Comparison of the Effects of Sublethal Doses of Triadimefon to Those of Rate-Reducing Resistance to *Erysiphe graminis* in Wheat

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ABSTRACT

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Attempts to control plant disease by the use of rate-reducing resistance were stimulated by the periodic demise of race-specific resistance genes selected to give almost complete control. Similarly, some systemic fungicides, used at rates determined to give almost complete control, result in the selection of fungicide-tolerant populations. Reasoning that these fungicides at sublethal dosages may affect the same components of disease development as rate-reducing resistance, we postulated that fungicides used in this way might enable management of some plant diseases at less cost and with reduced risk of causing rapid selection of fungicide tolerant populations. By testing triadimefon against powdery mildew of wheat, it was determined that disease efficiency and sporulation capacity were reduced greatly by amounts less than one-one hundredth of the recommended dosages. We conclude that studies of disease management with such small dosages are in order to see if such procedures will lessen the rate of development of fungicide tolerance and increase the commercial life of both cultivars and fungicides.

There are striking similarities between the selection of virulent plant pathogenic strains of fungi by race-specific resistance genes and the selection of fungicide-resistant strains by systemic fungicides. The first case has been called a selection for "vertical" virulence by vertical resistance (22). The specific modes of action of systemic fungicides act similarly, causing greater selection than broad action fungicides of strains called fungicide resistant or tolerant. Race-specific resistance can lose its value rapidly. Its merit is that it is relatively easier for plant breeders to handle. A defeated gene can, with considerable effort, be replaced or augmented by other genes. For fungicides, the solution is more complex; addition of different enzyme inhibitors to a fungicide requires costly new patents, testing, registrations, and market development. Because of chemical similarities among new fungicides, "cross-resistance" is a problem; one fungicide may select pathogen strains resistant to other fungicides (3–5).

In the last two decades, resistance breeding has pursued a second control strategy—the employment of what Vanderplank (19) called "horizontal" resistance, which we call by the epidemiological term "rate-reducing" resistance. Rather than employing resistance, which effectively stops pathogen population development, selection is made for lines on which disease will develop, but at rates low enough that final disease is below or near economic thresholds of loss. This strategy is particularly suitable for staple crops and has been demonstrated to be useful in potatoes (2) and cereals (12,15,18,20,21). The appeal of this second strategy is based on theoretical population genetics as well as experience. Allowing the pathogen to develop should reduce selection pressure for virulent strains. Such cultivars should have a longer effective life, ie, their resistance should be more "durable."

The technique of components analysis (23,24) is used to identify which segments of the disease monocycle are affected by rate-reducing resistance and to quantify the effects. For fungal foliar disease it has been reasoned and then demonstrated that increased latent period (15,17), fewer lesions per inoculum unit (reduced infection or disease efficiency) (8,12,16,21), and reduced sporulation (14,16,21) are the three most important attributes of rate-reducing resistance. Similarly, studies of the mode of action of new fungicides and of resistance to them have demonstrated production of spores that cannot germinate (1,7), reduced sporulation (2), and reduced lesion size (2,22), provided the dose is not lethal to almost all of the fungal population.

Dosage response studies of toxicants typically reveal a single pattern. A proportion of the population is very sensitive and is killed or affected by very low dosages. Most of the population is killed by relatively low dosages, but a certain proportion of the population is killed only by high dosages. This is due not so much to differing sensitivity within a population of spores as to the probability of random contact of fungus and fungicide molecules. A plot of the dosage response results in a "diminishing returns," negative exponential curve. These data may be transformed to fit a straight line (1). Different fungicides, pathogens, crops, and environments will produce different slopes of this line. For disease control in the field, it is usual to apply fungicide dosages great enough to kill nearly all of the population, ie, at ED_{95}, ED_{99}, or even much higher depending on cost of the fungicide, phytotoxicity, crop surface characteristics, compensation for weathering effects, bio- and photo-degradation, and the "safety factor" used. This practice, it is reasoned, not only selects for the most resistant strains of the pathogen, but may eliminate competitors from the environment, thus favoring their rapid increase (3).

If the use of such massive doses is analogous to the use of race-specific resistance in its selection of resistant strains, it seems reasonable to hypothesize that much smaller doses will mimic rate-reducing resistance, allowing disease to develop, but affecting length of the latent period, inoculum efficiency, and sporulation. If so, then the theory that rate-limiting resistance should suppress selection of virulent isolates logically leads to a second theory that sublethal doses should suppress selection for fungicide-resistant isolates.

