,with $P = 0.05$, was used to determined whether observed distribution of observations was significantly different (*) from random.

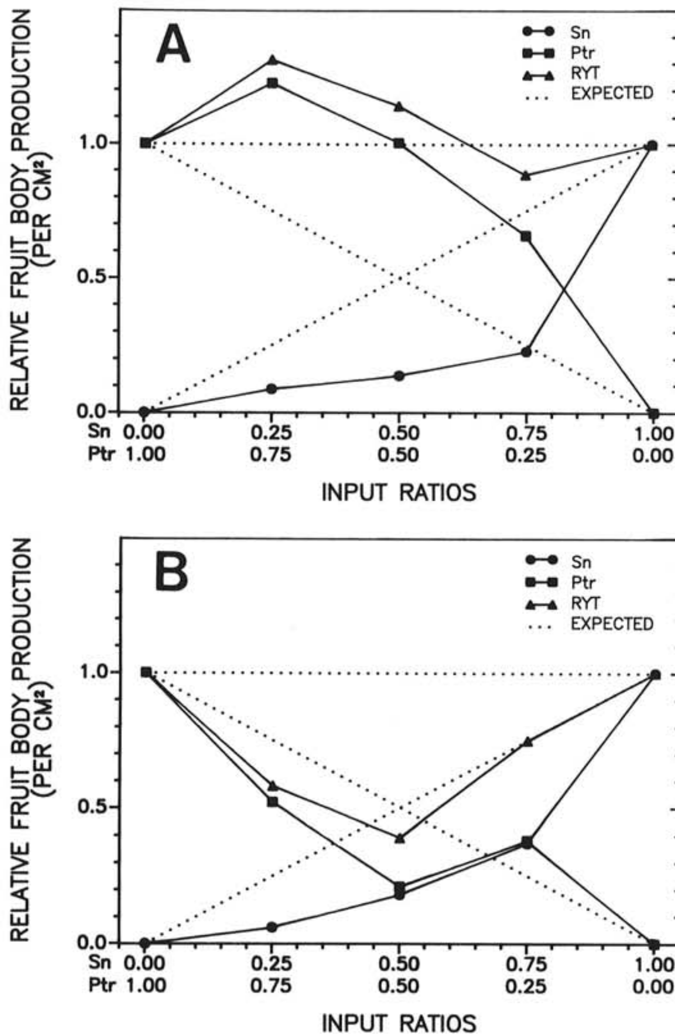

Fig. 3. Relative yield lines for *Pyrenophora tritici-repentis* and *Septoria nodorum* on the flag-2 leaf. **A,** Sporocarp production resulting from coinoculation with the two fungi. **B,** Sporocarp production resulting from time-lag inoculations, where *S. nodorum* was inoculated 4 days before *P. tritici-repentis*. Sn = yield of pycnidia of *S. nodorum*; Ptr = ascocarp yield of *P. tritici-repentis*; and RYT = relative yield total. Expected values (dotted lines) are reference values indicating equal inter- and intraspecific competition.

in fewer above-reference relative yield values for *P. tritici-repentis* than in the coinoculation experiments (Table 2); but the greater susceptibility of *S. nodorum* to competition remains, despite its advantage of prior colonization.

RYTs were reduced significantly in most of the coinoculation experiments and in all of the time-lag inoculation experiments for the flag and flag-1 leaves (Table 3), indicating strong interspecific interference between *P. tritici-repentis* and *S. nodorum*. None of the RYT values was significantly greater than 1.0. Plant ecologists report that RYTs significantly less than 1.0 indicate some mechanism of strong antagonism between the two species, such as allelopathy (13); the reduced RYTs we observed may similarly indicate the presence of a fungal antibiotic. Relative yields of *P. tritici-repentis* for the time-lag method were less variable than for the coinoculation method, indicating that first inoculating plants with *S. nodorum* removed some factor (at present unknown) that may cause variability in the response of *P. tritici-repentis*.

Our interpretation of replacement series experiments was based on descriptions given by plant ecologists. For infection of a host by plant pathogens, however, additional factors may influence the outcome of the competitive interaction. For example, infection of the wheat plant by *P. tritici-repentis* and *S. nodorum* may elicit toxic host metabolites to which one or both of the fungi may be sensitive. Additionally, resistance or susceptibility of a given cultivar could affect infection or colonization, thereby influencing the outcome. The presence of other microorganisms (that is, saprophytic fungi, bacteria, or yeast) (3) on the leaf surface may affect results. As wheat leaves senesce, saprophytic fungi commonly colonize the leaves and may prevent colonization of localized sites of senescent leaf tissue by plant pathogens. As mentioned, data collected from the third leaf position were highly variable due, perhaps, to colonization by saprophytes on the leaf.

We propose this type of experiment, and the indicated data analysis, as useful tools for quantitating competitive interactions between plant pathogens. The method is applicable to interactions occurring during the pathogens' parasitic phase, saprophytic phase, or both. It is more time consuming than some other techniques, but we think that it is more sensitive than in vitro methods and provides more insight into the nature and outcome of competitive interactions between pathogens.

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