THE RELATION OF VARIETY AND DISTANCE
FROM AN INOCULUM SOURCE TO
SEVERITY OF WHEAT LEAF
RUST INFECTION

By

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1963

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
MASTER OF SCIENCE
December, 1974

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Thesis Approved:

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ACKNOWLEDGEMENTS

The author wishes to express his sincere appreciation to his major adviser, Dr. Harry C. Young, Jr., for his guidance and assistance throughout this study and preparation of the manuscript. Appreciation is also expressed to the other committee members, Drs. J. E. Thomas and R. V. Sturgeon, Jr., for critical review and suggestions concerning the manuscript.

The author is grateful to Dr. R. D. Morrison for assistance in conducting the statistical analysis.

The author wishes to thank the Department of Botany and Plant Pathology of Oklahoma State University for providing the facilities needed for this study.

The author is deeply indebted to the Rockefeller Foundation for the fellowship which made this study possible.

Finally, to his wife, Halide Celik, and to his child, Neha, the author wishes to express his sincere gratitude for their encouragement, patience, and sacrifice which were invaluable in the completion of the research reported herein.

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CHAPTER I

INTRODUCTION

Many fungi have highly efficient methods of spore liberation and some kinds of inoculum remain viable for a long time. Another requisite for biological success is abundant, timely, and widespread dissemination. The biological success of a pathogen is certainly an indication of its destructive potential economically. The rapid increase of disease development in cereal rust epidemics is partly due to the large number of uredospores produced at each infection site, and to the effectiveness of these uredospores as dispersal units. The interaction of host susceptibility-pathogen virulence and host growth stage within the limits of the environment determine the rate of disease increase and consequently epidemic development. However, the development of epidemics over wide areas ultimately depends primarily on spore dispersal.

There are two types of uredial inocula available within any given wheat field; the spores disseminated within the field from established infections, and that carried into the field from outside sources of infection. Hereafter, these types of inocula will be referred to as autogenous and exogenous inocula respectively. After the initial phases of an epidemic, autogenous inoculum generally exceeds exogenous inoculum because of the dilution by distance from the source. Consequently the rate of rust development within a field of susceptible wheat is governed ultimately by the dispersal of autogenous inoculum.

Gregory 1968 (22) reported that infection gradients are of two kinds: (a) environmental gradients, due to variation across a field, of such factors as ecoclimate or soil; and (b) dispersal gradients due to spatial variation in the amount of inoculum arriving.

Chamberlain (14), Gregory (22) and Schrödter (27) have all developed theories on spore dispersal. These theories were derived from: (I) the movement of spores and particles in relatively short wind tunnels; (II) the dissemination of spores released from point sources in the field; (III) the study of plant disease gradients; and (IV) consideration of the physical laws of particle movement.

Although these theories may be used to describe gradients from natural sources, empirical evaluation has been lacking. For example, wind turbulence, a most important factor under field conditions, is minimal in wind tunnels; spore dispersal gradients from point sources are known to be steeper than those from area sources (21); plant disease gradients of the cereal rusts are dependent not only on spore dispersal gradients, but also resistance or susceptibility, germination and growth of the pathogen and favorable environmental conditions; each of which may often be a greater limitation than spore dispersal gradients.

Similarly, physical laws of particle movement are based on particles that are nearly spherical, with a constant shape and weight; however, uredospores in addition to being variable in size and weight at formation, change in both weight and shape under variable conditions of temperature and humidity (32).

The objectives of this research, therefore, were:

1) To determine the relationship between distance from the

inoculum source and disease development when uredospores of leaf rust are blown past moistened seedling wheat plants.

2) To assess differences in leaf rust severity among five cultivars exposed to uredospores blown past the moistened leaves.

CHAPTER II

REVIEW OF LITERATURE

Leaf rust of wheat caused by *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* has often been regarded as a chronic disease, common in all wheat growing areas but rarely injuring the crop to any serious extent. In 1938, leaf rust epidemic development caused a $12,000,000 loss of Oklahoma wheat (17). Analogous losses were reported from Texas to the Prairie Provinces of Canada as the disease followed the crop northward (15, 16).

Chester (15), in 1939, reported that leaf rust does not oversummer in Oklahoma but passes the summer months in other parts of North America and returns via northerly winds and is deposited on fall-sown wheat.

Ukkelberg (31), in 1933, was the first to make a precise study of the rate of free fall of leaf rust uredospores in calm air. He found much variation in the rate of fall of individual spores. They required 90-150 sec. to fall 180 cm averaging 12.62 mm/sec.; at this rate of fall it would take leaf rust uredospores about 6 hr. 43 min. to fall one thousand feet.

Rusakow (25), in 1929, reported trapping an average of 127 spores in a 15 m/sec. wind and only 30 in a 8.5 m/sec. wind. Boevski (4) showed that the direction of a wheat field relative to a source of infection is fully as important as its distance from the source of infection. He also illustrated the effectiveness of barriers in preventing local rust dissemination. He observed reduced concentrations of leaf rust uredia with distance as follows: at 14 feet from the source there was half as much rust as at the source; at 245 feet 1/4 as much; and at 700 feet only 1/8 as much (26).

