RELATIONSHIP BETWEEN LIGHT AND OAT STEM RUST INFECTION TYPES

by

Elkin Bustamante-R

A Thesis Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
MASTER OF SCIENCE

Major Subject: Plant Pathology

Approved:

In Charge of Major Work

Head of Major Department

Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1967

TABLE OF CONTENTS

INTRODUCTION

Oats (Avena sativa L.) are in demand for human consumption in Colombia and are one of the most promising crops for forage and silage in the cold highlands of the Andes, but severe attacks by oat stem rust (Puccinia graminis Pers. f. sp. avenae Erikss. and Henn.) have limited the development of adapted varieties (Crowder et al., 1967). When pathogenic races of the oat stem rust fungus were identified in Colombia, it was found that some were unusually virulent -- one, race 6C, was in fact, considered the most virulent race known at that time (Orjuela et al., 1962) and there was apprehension lest Colombian races reach the United States. Therefore, a P.L. 480 project was established in which the U. S. Department of Agriculture would cooperate with The Rockefeller Foundation and The Colombian Institute of Agriculture to study oat stem rust in Colombia and means of obtaining resistance to it.

That study revealed that certain oat stem rust resistance genes are light sensitive and that at the elevation of 9,000 feet or above where races are identified and oats are grown commercially in Colombia, light intensity is high enough that these resistance genes partially lose their effectiveness (Browning et al., 1967). In a sense, then, the races rated as "extra-virulent" in the Andes were "environmental" races rather than "genetic" races and, therefore, workers elsewhere had no reason to fear them.

The discovery of the light sensitivity of certain stem rust-oat host-parasite interactions led to many additional questions, however. One of these was, "Is the light sensitivity of the Puccinia graminis avenae-Avena sativa interaction peculiar to the races and environment of Colombia or is this a general phenomenon where the same varieties of the host are involved?" And, "What is the function of light quality and of photosynthesis per se in the light-sensitive host-parasite interactions?"

The objectives of this study, then, were to answer at least in part, the above questions using the same varieties and seed sources for the host, but using North American races of the pathogen.

LITERATURE REVIEW

The infection process of the rust fungi (Uredinales), like other fungi, is influenced by environmental factors. With the rusts, environmental factors affect the infection type, number of pustules, and/or duration of the latent period of infection. The influence of temperature, light, and CO_2 level on uredospore development has been observed in some host pathogen systems. Temperature of 27°C or more, for instance, can cause the breakdown of resistance to normally avirulent races of stem rust (Puccinia graminis Pers. f. sp. avenae Erikss. and Henn.) of oat varieties containing genes Pg-3 and Pg-4 (Welsh, 1937). This temperature effect was shown by Roberts and Moore (1956) to be a "local" reaction in the plant. When the distal portion of a leaf was exposed to 22°C and the basal portion to 27°C or vice versa, the portion receiving the lower temperature was resistant and the other susceptible. A temperature change from 22°C to 27°C between day and night or vice versa did not affect the infection type of two oat isogenic lines (genes Pg-4 and pg-4) to race 6 of the oat stem rust organism (Gregory, 1966). Other data showed that McMurachy wheat is normally susceptible at 24°C to stem rust (P. graminis Pers. f. sp. tritici Erikss. and Henn.) but it was resistant when it was exposed to 16°C for 16 hours between 75 and 91 hours after inoculation (Forsyth, 1956). Some oat selections were immune from race 203 of crown rust

(P. coronata Cda. var. avenae Fraser and Led.) at a temperature of 22°C but they were susceptible at higher temperatures (Rosen and Bailey, 1957). Some oat varieties were susceptible to crown rust as seedlings at 15°C but showed resistance when inoculated as mature plants (Simons, 1954). At 25°C these varieties were susceptible at all stages of growth. Under the extremely low temperature treatments of 1°C the latent period of infection of wheat stem rust was lengthened to 70 days (Melander, 1935).

Bever (1933), working with Puccinia glumarum (Schm.) Ericks. and Henn. and wheat found that with a day length longer than 12 hours, the infection type changed from 4 to 0. Response of the host to quality of light is widely variable among different host-pathogen pairs, as is the response to light intensity. For instance, naked barley infected with biotype 68-1 of brown rust (P. hordei Otth.) is heavily attacked in red or white light, but not in blue light. However, when biotype 118-2 is used the leaves are attacked in blue light but not in red or white light (Gaumann, 1950). Beans inoculated with Uromyces appendiculatus Fr. showed that red and green filters did not affect disease development but a blue filter had a depressing effect (Sempio, 1938). Ultraviolet radiation, however, tended to repress the pustule formation in the irradiated side of the leaf.

Under the normal sunlight of the Upper Mississippi Valley, plants of Hope wheat in various stages of development

beyond the seedling stage appeared to have considerable resistance to race 21 of the stem rust fungus (Hart and Zapesky, 1935). When light was reduced by shading, however, the plants were completely susceptible, just as in their seedling stage. Thus, Hart and Zapesky concluded Hope variety seems to have no protoplasmic resistance to race 21 when light intensity is reduced. Absence of light during the 48 hours after inoculation in some cases caused a local necrosis of host cells adjoining the focus of infection (Gaumann, 1950). At the same time, cereal plants grown in weak light were more resistant to rust attack. This was due mainly to the tendency of the tissues to become necrotic. As light intensity increased, the level of susceptibility increased to a definite optimum. However, different host-pathogen pairs showed characteristic reactions to light.

Gassner and Straib (1929) found that increasing the concentration of CO_2 in the air had effects on both the assimilation and the disease disposition of the host similar to those of increasing the amount of light. The lack of CO_2 resulted in an increase in the latent period of infection of several cereal rust diseases, and infection was less successful. The normal CO_2 content of the air was sufficient to facilitate good infection, but infection could be improved by artificially increasing the amount of CO_2. However, they found that the optimum concentration for infection lay between 0.2% and 0.7% of CO_2 for the most important cereal rusts.