In the experiments reported here, we tested the effects of low dosages of triadimefon on powdery mildew of wheat. Results of preliminary trials were reported earlier (13).

MATERIALS AND METHODS

Inoculum. *Erysiphe graminis* D.C. f. sp. *tritici* isolate 244, a single-colony isolate obtained from wheat (*Triticum aestivum* L. 'Titan') in Pennsylvania in 1980, was used in this study. Inoculum

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was obtained by inoculating 7-day-old seedlings of wheat cultivar Chancellor growing in a pasteurized soil mixture of Hagerstown silty clay loam, peat, and sand (2:1:1, v/v) in 5-cm-diameter clay pots. Glass lamp chimneys were placed over each pot at the time of planting and closed with two layers of tissue paper to prevent contamination. Inoculated plants were placed in a growth chamber (20 C, 12-hr photoperiod, and irradiation of 80 $\mu E \cdot m^{-2} \cdot sec^{-1}$) for 9 days to allow the increase of conidia for further inoculations. To ensure that newly formed conidia were used as inoculum, plants to be used for the inoculum source were shaken 24 hr prior to use to remove older conidia.

Plants for fungicide tests. Seeds of cultivar Chancellor were sown at two seeds per hole, four holes per side of 16.5 × 12 × 6-cm plastic flats in the soil mixture described above. Twelve days after planting, 16 primary leaves were draped over an 8 × 15 × 10-cm wire grid with the adaxial surfaces facing upward and were secured with masking tape, leaving exposed an area about 50 mm long × 3 mm wide; other leaves were removed.

Application of fungicide. The suggested field application rate of triadimefon (as Bayleton 50% wettable powder) is 142 g a.i./ha (2 oz a.i./acre) applied in 374 L/ha (40 gal/acre). This is the equivalent of 450 mg a.i./1,200 ml. We mixed 0.8, 1.6, 2.4, 4.0, and 6.0 mg a.i./1,200 ml water; 0.4 ml of Tween-20 was added to all suspensions as well as to the water control. Spraying was done with a special plot sprayer developed for turfgrass studies. This sprayer was equipped with conejet T 18x nozzles mounted about 46 cm above ground level and operated at 200 kPa. To approximate field application of 374 L/ha, flats were placed on the floor and the sprayer was wheeled over them at ~1 m/sec. Fungicides were applied 1 day before inoculation. There were four flats each of the 0, 0.8, 1.6, and 2.4 mg treatments; because trials showed greatly reduced colony numbers at higher dosages, seven flats were included in the 4- and 6-mg/1,200-ml treatments to obtain enough data for analysis.

Inoculation. A modified version of the Melching settling tower (9) with dimensions of 1.40 × 0.73 × 0.73 m was used. Infected leaves of Chancellor were placed in a funnel at the top of the chamber and short blasts of nitrogen gas (69 kPa) were used to dislodge conidia from colonies. While conidia settled, flats were rotated on a turntable at 42 degrees per second to yield a more uniform inoculum deposit. After each inoculation, flats were bagged and transferred to a growth chamber maintained at 20 ± 2 C with irradiation at the top of the trays of 80 $\mu E \cdot m^{-2} \cdot sec^{-1}$ and a 12-hr photoperiod. The bags were removed after 2 days and the trays were moved closer to the lights with irradiation of 170 $\mu E \cdot m^{-2} \cdot sec^{-1}$.

Data collection. Beginning on day 7 after inoculation, colonies were counted and conidia were harvested every other day through day 13. Conidia were removed by vacuum from all colonies on a leaf (10). Spore collection was discontinued after day 13 because of the appearance of daughter colonies from secondary infections. The spore collection tube contained 5 ml of 0.1% Tween-20. The nozzle of the collection apparatus was coated with organosilane (Prosil-28, PCR Research Chemicals Inc., SCM Corp., Gainesville, FL 32602) to inhibit adhesion of spores. Between collections, 1 ml of distilled water was drawn through the nozzle into the collection tube to minimize spore carryover to the next sample.

Spore counting. Twenty milliliters of a 1% NaCl solution was added to each tube and four 0.5-ml aliquots were counted with a model zB Coulter Counter (Coulter Electronics Inc., 590 West 20th Street, Hialeah, FL 33010). The aliquot counts were adjusted to compensate for the background count, then averaged and converted to mean number of conidia per colony per day.