Asai (1) reported higher or more turbulent surface winds during the day also accounted for higher spore concentration in the air. Winds of variable velocity, night or day, caused variable spore concentrations. It was evident that higher velocity winds carried the spores not only further but higher.

That spores are carried higher into the air in winds of higher velocity is in agreement with the findings of Best, as reported by Sutton (29). He found that values for vertical gustiness were directly affected by wind velocity. At a height of two meters above grassland, he found that the mean value of vertical gustiness increased with mean wind velocity, especially during temperature inversions.

It is evident, then, that the dispersal of spores is a function of both vertical and horizontal forces of gravity and air movement. The first stage in dispersal is the liberation of spores from the structures in which they were formed. The mechanisms of spore discharge in the fungi were the subject of an extensive series of researches by Buller 1909-34 (10). Each biologically successful organism has a unique and specific mode of spore liberation. In leaf rust the uredospores are produced above the leaf surface where minute air currents can dislodge the mature spore. In still air, spores fall slowly under gravity, as mentioned earlier.

The period after discharge during which a basidiospore, for instance, is undergoing a positive acceleration due to gravity is very short on account of the small mass of the spore in comparison with its area. Working with the basidiospores of *Amanitopsis vaginata*, Buller (10) found that acceleration of spore fall was balanced by increased air resistance after a fall of less than one diameter of the spore (10μ) and that the fall continued thereafter at a constant terminal velocity. He concluded that this velocity might even decrease if desiccation further reduced the mass of the spore. Stokes's Law (21), which may or may not apply to fungus spores, describes the relation between the size and velocity of fall of a smooth sphere in viscous fluid in the following terms:

$$v = \frac{2}{g} \cdot \frac{P-\sigma}{u} gr^2$$

where v = terminal velocity, P = density of the sphere, σ = density of the medium, g = acceleration due to gravity, r = radius of the sphere, and u = viscosity of the medium.

Ukkelberg (31) showed that differences in rate of spore fall of uredospores and aecidiospores of *Puccinia graminis tritici* and *P. g. secalis* were probably due to differences in size, but it remains to be shown whether differences in the average terminal velocity within a population are also due to differences in size.

Basidiospores of certain fleshy fungi have been shown by Buller (10) to carry a small electric charge while falling through the air. It is also known that small particles tend to move down a temperature gradient (13).

Besides the vertical force of gravity, spores are also acted on by a wind force acting horizontally. The air is seldom still and its movement has been studied extensively.

Bilham (3) in England reported from 3,625 observations at two locations wind speeds over 96 percent of the time were above 0.3 m/sec. Highest speeds were from 3.5 to 7.9 m/sec. Wind speeds, therefore, are commonly 300 times, and usually at least 100 times, as great as the rate of fall of spores under gravity. Undoubtedly wind is a major factor in controlling spore dispersal, and may also play a part in the number of spores liberated into the air as was reported by Stepanoff (28).

Previous estimates of the probable limits of spore dispersal have usually been based on the trajectory of an individual spore considered as the resultant of its vertical fall under gravity and its horizontal transport by wind. Data on the slow speed of fall have been quoted as evidence that spores may be carried for great distances.

McCubbin (23) in 1918 reported that: "The problem of spore dispersal is vitally a question of the maximum dispersal distance" (page 36). Of main interest are those spores which fall most slowly, and therefore, are likely to be carried farthest in air currents. If such spores take approximately five minutes to fall a distance of eight feet, they will be carried 2.5 miles in a 30 mph. wind.

Christensen (18) calculated the approximate theoretical dispersal distance of spores falling under gravity from a height of one mile in a 20 mph. wind to be 740 miles, for a uredospore of about 28 x 17μ. Ukkelberg (31) calculated that if a uredospore of *P. graminis tritici* reached an altitude of 5,000 feet, its dispersal distance in a 30 mph. wind would be about 1,100 miles.

The foregoing discussion considered the motion of a spore in terms of a vertical motion of 1 cm/sec., and of a larger but more variable horizontal component varying from 30 to 2,500 cm/sec., with a mean near 300 cm/sec. These conditions only approximate the motion in comparatively rare cases on non-turbulent air movement such as under extreme temperature inversions. According to Brunt (9) there are usually present in the atmosphere large numbers of small scale eddies whose periods are in the order of one second, and at least two-thirds of the eddying energy is associated with eddies of periods of less than five seconds. The action of the numerous eddies of varying size on the very numerous spores produced from a given source makes regularity in the dispersal pattern impossible.

Finally, Todd and his associates (30) studying wind velocity in relation to physiological activities in wheat found that wind velocities of four to five m/sec. significantly effected stomatal opening and closing. This in turn, conceivably could effect infection and, ultimately, rust severity.

CHAPTER III

MATERIALS AND METHODS

Race UN 9 (2) of *Puccinia recondita* f. sp. *tritici* was used in this investigation. This race was isolated from a field of a susceptible cultivar grown in Oklahoma and at the time of this writing comprises about 5 percent of the population.

