Growth of the Sporulating Zone of Puccinia striiformis and Its Relationship to Stripe Rust Epiphytology

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ABSTRACT

Sporulation zones of *Puccinia striiformis* were measured daily for 5-12 days on several cultivars of wheat at different growth stages in the greenhouse and field. The sporulating zones showed a definite and continuing increase in area over time. The growth of the measured lesions was linear during the measurement period, but the rate of growth of the lesions on certain cultivars appeared to decrease with maturation. The characteristic of lesion enlargement permits an intensification of disease in the absence of conditions conducive to reinfection and profoundly affects the epiphytological aspects of the disease.

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Additional key words: predictive model, cereal rust, daily multiplication factor, removals.

Since 1958-60, when stripe rust, caused by *Puccinia striiformis* West., initiated so much damage to the wheat (*Triticum aestivum* L.) of the Pacific Northwest, interest has been directed toward the epiphytology of this disease. During the same period interest in epiphytological models has accelerated. *P. striiformis* shows a characteristic that is unique among cereal rusts, and is of utmost importance to its rate of increase in the field. This is the systemic growth of the organism within the leaf of the host; it is manifested by the continual enlargement of the sporulation zone. Thus, stripe rust infection intensifies in the absence of conditions necessary for reinfection. This characteristic is important to the epiphytology of the disease and to the development of predictive models. Current epiphytological models of cereal rust development are concerned with stem or leaf rusts or both. When stripe rust is referred to in relation to these models, there is little or no mention that the sporulating zone continue to increase, or that the increase affects the model structure.

We conducted a series of experiments to determine the increase per day of the sporulating zone and the influence of the host cultivar on the rate of increase. Measurements of the sporulating zones of stripe rust on several host cultivars and growth stages were made daily.

MATERIALS AND METHODS.—Studies were conducted in the greenhouse on the wheat cultivars Baart, Gaines, Nugaines, Adams, and Luke; and in the field on Omar, Golden, McCall, and Adams. In the greenhouse, leaves of 8- to 10-day-old plants were inoculated in a settling tower (2) with 3 mg of uredospores of *P. striiformis* germinating at 65-80%. (It has been previously determined that 5 mg of spores used in the settling tower would produce about 9-10 infections per leaf, thus a dosage level of 3 mg produced not more than three infections per leaf.) Infection was established by holding the inoculated plants in a dark dew chamber for 16 hours at an air temperature of 10 C. The plants were then placed in a greenhouse maintained at 20 ± 2 C. When sporulation was visible and the zone measurable (about 1 mm in diameter), 10 plants each supporting one infection per leaf were selected from each cultivar; the others were discarded. The leaves were numbered, and the diameters, lengths, and widths of the sporulating lesions were measured at about the same time each day for 5-7 days. During the seedling and tillering stages, the growth of the lesion was unrestricted so it eventually covered the entire leaf. In the late tillering and subsequent stages, growth was restricted by the leaf veins, thus forming the characteristic stripes.

The field experiments were carried out in conjunction with epiphytological studies at the Agricultural Experiment Station, Pendleton, Oregon. Omar wheat was seeded in October, 1972, and inoculated at three dosage rates (0.0041, 0.041, and 0.41 g/hectare) with uredospores of *P. striiformis* supplied by the Department of Botany and Plant Pathology, Oregon State University. During the late tillering stage of plant growth (7-18 May 1973), leaves supporting not more than three well distributed infections were tagged for measurement of the sporulating zones. This procedure was repeated at the joint stage (31May-8 June 1973) and at the early milk stage (13-20 June 1973). The infections measured during the milk stage were on the flag leaves as were those on the cultivars Golden, Adams, and McCall in an adjacent inoculated nursery. The measurements were made about the same time each day for 7-12 days, but were not continued past the 12th day because new infections would tend to overrun those being measured or would coalesce. When such interference did develop, the measurement of that sporulating area was discontinued. However, near drought conditions existed during this experiment, which resulted in a low incidence of reinfection, and only a few discards were necessary.

RESULTS.—*Greenhouse.*—The sporulation zones showed a definite and continual increase in area over time. The amount of increase ranged from 8.8 to 18.8 mm^2/day (Table 1). Analysis indicated that the means of the daily increases did not differ significantly at $F_{0.95}$, but did at $F_{0.99}$ except for Gaines and Adams. The average daily increase of the sporulating zones closely agreed with the slope (b) computed from the average daily sizes of the sporulating zones (Table 1). This agreement suggests linear growth of the sporulating areas. A test for linearity of regression yielded F values smaller than those for $F_{0.95}$ in each instance (Table 2).

Field.—Sporulation zones measured in the field had the same characteristic as those in the greenhouse: the

TABLE 1. Evaluation of average daily increase in size (mm^2) of the sporulating zone of *Puccinia striiformis* on seedling leaves of several greenhouse-grown wheat cultivars

Cultivar	Initial size (mm^2)	Increase (mm^2)[a]	b[b]	r[c]	$S_{y.x}$[d]	s[e]
Baart	1.2	13.2 ± 2.28	13.41	0.998	1.359	2.61
Gaines	1.1	18.4 ± 6.02	18.93	0.995	3.515	6.86
Nugaines	1.2	15.8 ± 4.56	16.33	0.996	2.768	5.19
Adams	4.2	18.2 ± 4.79	18.36	0.994	3.779	5.46
Omar	0.4	8.8 ± 4.3	9.39	0.974	4.075	4.92
Luke	21.6	18.8 ± 5.67	18.44	0.982	8.624	7.66

[a] $P = 0.05$.
[b] b = slope of size on days.
[c] r = correlation coefficient.
[d] S_{xy} = standard error of estimate.
[e] s = standard deviation of size increase.

average daily size increase and the slope closely agreed (Tables 2 and 3). However, the average daily growth rate of the sporulating zones on the cultivar Omar (Table 3) appeared to decrease with increasing age of the host.