Dosage-mortality analysis. The classical method of Bliss (1) was used in which dosage, as the abscissa, was rendered as log dosage, and colony numbers were converted to probit percent survivors, survivors at zero dosage being taken as 100%. Data for the zero dose were omitted from these linear regression analyses because the log of zero may not be taken and the approximation of −3 affected the regression disproportionately.

Estimation of mean latent period. An attempt was made to apply the probit technique of Shaner (17) to colony numbers per leaf over time with the knowledge that this would be an estimate of incubation period rather than latent period.

RESULTS

Reduction in colony numbers. Table 1 shows that colony numbers per leaf declined as dosage increased, and colony numbers increased gradually with time for all dosage levels. Linear regressions obtained by transforming colony numbers to probit percent survivors and dosage to log dose show that quite similar dosage responses were obtained on days 9 through 13. The r^2 values are judged satisfactory. The range of ED_{50}, ED_{95}, and ED_{99} (in milligrams) obtained with the three regression equations is given.

Fig. 1 shows, for day 11 only, the actual data obtained, the transformed dosage-mortality curve, and the detransformed dosage response curve. In these tests, triadimefon showed a strong ability to reduce colony numbers at quite low dosages.

Latent period. Inspection of Table 1 reveals a lengthening of the incubation period (time from inoculation until the appearance of first colonies) by the two highest doses. It follows that latent period would be similarly affected. The technique of Shaner (17) to obtain values for mean latent period could be applied only to dosages of 0,

TABLE 1. Effect of sublethal dosages of triadimefon on numbers of *Erysiphe graminis* colonies per leaf of wheat

Dosage (mg)	Days after inoculation			
	7	9	11	13
0.0	7.57	9.51	10.66	11.17
0.8	2.54	3.16	3.78	4.09
1.6	1.60	2.02	2.29	2.43
2.4	0.75	1.50	1.58	1.63
4.0	0	0.91	0.93	0.95
6.0	0	0.60	1.03	1.08
Regressions: Y^a =		$4.46 - 1.26x$	$4.46 - 1.15x$	$4.47 - 1.19x$
r^2		0.98	0.94	0.93
ED_{50} (mg)[b]		0.37	0.33	0.36
ED_{95}		7.4	9.0	8.6
ED_{99}		26.0	36.0	33.0

[a] Y = probit percent colonies; x = log of fungicide dose.
[b] ED signifies the dose calculated by regression analysis to be effective against the proportion of the population indicated by the subscript, eg, ED_{50} is the dose effective against 50% of the population.

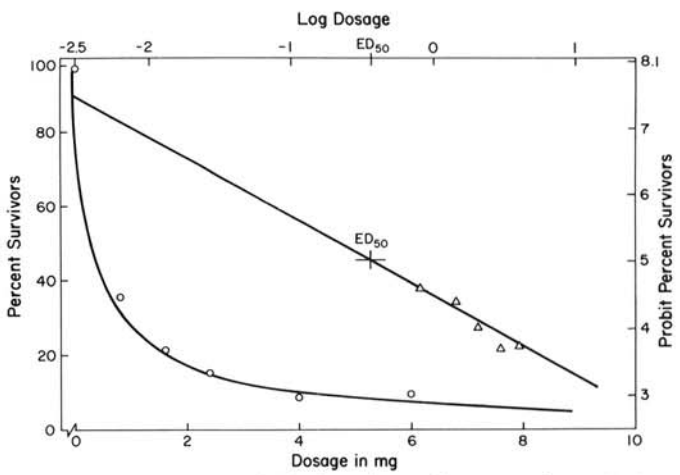

Fig. 1. Dosage response to triadimefon of *Erysiphe graminis* f. sp. *tritici* on wheat leaves. The straight line is the regression of probit percent survivors against log of dose. Actual data (zero dose omitted) and the ED_{50} are indicated. The curved line is the plot of percent survivors against dosage obtained by detransforming the straight line; actual data, including zero dose, are indicated.

0.8, 1.6, and 2.4 mg; values of 6.3, 6.9, 6.5, and 6.9 days, respectively, resulted. From this test no latent period lengthening effect could be ascribed to these lower dosages.