The five cultivars of wheat *Triticum aestivum* L. em. Thell., used in this investigation were, with one exception, susceptible, in the seedling stage, to this race. They were:

Danne C. I. 13876 (Dne)(5) was released in 1970 by the Oklahoma Agricultural Experiment Station and the Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture. It is a selection from material bequeathed to Oklahoma State University in 1959 by the late Joseph E. Danne. According to Mr. Danne's records the cross, made in 1950, was between Super Triumph and Western Prince. Danne is one of the widely grown cultivars in Oklahoma, has a high yield potential but is susceptible to leaf rust at all stages of growth.

TAM Wheat 101 C. I. 15324 (TAM W-101) is a short-statured wheat released by the Texas Agriculture Experiment Station in cooperation with the Crops Research Division, U. S. Department of Agriculture. Its pedigree is: Norin 16/3/ Nebraska 60 // Mediterranean / Hope / 4 / Bison. It has no known resistance to leaf rust.

Triumph 64 C. I. 13679 (Tmp 64) is a selection from the cross Danne

Beardless Blackhull /3/ Kanred / Blackhull // Florence /4/ Kanred / Blackhull // Triumph. The last cross was made in 1934 by a private plant breeder, Joseph Danne, El Reno, Oklahoma, and was released by him with the name "Rust Resistant Triumph." This cultivar has at least one rust resistance gene, probably the same gene as one found also in the older cultivars Westar and Concho. In 1964 the seed source was purified and released with the name Triumph 64 by the Oklahoma Agriculture Exteriment Station.

Scout C. I. 13546 (Sut) traces to a plant selection in the F_3 generation of the cross Nebred // Hope / Turkey /3/ Cheyenne / Ponca. The Nebraska Agricultural Experiment Station and the Agricultural Research Service, USDA, participated in the development and release of the cultivar. An early generation selection, it has exhibited some heterogenicity in several agronomic characteristics. It has one, and perhaps other genes, for resistance to leaf rust in the seedling stage.

Chinofuz C. I. 15350 (Cnf), is a short-statured line that attains only approximately half the adult plant height of the other cultivars used in this study. It has at least one gene for resistance to leaf rust in the seedling stage, effective against race UN9 used in this study, and one gene for resistance in the adult-plant stage effective against all cultures of the pathogen so far recognized in Oklahoma. The cultivar was developed in Oklahoma from a cross originally made at Purdue University, Lafayette, Indiana, and was released as leaf rust resistance germ plasm and not for commercial production (34).

Air movement for the experiments was provided by a Dayton forward curved centrifugal fan model 2C 944 9 modified at the outlet to provide a uniform air velocity of about 20 mph (10 m/sec.). The air velocity for each of the experiments was measured at each distance from the inoculum source with an anemometer. These velocities are given in Table I.

TABLE I

WIND VELOCITY FOR EACH DISTANCE FROM THE FAN OPENING TO THE PLANTS TO BE INOCULATED

Distance	Experiment I m/sec.	Experiment II m/sec.
00 cm	10.95	10.95
25 cm	9.59	8.48
50 cm	6.78	5.62
75 cm	3.65	2.84
100 cm	1.99	1.58
125 cm	2.18	1.28

Five distances from the inoculum source in increments of 25 cm, beginning with 25 cm were used in each of two experiments. In this study, distances represent whole plots and cultivars were arranged in a randomized complete block design. The design is shown in Figure 1. The same experimental design was used in both experiments, the difference between them being the way the inoculation was accomplished. This difference will be discussed later.

In each experiment 40 "Arasan" (50 percent Thiram) treated seeds

1 = Chinofuz; 2 = Tam Wheat 101; 3 = Triumph 64 Wheat; 4 = Scout; 5 = Danne [1]

Distance	Replication	Randomization of Cultivars[1]				
25 cm	1	1	2	3	4	5
	2	3	4	5	1	2
	3	4	5	2	3	1
	4	5	3	1	2	4
50 cm	1	1	2	3	4	5
	2	3	4	5	1	2
	3	4	5	2	3	1
	4	5	3	1	2	4
75 cm	1	1	2	3	4	5
	2	3	4	5	1	2
	3	4	5	2	3	1
	4	5	3	1	2	4
100 cm	1	1	2	3	4	5
	2	3	4	5	1	2
	3	4	5	2	3	1
	4	5	3	1	2	4
125 cm	1	1	2	3	4	5
	2	3	4	5	1	2
	3	4	5	2	3	1
	4	5	3	1	2	4

Figure 1. A Diagram of the Experimental Design

of each cultivar were planted in each of forty 10.16 cm pots. Each pot was firmly packed with 400 gm of a uniformly mixed soil composed of six parts of clay loam, one part fine sand and one part peat moss. The seeds were uniformly spread on top of the soil surface and firmly covered with an additional 100 gm of the soil mixture. Water was slowly added to each pot until the water began to drain at the base of the pot. Eight pots were used for each variety.

The pots were then placed in a greenhouse room maintained at 21 $\pm$ 3 C during both the night and day period. The pots remained seven days in the greenhouse until the primary leaves were well emerged. During this period soil moisture was maintained near optimum and the plants never were subjected to moisture stress. Beginning the third day after planting the plots were watered every other day.