Rosen and Bailey (1957) found that oat varieties normally resistant above 21°C to a race of crown rust were susceptible when plants were grown with CO_2 added to the atmosphere or when sucrose was applied to the leaves. In this case, the carbohydrate metabolites appeared to play a very important role in the host-pathogen system. The level of CO_2 was found markedly toxic at a level of 9.0% in the Uromyces appendiculatus-bean system in any period of disease development (Sempio, 1938).

MATERIAL AND METHODS

General Procedure

Seed of the differential and supplemental differential oat varieties not available locally, and cultures 102 (race 11A), 103 (race 8A), and 104 (race 10A) of the oat stem rust fungus were obtained from the USDA Cooperative Rust Laboratory. Selections of ICA-Bacata, the Yugoslavian variety Kyto, and lines of Bt-SF x C.I. 6969 and Sac-HJ x C.I. 6969 were obtained from Colombian Agricultural Institute personnel in Colombia. The varieties and their probable genotypes are shown in Table 1. The material was grown 10-12 plants/4" pot of greenhouse soil (1 sand: 1 muck: 2 field soil). Approximately 10 days after planting, primary leaves were inoculated with uredospores suspended in Mobilsol 100 using a venturi glass atomizer (Rowell, 1957). The seedlings later were atomized with 0.5% solution of Tween-20 and kept overnight in a moist chamber. Next morning, the moist chamber was opened so the plants could dry gradually for 4 hours; they were then transferred to the place provided for a given experiment.

Data were taken on the first appearance of flecks and uredia, infection type, and number of pustules per leaf. The infection types used were adapted by Browning and Bustamante (unpublished) from those of Bailey (1925). The description of these infection types is as follows:

0. No macroscopic evidence of infection.

Table 1. Oat Varieties used in this study and their probable genotypes according to the original and the new standardized system[a]

Variety or Cross	C.I. or P.I. No.	Probable Genotype	
		Original System	Standardized New System
Minrus	2144	D	Pg-1
Richland	787	A	Pg-2
Jostrain	2660	E	Pg-3
Rodney	6661	B	Pg-4
Ada	7144	AD	Pg-1,2
Abda	7145	ABD	Pg-1,2,4
New Garry	6662	AB	Pg-2,4
Burnett	6537	BD	Pg-1,4
Saia	4639	Undetermined	Undetermined
Hajira X Joanette (H-J)	4023	BEF	Pg-3,4,pg-8
Eagle x C.I. 4023	8111	F	pg-8
Bonham	6102	D	Pg-1
Cherokee	6003	D	Pg-1
Nemaha	6004	D	Pg-1
Clinton	6034	D	Pg-1
ICA-Bacata	____	BD	Pg-1,4
Sac-SF x C.I. 6969	____	BDE	Pg-1,3,4
Bt-SF x C.I. 6969	____	BDE	Pg-1,3,4
Kyto sel. 2	221285	Undetermined	Undetermined
_____	5844	H	pg-9
Markton	2053	abdef	pg-1,2,3,4

[a]Simons, Zillinsky & Jensen (1966).

0; Hypersensitive flecks but not uredia present. Necrosis develops slowly.

1, Uredia approximately 1 mm or less in diameter, surrounded by chlorosis at 14 days and possible necrosis at 18 days. The uredia seldom become linear; they are nearly always circular.

2. Uredia varying in size from smaller, 0.3 - 0.8 mm x 0.9 - 1.1 mm to larger, 0.5 - 0.6 mm x 2.5 - 3.0 mm. A green island may surround the uredia and they may be marked by distinct or indistinct chlorotic rings.

3. Uredia vary from 0.6 x 2.5 mm to 0.6 x 6.5 mm. Uredia are surrounded by varying degrees of chlorosis.

4. Uredia vary from 1.5 x 3.5 mm to 2.5 x 6.0 mm or even longer. Pustules tend to be diamond shaped and pustules are surrounded by about 1 mm of chlorotic tissue regardless of the size of the sporulating area.

X. Infection types 0;, 1, and 2 (X^{-}); or 0;, 1, 2, and 3 ($X^{\pm}$); or 2, 3, and 4 (X^{+}) on the same leaf constitute a mesothetic (X) reaction. No mechanical separation is possible.

Besides the infection type, superscript "+" and "-" signs are used to distinguish the variation within a given reaction. For instance, "++" indicates the upper and "-" the lower limits for each type. A dash indicates a continuous range of

reaction. For instance, the reading "0; - 1^+" is read fleck dash one plus" and indicates a continuous range from flecks to pustules somewhat larger than those described as infection type 1.

Varietal Response to Light

Light was supplied by Sylvania VHO cool white fluorescent bulbs for a 14-hr. photoperiod in Plant Growth Labs[a]. All varieties were tested under 1,000 ft-c and 3,500 ft-c. Light measurements were taken with a Weston Meter Model No. 756. Ambient temperature was held during 3 experiments at 20°C ± 1.5°C and in another one at 24°C ± 1.5°C.

Light Quality

Cool white fluorescent lights were the source of light in most experiments. Besides that source, however, Cool Beam incandescent, blue, red, and UV sources were tested. Incandescent light was provided by General Electric 75 PAR38/2 FL and 150 PAR 38/2 FL Cool Beam lamps. The lamps were located 62 cm above the tops of the pots so that the 75w and 150w bulbs gave 1,000 ft-c and 3,200 ft-c, respectively, at the level of the seedling leaves.

---

[a]Model No. PGW-132 manufactured by the Percival Refrigeration Co., Des Moines, Iowa.

Sheets of Cinemoid[a] number 6, primary red (625-700 mu), and number 20, primary blue (400-500 mu), were used to check the influence of monochromatic light. Light was provided by G.E. 300 PAR56/2MFL Cool Beam lamps fixed at the appropriate distance to produce 3,000 ft-c of monochromatic red or blue light on the seedlings, as measured by the Weston meter. A container with distilled water was inserted above each filter to absorb the infrared wavelengths.