DISCUSSION.—Close agreement of the average daily increase of the sporulating zone with the slope (b) of the daily size of the lesions and the small deviation(s) (Tables 2 and 3) indicate that the rate of growth of the lesions was linear over the measurement periods. The agreement was evident in every experiment, whether in the greenhouse or in the field. The decreased rate of growth of the lesion on some cultivars; e.g., Omar, as the plant matured was probably a physiological host response and not a direct effect of the environment.

P. striiformis is systemic within the leaf of the host, but very little has been reported about its rate of growth as manifested by the enlargement of the lesion. Thus, the relationship of the lesion growth rate to the epiphytology of the disease has been ignored. Data presented here indicate that the sporulating zones increase significantly each day. This linear increase is of paramount importance in the epiphytology of stripe rust. Preliminary data indicate that about 200 uredospores are produced per mm^2 per day. This rate of spore production occurred for up to 12 days. Thus, the number of spores increased significantly in the absence of new infections.

The enlargement of the stripe rust lesion has a pronounced effect on the duration of the period that inoculum is available to initiate new infections, on the daily multiplication factor (DMFR) (number of effective spores produced per day per lesion), and on the removals (areas in which active sporulation ceases). The constant value of DMFR referred to by Zadoks (4) and used in relation to reinfection would seem to assume that the lesion does not appreciable enlarge and that, therefore, about the same number of spores is produced each day. In stem and leaf rusts, this value may be essentially constant after the lesion reaches its full size. Stripe rust lesions,

TABLE 2. Test for deviation from linearity of regression of size (mm^2) of sporulating zones of *Puccinia striiformis* on wheat cultivars in greenhouse and field

Cultivar	Plant stage	Computed F	df	$F_{0.95}$
Greenhouse				
Luke	Seedling	1.38	6,72	2.24
Gaines	Seedling	1.208	4,54	2.554
Nugaines	Seedling	1.41	4,54	2.554
Baart	Seedling	0.233	4,54	2.554
Adams	Seedling	1.26	4,54	2.554
Omar	Seedling	0.36	4,44	2.549
Field				
Omar	Tiller	0.272	7,166	2.01
Omar	Joint	0.47	10,101	1.93
Omar	Milk[a]	0.128	5,36	2.482
Golden	Milk	0.004	6,68	2.241
McCall	Milk	0.08	6,72	2.236
Adams	Milk	0.099	6,42	2.331

[a] All measurements during the milk stage were made on the flag leaf.

TABLE 3. Evaluation of average daily increase in size (mm^2) of the sporulating zone of *Puccinia striiformis* on several field-grown wheat cultivars

Cultivar	Plant stage	Initial size (mm^2)	Increase (mm^2)[a]	b[b]	r[c]	$S_{x.y}$[d]	s[e]
Omar	Tiller	12.15	4.56 ± 1.48	4.5	0.993	1.46	1.77
Omar	Joint	9.3	6.19 ± 1.71	6.5	0.997	1.77	2.54
Omar	Milk[f]	7.2	2.06 ± 1.94	2.0	0.977	0.82	1.57
Golden	Milk	22.1	3.26 ± 0.78	3.2	0.998	0.54	0.84
McCall	Milk	12.9	2.76 ± 1.06	2.6	0.990	0.88	1.14
Adams	Milk	13.1	1.95 ± 2.72	2.0	0.947	1.30	2.19

[a] $P = 0.05$
[b] b = slope of size on days.
[c] r = correlation coefficient.
[d] $S_{x.y}$ = standard error of estimate.
[e] s standard deviation of size increase.
[f] All measurements during the milk stage were made on the flag leaf.

however, enlarge each day until they coalesce, reach the extremities of the leaf, or the plant tissue senesces due to maturation or because of adverse climatic conditions. The DMFR, therefore, cannot be considered a constant value in stripe rust epiphytotics. Removals are considered by van der Plank (3) as unimportant in cereal rust models. Zadoks, however, includes them in his system analysis (4). If removals are to be considered as the area in which active sporulation ceases because of lesion age, then removals are not a factor in stripe rust epiphytology. Sporulation of *P. striiformis* appears as profuse at the original site of infection as at the extremities of the enlarging lesion, so in stripe rust a removal can only occur at the death of the leaf, either with age or because of adverse climatic conditions.

The prolonged period of spore production, the increasing DMFR, and lack of influence of removals results in a nearly constant infection rate after the infection logarithmic phase. This result is evidenced by the straight line increase of the disease, and the reduced plateau of the slope (1). This "flattening" of the slope, so characteristic of other cereal rusts, is explained by van der Plank (3) as caused by the amount of noninfected tissue available for infection. The availability of infectible tissue also decreases as stripe rust infection increases, thereby reducing the chance for reinfection. However, the sporulating zones of the existing infections increase at a definite rate each day, and so result in increasing severities without new infections. This result evidently permits the infection slope to continue in an upward pattern until plant maturation begins.

The influence of the expanding sporulation zone on the dynamics of stripe rust epiphytology cannot be ignored in the development of predictive systems.

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