The wheat seedlings were thinned to thirty plants per pot seven days after planting.

The inoculum for the experiments was prepared by increasing the rust uredospores twice on the cultivar "Cheyenne." The first increase was made by dipping pots of ten-day old seedling plants in water in which stored uredospores of the rust culture were dispersed. Then, 12 days after inoculation these rusted plants were used to brush inoculate (7) other pots of seedlings which would be used as the inoculum source in the experiments.

Inoculations were made when the five cultivars to be inoculated were seven days old and when the inoculum was ten days old. The two experiments were inoculated in the same manner except that in Experiment I each replicate of each distance was inoculated separately, while in Experiment II all distances were inoculated at once and each replicate separately (Figure 2). Each time, the source of inoculum was placed five cm from the outlet opening of the fan (Figure 3) which was activated for 30 seconds each time to disperse the spores (Figure 4).

In each experiment, the plants to be inoculated were sprayed with a solution containing tap water and a surfactant, "Tween 20" (polyoxyethelene 20 sorbitan monolaurate) at 3 to 4 drops/1000 ml water, sufficiently to wet the seedlings.

The inoculated plants were placed in glass-covered moist chambers for a period of twelve hours, after which they were removed to a growth chamber for seven days for disease development. At the end of that time ten leaves were taken randomly from the 30 leaves of each pot and the number of pustules per leaf were counted.

Figure 2. Arrangement of Pots to be Inoculated in Experiment II in Position in Front of Fan Opening (Inoculum Not in Place)

Figure 3. Inoculum in Place in Front of Fan Just Prior to Inoculation (Experiment I, 25 cm Distance)

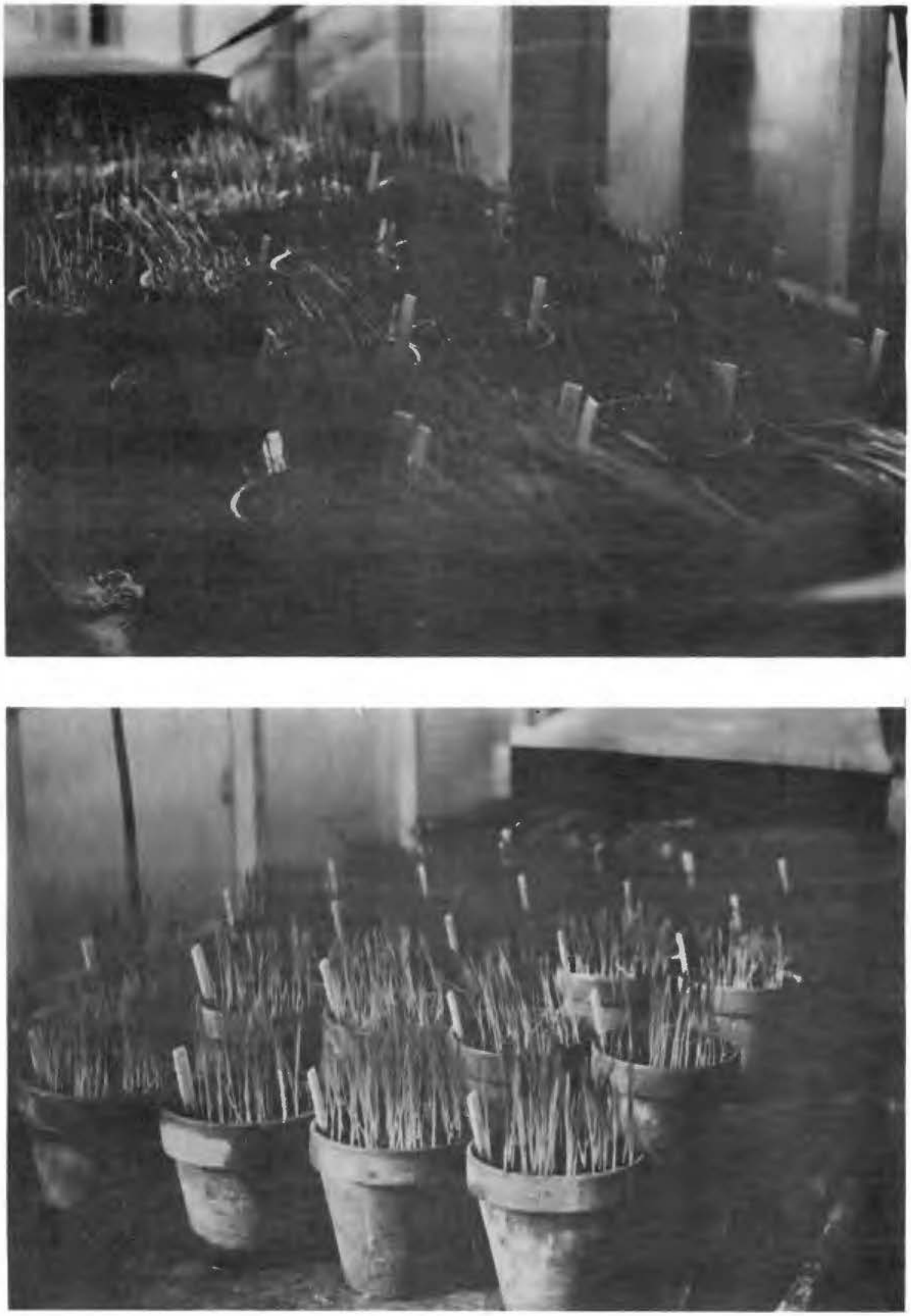

Figure 4. Inoculation Process in Operation (Experiment II)