The growth chambers were equipped with barriers of "Weatherable Milar"[b] which intercepts almost all the ultraviolet emission from the cool white fluorescent bulbs; therefore, an experiment with additional UV was run. The UV radiation was supplied by one 40w fluorescent black light lamp (Phillips MCF/U40/8) situated 20, 40 and 60 cm from the seedlings.

Carbon Dioxide

Three levels of CO_2 (100, 300 and 3,000 ppm) were supplied in biological atmospheres of CO_2 and air[c]. Pressures were regulated to 10 lb/in^2 and the flow rates were

---

[a]Manufactured by Kliegl Bros., Universal Electric Stage Lighting Co., Inc., Long Island City, N. Y.

[b]Manufactured by E.I. Dupont de Nemours and Co., Wilmington, Delaware.

[c]Supplied in compressed gas cylinders by The Matheson Co., Inc., Joliet, Ill.

20 liters/hour. The plants were enclosed in chambers 19" x 14" x 10" high lined with "Milar" film 3u thick. Milar has an extremely low permeability to CO_2 and a high resistance to tearing. The film was attached to frames so as to get a gas tight seal. The Milar has a spectral transmission between 300 and 800 mu, and transmission is about 85%.

RESULTS

Effect of Light Intensities on Infection Types

Cultures of Puccinia graminis avenae races 8A, 10A and 11A were tested initially on all 22 oat varieties. The rust reactions to these races at low and high light intensities are presented in Table 2. The host-pathogen interactions were similar to those described with cultures of Colombian races 4A, 6B or C, and 13B (Browning et al., 1967). Plants kept in low light intensity had developed flecks by six days after inoculation. Uredia were erumpent nine days after inoculation and a well developed primary sporulation was obtained by ten days. On the plants kept in high light intensity, flecks were present four days after inoculation and an abundant primary sporulation appeared by eight days. Kyto selection was always the first in showing flecks. The material in high light intensity matured sooner. Hence, notes were taken 13 and 15 days after inoculation.

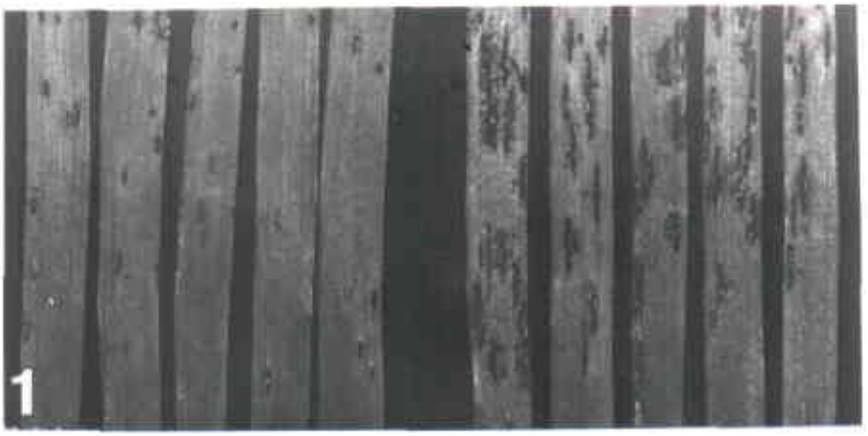
The results of this experiment (Table 2) indicate that varieties with genes Pg-1 or pg-8 are highly sensitive to light intensity. Figures 1 to 4 show the breakdown of resistance conditioned by gene Pg-1 in Bonham, Cherokee, Clinton and Nemaha varieties, respectively. Differences from variety to variety were not great; however, the infection type 2 of Bonham at low light intensity (Fig. 1) was larger, the green island was not so sharp, and the uredial development was more

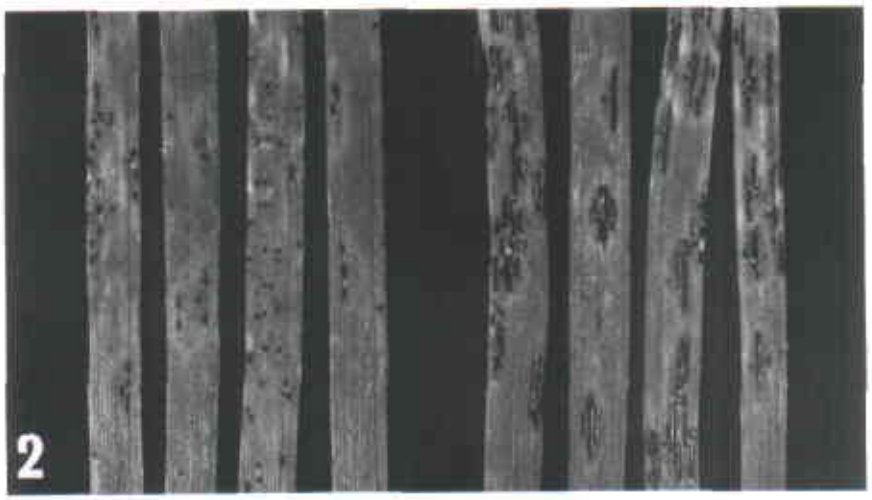
Table 2. The effect of light intensity[a] on the infection type produced by races of Puccinia graminis avenae on 22 varieties of oats