Sporulation. Reading downward in Table 2, the effect of increasing fungicide dosage is seen for each sampling day. For all days, a dosage of 6 mg reduced spore numbers by >70%. Further, the effect of increasing dosage can be seen clearly for any day. There were, of course, no spores on day 7 for the two highest doses because there were no colonies. Reading across, one sees the increase in numbers of spores per colony during the 6-day sampling period; these data are of spores produced in each 2-day interval. From other studies (J. R. Pelletier, *unpublished*) of wheat mildew, it is known that cumulative sporulation is represented by a sigmoid curve, the upper inflection of which, for this cultivar-isolate combination, is well after day 13. These present data, being in the exponential segment of this curve, were renderable as a straight line by transforming to the natural log of accumulated spores; then linear regression analysis could be used to compare dosage effects. This analysis (Table 3) reveals that although increasing dosage reduced the cumulative numbers of spores at any observation time, the rate of sporulation (slope of the regression) was not affected greatly by dosages 0 through 2.4 mg. The two highest doses show a greater effect on rate, but the regressions are derived from only three data sets and may be less reliable. We conclude that there is some effect on rate of sporulation but that repression of sporulation is also a function of delay in reaching the sporulating state, as shown by the y-intercepts for dosages 0 through 2.4. Fig. 2 is a linear plot of the effect of each dosage on accumulated spores per colony.

A plot of cumulative spores per leaf, rather than of spores per colony, integrates all effects measured in these studies—increased latent period, decreased infection efficiency, and repressed sporulation—and provides a grasp of their potential epidemiologic effect. The values plotted in Fig. 3 are the product of mean number

TABLE 2. Effect of sublethal dosages of triadimefon on mean number of spores per colony of *Erysiphe graminis*

Dosage (mg)	Days after inoculation			
	7	9	11	13
0.0	72	2,725[a]	10,689	36,349
0.8	52	2,075	8,696	27,755
1.6	48	1,237	6,424	22,365
2.4	21	1,136	5,348	16,126
4.0	0	872	5,672	15,752
6.0	0	480	2,898	10,300

[a] Each entry, beginning with day 9, indicates the mean number of spores produced per colony in the 2-day interval since the previous collection.

TABLE 3. Effect of triadimefon on cumulative spore production per colony and on the rate of spore production of *Erysiphe graminis*

Dosage (mg)	Day (X)	Mean no. spores per colony ($\times 10^{-3}$) (Y)	ln Y	Regression[a]	r^2
0.0	7	0.072	−2.63	$-9.37 + 1.06X$	0.94
	9	2.797	1.03		
	11	13.386	2.6		
	13	49.834	3.91		
0.8	7	0.52	−2.96	$-9.77 + 1.07X$	0.93
	9	2.127	0.75		
	11	10.823	2.38		
	13	38.578	3.65		
1.6	7	0.048	−3.04	$-9.89 + 1.06X$	0.96
	9	1.284	0.25		
	11	7.708	2.04		
	13	30.079	3.4		
2.4	7	0.021	−3.86	$-11 + 1.13X$	0.93
	9	1.157	0.15		
	11	6.506	1.86		
	13	22.632	3.12		
4.0	7	0.0	···	$-7.29 + 0.81X$	0.98
	9	0.872	−0.14		
	11	6.544	1.88		
	13	22.296	3.1		
6.0	7	0.0	···	$-8.17 + 0.84X$	0.99
	9	0.48	−0.73		
	11	3.378	1.22		
	13	13.678	2.62		

[a] The regression is an estimate of ln Y (mean number of spores per colony).