CHAPTER IV

RESULTS

Experiment I was designed to measure the effect of distance from the inoculum source on leaf rust severity on several cultivars of wheat. In this experiment each distance was inoculated separately so that each succeeding distance would not be influenced by the plants at a shorter distance creating turbulence in the air flow patterns. The data are presented in Table II. It was found that distance from the source of inoculum did affect leaf rust severity. Significantly higher severities occurred on all cultivars at 50 and 75 cm from the inoculum source than at 25, 100 and 125 cm. It was also found that the cultivars tested did not all develop the same severity. The greatest amount of rust was found on the cultivar Danne (Figure 5) which was significantly higher than TAM Wheat 101, which, in turn was higher than Triumph 64 or Scout. The later two were not different from each other. The resistant cultivar Chinofuz had the least severity.

There was no significant interaction between distance and cultivar in this test, which means that all cultivars behaved similarly at all distances. This effect is illustrated in Figure 6 which adapts the data presented in Table II.

Experiment II was designed to test the same factors as Experiment I except that all plants were placed at the different distances and inoculated at the same time. Turbulence in air flow caused by plants closer to the inoculum source would then be expected to influence the inoculation of those further away. This, indeed, did happen. The highest severities were found at 100 cm from the inoculum source in this experiment where the highest severities in Experiment I were found at 75 cm (Table III).

TABLE II

THE NUMBER OF PUSTULES DEVELOPED PER LEAF OF FIVE CULTIVARS LOCATED AT FIVE DISTANCES FROM AN INOCULUM SOURCE BLOWN OVER THE PLANTS BY A 20 MPH WIND. EACH DISTANCE INOCULATED SEPARATELY (EXPERIMENT I)

	Distance From Inoculum in cm					
Cultivars[1]	25	50	75	100	125	$\bar{x}$ [2]
Cnf	37	64	102	41	25	54
TAM W-101	68	159	189	93	75	117
Tmp 64	54	117	161	68	59	92
Sut	63	110	163	60	54	90
Dne	136	194	265	117	96	162
$\bar{x}$ [3]	72	129	176	76	62	

[1]Abbreviations used are those proposed by Briggle et. al. (5).