Variety or Cross	Probable Genotype	Reaction at designated light intensity					
		Race 11A		Race 10A		Race 8A	
		1,000	3,000	1,000	3,000	1,000	3,000
Minrus	Pg-1	2	$3^{\pm}$	2	3^{+}	2	3^{+}
Bonham	"	2	3^{++}	2^{+}	3^{++}	2^{+}	3^{++}
Cherokee	"	2^{+}	3^{++}	2^{+}	3^{++}	2^{+}	3^{++}
Nemaha	"	2^{+}	3^{++}	2^{+}	3^{++}	2^{+}	3^{++}
Clinton	"	2^{+}	3^{++}	2^{+}	3^{++}	2^{+}	3^{++}
Richland	Pg-2	4	4	4	4	4	4
Jostrain	Pg-3	0;-1	0;-1	X	$X^{\pm}$	4	4
Rodney	Pg-4	4	4	4	4	4	4
Eagle x C.I. 4023	pg-8	2	$3^{\pm}$	2	$3^{\pm}$	2	3^{+}
C.I. 5844	pg-9	4	4^{+}	4	4^{+}	4	4^{+}
Ada	Pg-1,2	2^{+}	3^{++}	2^{+}	3^{++}	2^{+}	3^{++}
Burnett	Pg-1,4	2^{+}	3^{+}	2^{+}	3^{+}	2^{+}	3^{++}
ICA-Bacata	Pg-1,4	2^{+}	3^{+}	2^{+}	3^{+}	2^{+}	3^{++}
New Garry	Pg-2,4	4	4	4	4	4	4
Abda	Pg-1,2,4	2^{+}	3^{++}	2^{+}	3^{++}	2^{+}	3^{++}
Sac-HJ x C.I. 6969	Pg-1,3,4	0;-1	0;-1	X	X	2^{+}	3^{++}
Bt-SF x C.I. 6969	Pg-1,3,4	0;-1	0;-1	X	X	2^{+}	3^{++}
Saia	Undeter.	0;-1	0;-1	0;-1	0;-1	0;-1	0;-1
Kyto sel 2	Undeter.	0;-1	0;-1	0;-1	0;-1	0;-1	0;-1
Markton	pg-1,2,3,4	4	4^{+}	4	4^{+}	4	4^{+}

[a]Light intensity is given in foot candles. Light was supplied by Sylvania cool white VHO fluorescent lamps in a 20°C growth chamber.

Fig. 1-3. Response of seedling oat leaves to culture 102 of Puccinia graminis avenae. The lefthand group of leaves received 1,000 ft-c of light, the righthand group 3,500 ft-c. Photoperiod was 14 hours, temperature 20°C. The photographs were taken 14 days after inoculation. Fig. 1 shows the oat variety 'Bonham'; Fig. 2, 'Cherokee'; and Fig. 3, 'Clinton'.


1


2

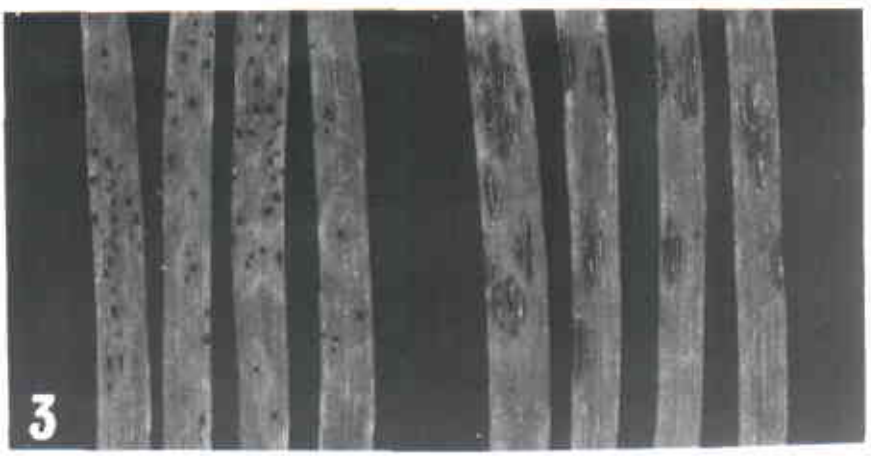
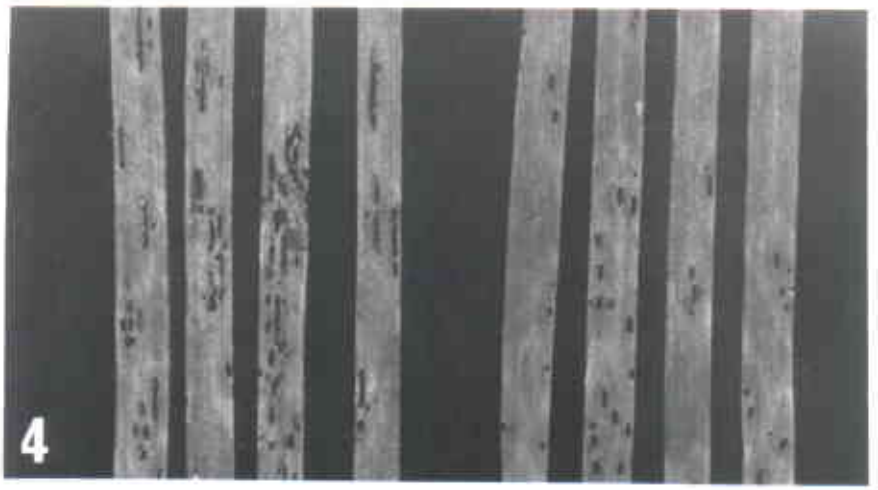
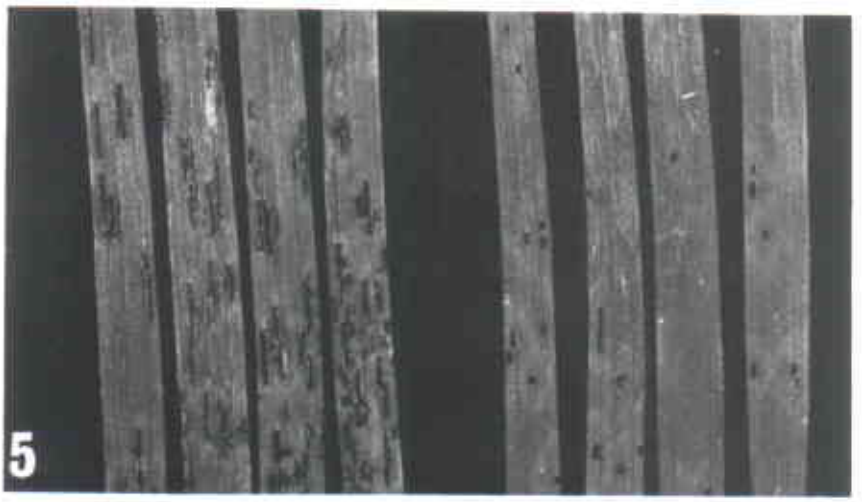
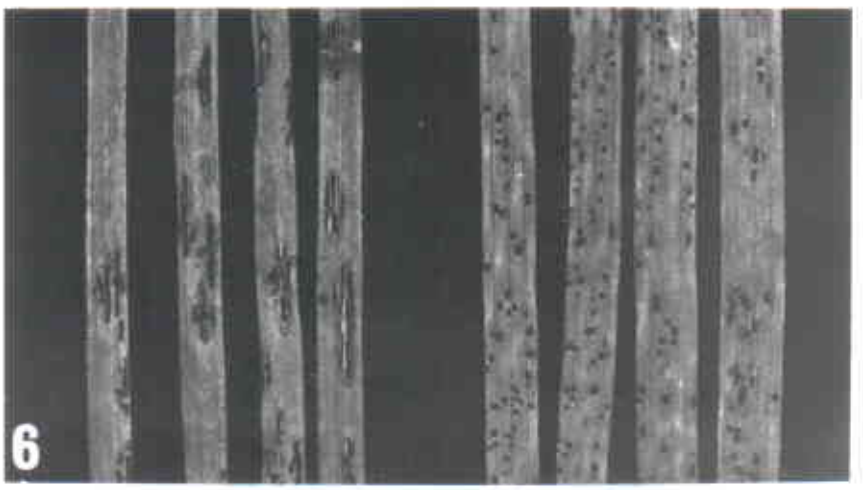