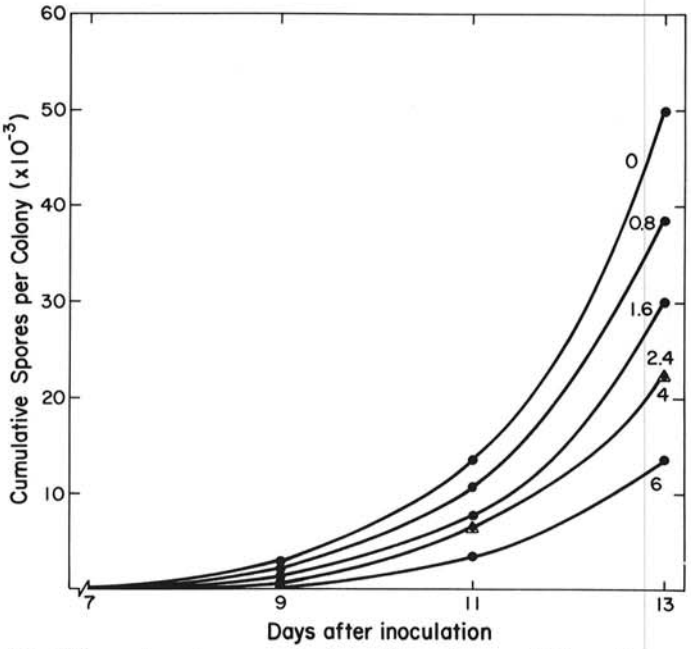

Fig. 2. Depression of spore production of *Erysiphe graminis* f. sp. *tritici* on leaves of wheat cultivar Chancellor by six dosages (in milligrams per 1,200 ml) of triadimefon.

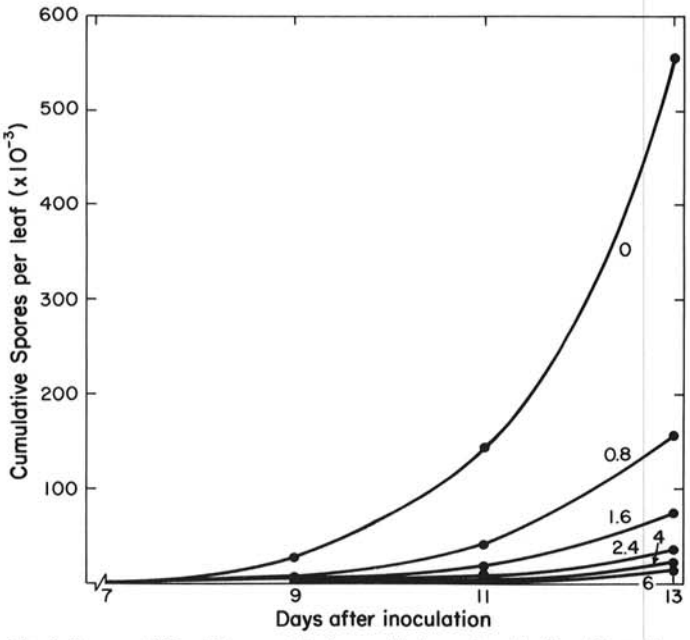

Fig. 3. Spores of *Erysiphe graminis* f. sp. *tritici* per wheat leaf as affected by six dosages (in milligrams per 1,200 ml) of triadimefon, showing the combined effects of reduced colony numbers per leaf as well as reduced spores per colony.

of colonies per leaf and mean accumulated spores per colony. The effect of increasing dosage is clear. If the data for day 13 in Fig. 3 are plotted, as a function of dosage, Fig. 4 results. Spores available for secondary cycles are reduced more than one order of magnitude, from 5.6×10^5 to 1.5×10^4, or to about 3% of the control. Even the lowest dosage, 0.8 mg, reduced accumulated spores per leaf to 28% of the control.

DISCUSSION

The purpose of this study was to demonstrate that dosages smaller than normally recommended, dosages termed by Dekker (3) as "sublethal" to populations, would induce fungal responses similar to those conditioned by partial or rate-reducing genetic resistance of host. We believe that the data presented demonstrate adequately, at the laboratory level of investigation, that this is so. Colonies per leaf were reduced to about 10% of the controls by a dosage of 6 mg; the suggested field dose is 225 mg. Sporulation per colony was reduced to <30% of the controls by a 6-mg/1,200 ml dose. Incubation period was obviously affected by the two highest dosages; the data suggest that all dosages had some repressive effect on colony development and so tended to delay the onset of the infectious period, even if not at epidemiologically significant levels. Spore production was progressively repressed by increasing dosage.

Our central theme is that if sublethal doses affect components of the monocycle in a way similar to the effects of rate-reducing host resistance, then the same strategy of disease management may be used. Such use would be most apt on staple crops in nonintensive agriculture (for which fungicide management is normally contraindicated) or in any crop plant disease for which management within the economic loss threshold is satisfactory. Obviously, the idea needs field testing. One would not expect the laboratory dosages to be so effective in the field, but the difference between 6 and 225 mg suggests that there is ample range for field testing. We can only mention in passing that a field test in a year of very little wheat mildew, when severity level effects could not be measured, incidence was reduced to one-half that of the controls by a dosage one-quarter of that recommended. Such a test is ample justification for moving to full-scale field tests. This raises the question: How great an effect on monocycle components must a rate-reducing cultivar or fungicide have in order to slow disease development satisfactorily? Vanderplank (19, pages 101–106 and 268) provided a theoretical way to answer this question, using R_c (the corrected basic infection rate or effective daily multiplication factor) and the threshold theorem. R_c may be estimated if one knows r_l, the exponential growth rate, or substitutes for it, r, the apparent infection rate, using the equation