[2]LSD (0.05) for comparing cultivar means = 18

[3]LSD (0.05) for comparing distance means = 51

Although the differences in rust severity between distances in

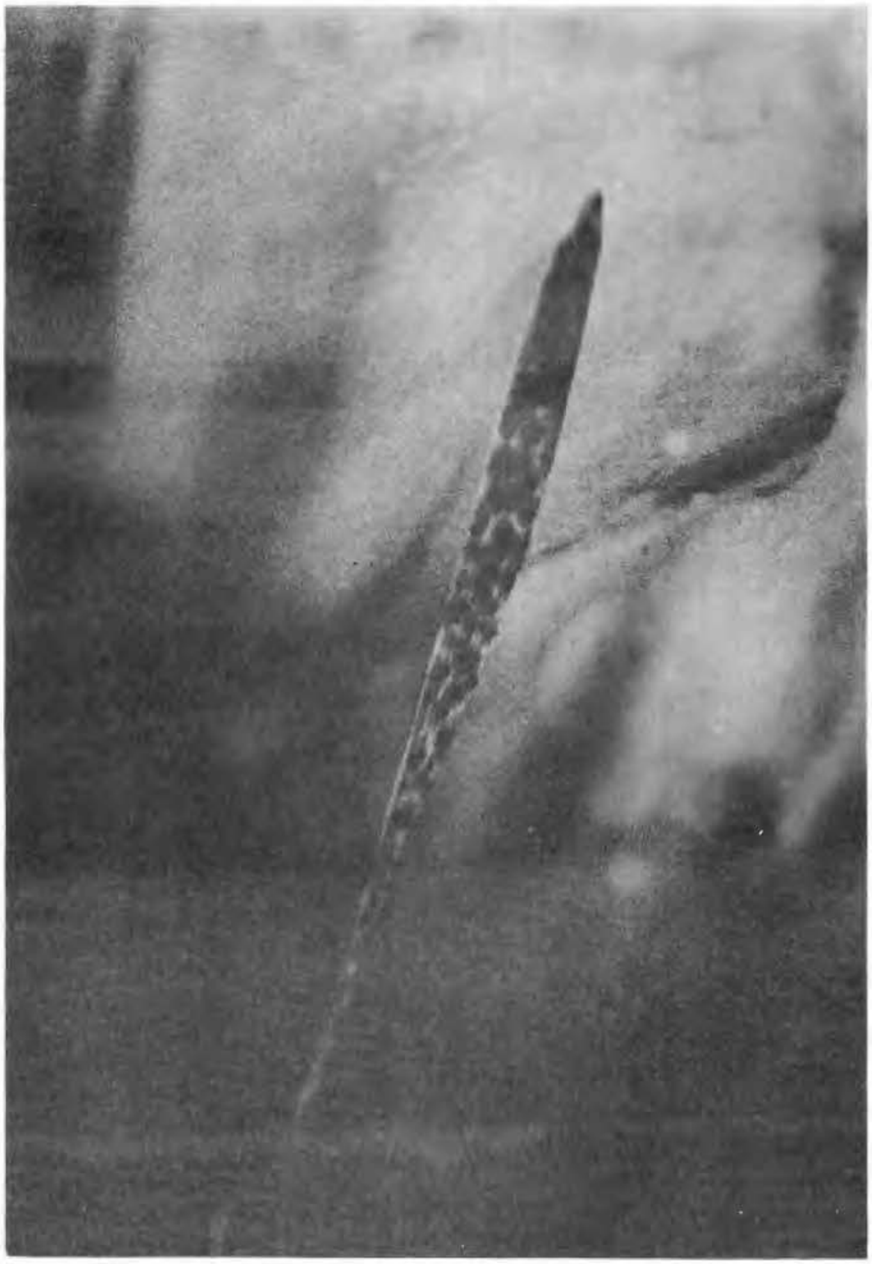

Figure 5. A Leaf of the Cultivar Danne Ten Days After Inoculation Indicating the Severity of Infection Developed at 75 cm From the Inoculum Source (Experiment I)

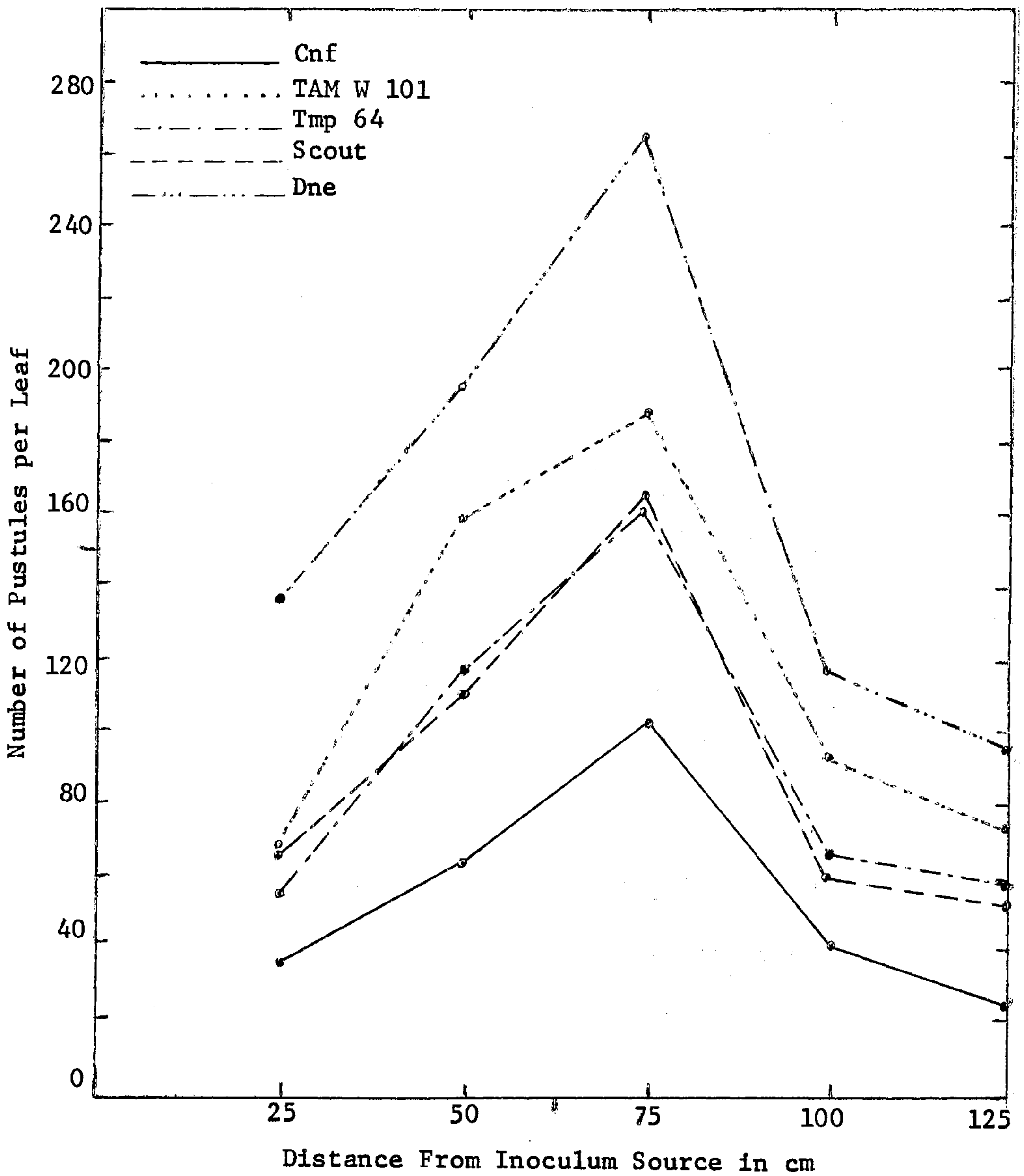

Figure 6. Number of Pustules per Leaf of Five Cultivars of Wheat at Five Different Distances From Inoculum (Experiment I)

Experiment II were not statistically significant, the trend found in both experiments was the same. For example, the lowest severities were found at distances close to or far from the inoculum source in both experiments. Similarly, the highest severities were found at the intermediate distances.