3

Fig. 4-6. Response of seedling oat leaves to culture 102 of *Puccinia graminis avenae*. The lefthand group of leaves received 1,000 ft-c of light, the righthand group 3,500 ft-c. Photoperiod was 14 hours, temperature 20°C. The photographs were taken 14 days after inoculation. Fig. 4 shows the oat variety 'Nemaha'; Fig. 5, 'Burnett'; and Fig. 6, 'ICA Bacata'.


4


5


6

linear than in the others (Fig. 2-4). The response of varieties with genes Pg-1 and pg-8 was not influenced by temperature when it was raised from 20 to 24°C. Burnett and ICA-Bacata varieties (Fig. 5 and 6) are examples of the breakdown of resistance in plants with Pg-1,4 genes. Pg-4 is a temperature sensitive gene (Roberts and Moore, 1956) with a critical point near 27°C, but the temperature level was kept below 20°C in this experiment. The fungus sporulated less on ICA-Bacata than on Burnett.

The interaction of varieties with genes Pg-2, Pg-4 and pg-1,2,3,4 with light intensity showed their infection types were not altered but their latent periods of infection were longer by at least two days, at the lower light intensity.

Knowing the sensitivity of gene Pg-1 to light, an experiment was planned to determine when after inoculation light is effective in the breakdown of the resistance conditioned by gene Pg-1. Seedlings of Burnett and Clinton were inoculated with culture 102 of race 11A. After removal from the moist chamber the plants were kept in a growth chamber at 1,000 ft-c for 14 hours/day throughout the experiment with the exception of those days they were selected to be kept at 3,500 ft-c per 14 hour/day (Fig. 7). Figure 8 shows graphically when after inoculation the exposition to high light intensity was effective in breaking down the resistance of gene Pg-1. The infection type increased (from 2-2^{+} to 3$^{\pm}$ to 4^{-}) as the exposition to intense light approached the