$$R_c = r_l e^{(i+p)r_l} / e^{ir} l - 1$$

in which p is the length of the latent period and i is the length of the sporulation period. In these studies, p was 6.3–7.0 for the control. In a study of four cultivars against two isolates (J. R. Pelletier, *unpublished*), i had a range of 15–28 days; 21 days is a value satisfactory for this estimate. Elliot (6) found r to be about 0.12 per day on Chancellor in the field. Substituting these values into Vanderplank's equation gives a value for R_c of 0.29 per day. The threshold theorem (19) states that disease will not increase unless $iR_c > 1$. Translated, the theorem says that the product of the number of sporulating days times the number of daughter lesions per mother lesion per day must be ≥ 1 if the organism is to survive and >1 if the population is to increase. In the present case, $iR_c = 6.1$. To stop an epidemic, a resistant cultivar or a fungicide would have to let not more than one germinating spore in six survive. This ratio, 0.17, means that if sporulation is reduced to ~17% that of the control, the epidemic will be stopped as long as the impeding factor—the fungicide or the resistance—is active. Fig. 4 shows that in these laboratory studies all dosages except the lowest would have effectively stopped the epidemic. In field studies the dosages will need to be higher to be effective, because of (among other factors) weather degradation of the fungicide and the greater coverage required.

Certain possible long-term effects of such a management strategy now come to our attention. The appeal of rate-reducing host resistance is that, in theory, while it manages disease within economic loss thresholds, selection and increase of virulent and aggressive isolates are repressed. Such cultivars promise durability of resistance, and so, longer commercial lives. We hypothesize that use of sublethal dosages should have a similar effect on the pathogens. In this point we differ from Dekker (3, page 422). A pathogen population consists of a diverse group of genotypes, each with a given level of virulence and fitness. In a situation in which that population is exposed to a sublethal dosage of a systemic fungicide, we visualize that the entire population will persist at some reduced level. Each genotype will infect and reproduce, although not all to the same degree. If a mutation results in some level of tolerance to the sublethal dosage, the mutant genotype will not command the selective advantage it would have had if it were the only surviving genotype. We speculate that no massive population shift will occur, although we recognize that it is impossible to speculate on the rate of directional mutation. The situation, at least as we view it, seems analogous to that of a pathogen confronted with rate-reducing resistance. The truth of the matter awaits adequate testing.

The use of sublethal or minimal dosages would also lessen the dangers of gradual buildup of some fungicides in the upper layers of arable soils as discussed by Rawlinson et al (11).

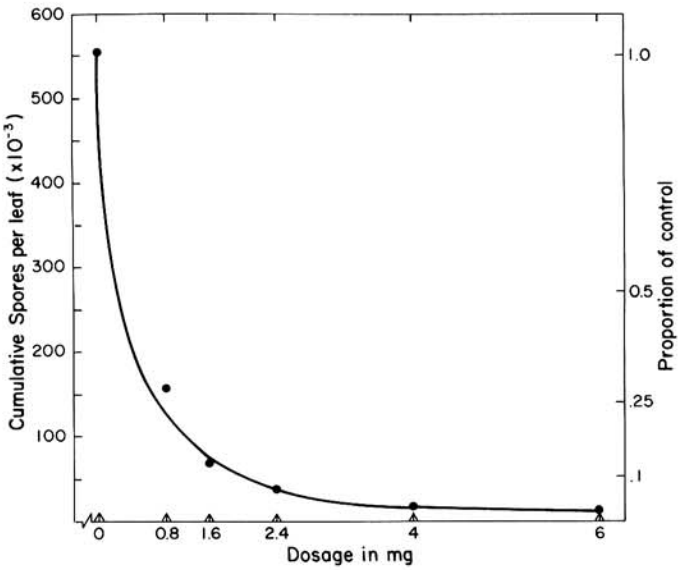

Fig. 4. Total spores per leaf produced by day 13 after inoculation by *Erysiphe graminis* f. sp. *tritici* as affected by six dosages (in milligrams per 1,200 ml) of triadimefon.

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