TABLE III

THE NUMBER OF PUSTULES DEVELOPED PER LEAF OF FIVE CULTIVARS LOCATED AT FIVE DISTANCES FROM AN INOCULUM SOURCE BLOWN OVER THE PLANTS BY A 20 MPH WIND. ALL DISTANCES INOCULATED AT ONE TIME (EXPERIMENT II)

	Distance From Inoculum in cm					
Cultivars[1]	25	50	75	100	125	$\bar{x}$ [2]
Cnf	31	33	38	40	34	35
TAM W-101	86	110	120	123	111	110
Tmp 64	75	85	100	112	105	96
Sut	47	82	92	103	88	88
Dne	126	138	149	150	132	139
$\bar{x}$ [3]	73	90	100	106	94	

[1]Abbreviations used are those proposed by Briggle et. al. (5).

[2]LSD (0.05) for comparing cultivar means = 18

[3]LSD (0.05) for comparing distance means = 49

The differences in severity among the five cultivars used in Experiment II were statistically significant. Again, Danne had the most rust and Chinofuz the least. TAM Wheat 101, in this experiment was not significantly different from Triumph 64, although it maintained the same relative position between Triumph 64 and Danne. As in Experiment I, there was less rust on Scout than on Triumph 64 but this difference was not statistically significant.

There was no interaction between cultivars and distance as can be noted in Figure 7. A comparison of Figures 6 and 7 will indicate the differences in the pattern of rust severity at various distances from the inoculum source in the two experiments.