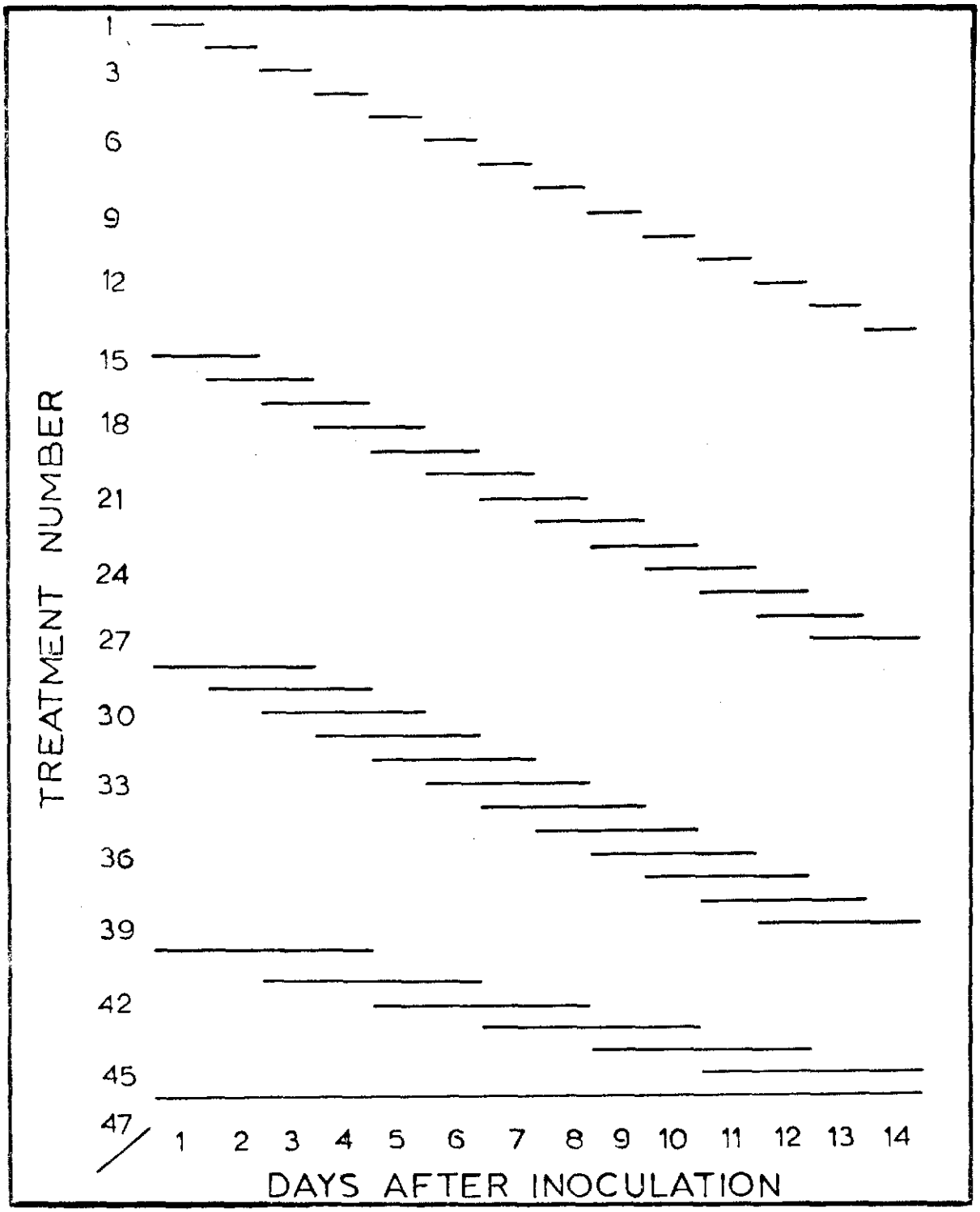


Fig. 7. Light exposition of Clinton oat seedlings after inoculation with Puccinia graminis avenae. The solid lines indicate the period when pots in each treatment were exposed to 3,500 ft-c of light. At other times plants were held at 1,000 ft-c.

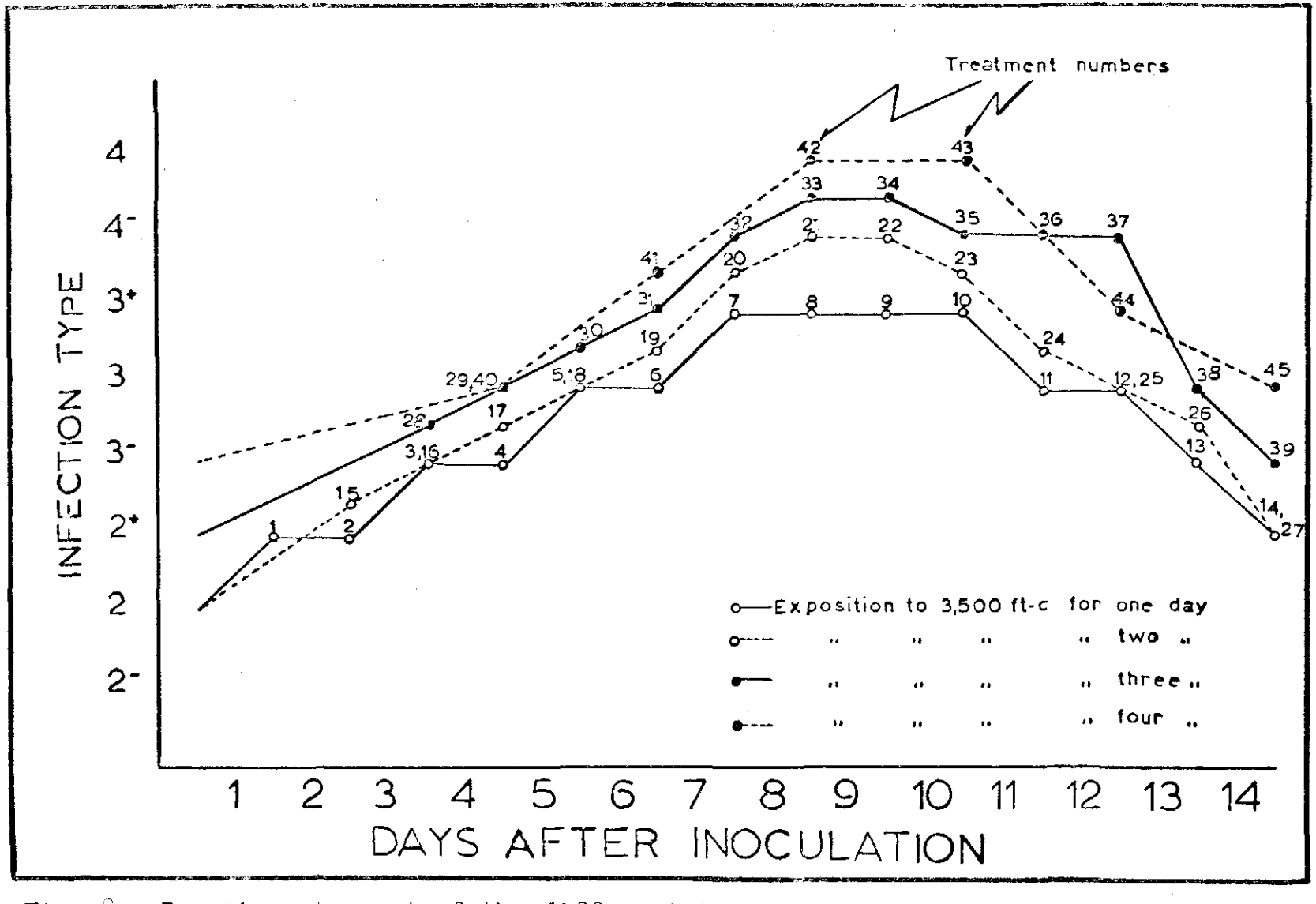


Fig. 8. Reactions to rust of the different treatment diagrammed in Fig. 1.

eighth day after inoculation. It stabilized from the ninth to eleventh days, and then it decreased again (3-3^{++} to 3^{+} to 2-2^{+}). Thus, a clear breakdown was observed from the eighth to the eleventh day after inoculation (Fig. 8). These results are similar to those obtained with Colombian races and Pg-1 varieties (Instituto Colombiano Agropecuario, 1964). Secondary sporulation was present in all the plants exposed to high light intensity after the eleventh day. This secondary sporulation was similar to that of Marquis wheat when plants were transferred from high to low temperature after rust sporulation had begun (Silverman, 1959). Plants receiving intense light for more than one day in the "critical breakdown period", eight to eleven days after inoculation, showed a more intense reaction and sporulation (infection type 3^{++}- 4^{-}) than those exposed one day only (infection type 3-3^{++}). Plants exposed during all the time to high light intensity did not give a more complete breakdown than plants exposed three or four days to high light intensity during the "critical breakdown period".

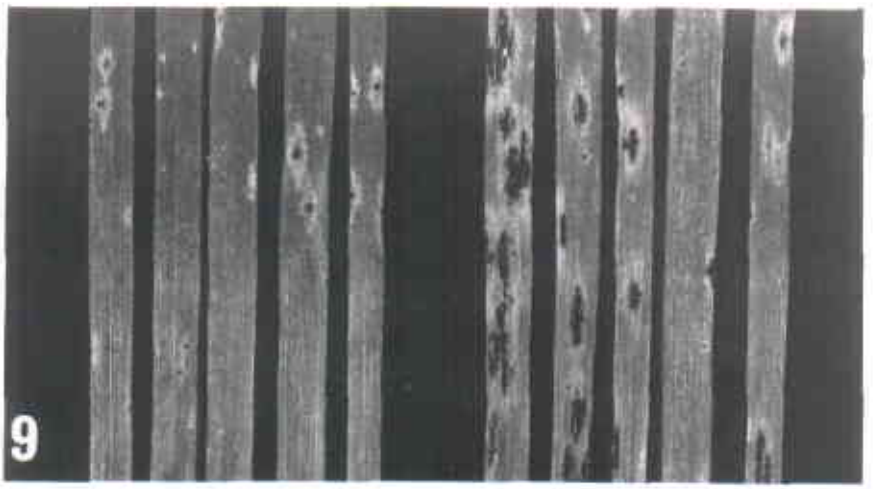
Jostrain with gene Pg-3, apparently was only changed by temperature (Fig. 9). It is sometimes difficult to get good infection with this variety. The cuticle has a thick waxy layer and rust development is slow. The response of Jostrain to temperature was quite clear but the possible light influence is uncertain.

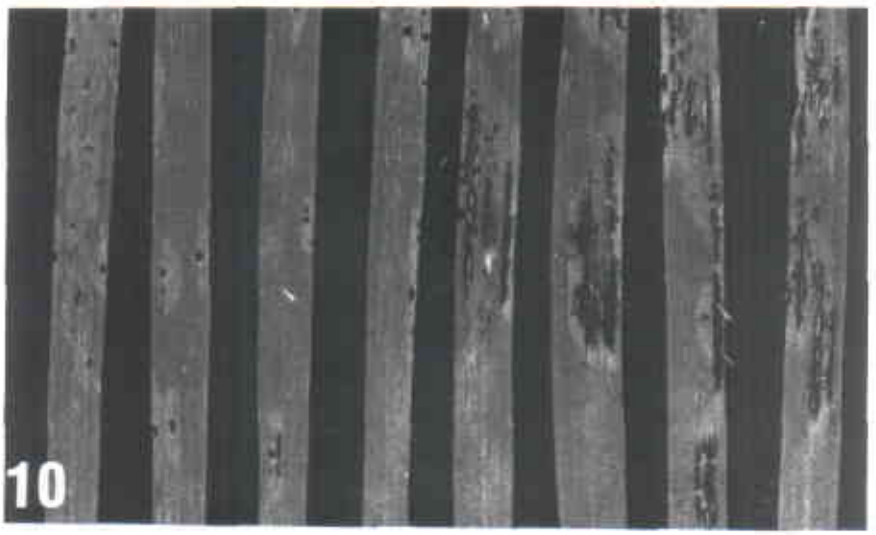
The Kyto selection which was tested with culture 102 of

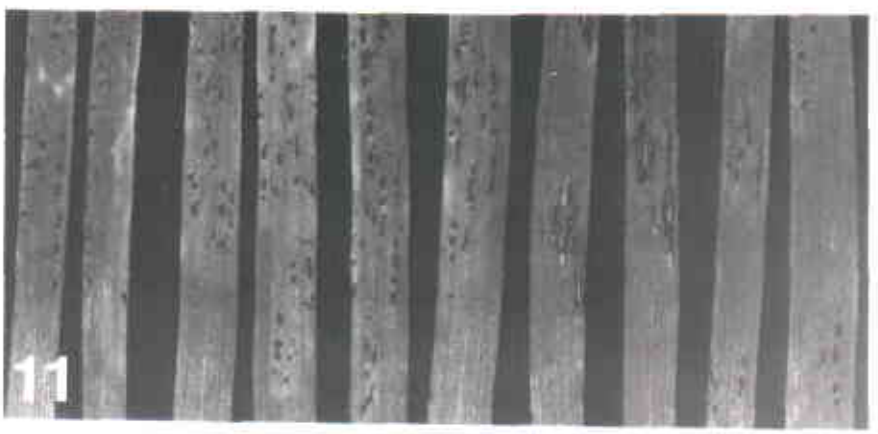
Fig. 9. Response of seedling leaves of the oat variety 'Jostrain' to Culture 102 of *Puccinia graminis avenae* at 20°C (left 5 leaves) and 24°C (right 5 leaves). Light intensity was 3,500 ft-c, photoperiod 14 hr. The photograph was taken 15 days after inoculation.

Fig. 10. Response of seedling leaves of the oat variety 'Kyto' to Culture 102 of *Puccinia graminis avenae* at 20°C (left 4 leaves) and 28°C (right 4 leaves). Light intensity was 3,500 ft-c, photoperiod 14 hr. The photograph was taken 15 days after inoculation.

Fig. 11. Response of seedling leaves of the oat variety 'Clinton' to Culture 102 of *Puccinia graminis avenae* under conditions of different qualities of light: From left to right, leaf pairs received, respectively, blue (3,000 ft-c 28°C), red (3,000 ft-c 28°C), Cool Beam incandescent (3,000 ft-c 28°C), cool white fluorescent (3,000 ft-c 20°C) and cool white fluorescent (1,000 ft-c 20°C). Photoperiod was 14 hr. The photograph was taken 15 days after inoculation.