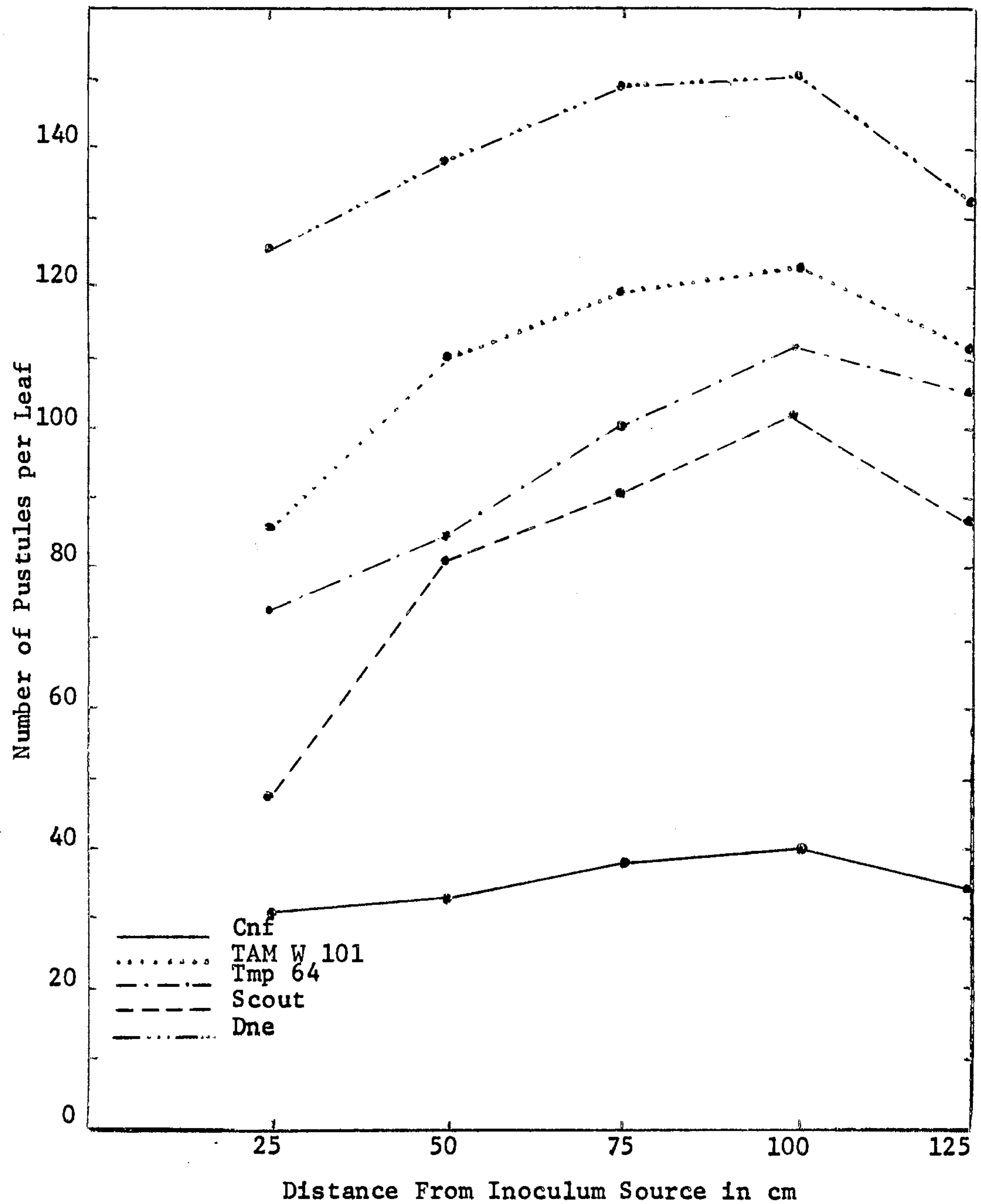

Figure 7. Difference of Leaf Rust Severity on Five Varieties of Wheat at Five Different Distances From the Source of Inoculum in Experiment II

CHAPTER V

DISCUSSION

It will be assumed for this discussion that the rust severity which developed is directly related to uredospore concentration and perhaps deposition. While it may not be a strictly valid assumption, certainly any discrepancy caused by such an assumption would not be large. The deposition of spores in the first experiment, then, does not follow the results of those who have indicated a strictly proportional reduction of inoculum with distance from the source. Greatest deposition of spores occurred at 75 cm, not 25 cm as might have been expected. This would appear to be related to the development of eddies and turbulence as the air moved away from the fan opening. Other factors must also be involved, however, since the deposition of spores decreased at distances beyond 75 cm, even though eddies and turbulence could be expected to continue to increase with distance. The relationship between rust severity and distance from the source seemed to follow a more or less normal curve. One explanation could certainly be that the air velocity was too high to permit maximum spore deposition close to the fan opening (at 25 cm, 9.59 m/sec.) and too slow to permit maximum deposition or contact between leaf and spore at the farthest distance (125 cm, 2.18 m/sec.).

When all of the distances from the inoculum source were inoculated at once in the second experiment it was expected that eddies and turbulence would be increased. This in turn would be expected to bring about a more even distribution of spores, and indeed it did. Peak disposition was found at 100 cm however, instead of 50 cm or closer which was expected. The differences in rust severity at different distances in this experiment were not statistically significant, so perhaps the peak at 100 cm was only by chance. It does appear, however, that the distribution of inoculum was not proportional to the distance from the source in this experiment either.

How these data relate to the actual distribution of autogenous inocula in the field awaits further study, but the implications are that such a study would prove useful in epidemiology.

The implications of the gene-for-gene phenomenon (19, 20, 24) in the use of specific resistance in cereals has led to researches for other types of resistance (33, 11). While the severity of rust on each cultivar maintained a relative rank at each distance in both experiments of this study, the cultivars did not develop the same severity of rust. This fact not only substantiates that spore concentration and perhaps deposition and the resulting rust severity are directly related, but also indicates some mechanism of resistance was operative. Assuming, again, equal deposition of spores, some phenomenon prevented an equal completion of infection and development of equal severities.

It can be speculated that perhaps actual deposition of spores on the leaves was not equal among the cultivars even though the availability of spores in the air stream was equal. This could be due to leaf surface texture density or shape of hair or pubescence, rigidity or turbidity of the leaves themselves or other factors. None of these were investigated in this study, but certainly warrant further interest.

Regardless of what caused the difference in rust severity among the cultivars, it is significant that the two cultivars with the highest severity, Danne and TAM Wheat 101, were those that have no known genes for specific resistance. The two cultivars that are known to have one or more genes for specific resistance (although not effective against the race used in these studies) had significantly less rust than the completely susceptible cultivars. The infection type for all four of these cultivars with race UN9 is 99P (6, 8), while the infection type developed with the cultivar Chinofuz and race UN9 is 35N. Again, in these studies with the cultivar Chinofuz both the size and the number of pustules was significantly smaller than with the other cultivars used. These results may well substantiate the theory that genes for specific resistance may well influence rust development in other ways than infection type alone, and that the stacking of specific genes may well lead to significant reductions in rust severity, and may be one of the factors involved in the so-called "slow rusting" form of resistance (12).

CHAPTER VI

SUMMARY

1. When each of five distances from the inoculum source was inoculated separately significant differences between rust severity at different distances were obtained. Lowest severities occurred on plants closest to the source of inoculum (25 cm) and farthest from the source (125 cm). Maximum infection occurred at 75 cm from the inoculum source.

2. When all five distances were inoculated at once, no statistically significant differences in rust severity occurred, although there was a tendency for the lowest severities to be at both extremes of distance.

3. Significant differences in rust severity were found on the five cultivars used. Danne and TAM Wheat 101 had the highest severity, Triumph 64 and Scout had lesser severities, and the cultivar Chinofuz had the least severity.

4. There was no interaction between distances and cultivars in rust severity in this study.

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