9


10


11

race 11A, culture 105 of race 6AF, and culture 106 of race 6AFH showed a resistant reaction to those races in the seedling stage. The resistant reaction was not influenced by light intensity; however, when the temperature was increased to 24°C the reaction was mesothetic and at 28°C the infection type was 4++ (Fig. 10). Rust developed on Kyto linearly with increase in temperature from 18° to 28°C which gave a biological indicator for checking the temperature.

Effect of Light Quality on Infection Type

The influence of cool white fluorescent light was described in the previous experiments. That source of light has a Blue-Red ratio (B:R) greater than one. On the basis of the wide response to light intensity of the interaction between stem rust culture 102 of race 11A and varieties with genes Pg-1 and pg-8, these were selected to be tested with other light sources.

Ultraviolet light experiment

The ultraviolet experiment was designed to test the effect of this wavelength on the host-pathogen system. "Weatherable Milar", used as barriers beneath the lights in the growth chambers, is considered to intercept almost all the UV radiation from the fluorescent bulbs. Thus, it was necessary to add light of this wavelength, which is naturally present in sunlight. The response of oat plants containing genes Pg-1, pg-8, pg-1,2,3,4 and Kyto, in high and low

light intensities with additional UV radiation was similar to that of the control plants. Differences in the length of the latent period of infection and sporulation were not observed either.

Incandescent light experiment

Richardson (1967) found that Cool Beam lamps (Fig. 12) appeared to be as effective as natural sunlight in supplying the energy for fixation of CO_2 and photosynthetic response in cotton. These lamps produce relatively less energy than sunlight at the shorter wavelengths but they produce proportionally more at longer wavelengths. Clinton and Eagle x C.I. 4023, containing Pg-1 and pg-8 genes, respectively, were inoculated with culture 102 of race 11A. After removal from the moist chamber the plants were kept in a room where the temperature fluctuated between 18°C and 28°C. A spore germination test was run 15 days after inoculation to compare the germinability of spores which developed under different light sources.

The material under low and high light intensities showed flecks at five and six days, respectively. Complete uredial development was observed eight (high intensity) and nine (low intensity) days after inoculation. Abundant secondary sporulation was present in both intensities. The tendency of the uredial development was linear, especially in high intensity; however, the infection type was a 2-2$^+$ to 3$^-$ which is closer

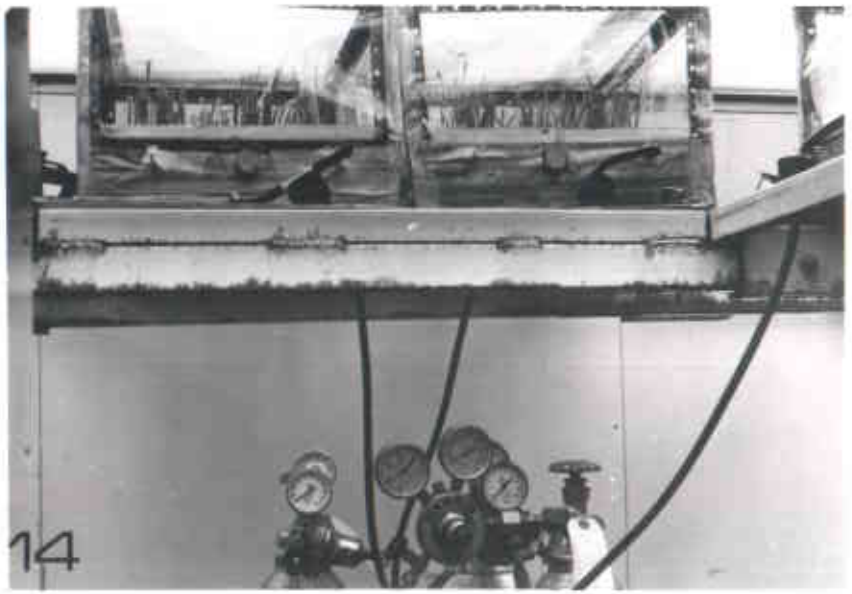
Fig. 12. Cool Beam incandescent light experiment. Left, 'Clinton' and 'Eagle x C.I. 4023' inoculated with Culture 102 of Puccinia graminis avenae and exposed to 1,000 ft-c from 75w bulbs; right, the same varieties exposed to 3,000 ft-c from 150w bulbs. Temperature was 28°C, photoperiod 14 hr. The photograph was taken 15 days after inoculation.

Fig. 13. Response of 'Clinton' oats inoculated with Culture 102 of Puccinia graminis avenae and exposed to blue (left) and red (right) light by filtering light from 300w Cool Beam bulbs with Cinamoid plastic sheets secured under the containers of water. Light intensity was 3,000 ft-c, temperature 28°C, photoperiod 14 hr. The photograph was taken 9 days after inoculation.

Fig. 14. Carbon dioxide experiment. Plants were kept in the small Milar chambers inside a growth chamber and received 3,000 ft-c of light. Temperature was 20°C, photoperiod 14 hr. CO_2 was supplied at 100, 300, and 3,000 ppm in biological atmospheres with air.


12


13


14

to the rust reaction found under fluorescent light at low light intensity (Fig. 11 and Table 3). The Cool Beam lamps used in this experiment normally intercept two-thirds of the infrared radiation. The use of a container of distilled water probably eliminated most of the remainder. Rust development, however, was similar to that under incandescent lights without water to remove infrared.

Table 3. Effect of light quality and intensity on reactions of Clinton and Eagle x C.I. 4023 oat varieties to Puccinia graminis avenae race 11A culture 102

Variety	Reactions at designated light quality and intensity					
	Cool White (Fluorescent)		Cool Beam (Incandescent)		Red	Blue
	1,000[a]	3,000	1,000	3,000	3,000	3,000
Clinton	2-2^{+}	3-3^{++}	2^{-}-2^{+}	2^{+}	2^{+}	2$^{=}$-2
C.I. 8111	2$^{=}$-2	3-3^{+}	2-2^{+}	2-2^{+}	2-2^{+}	2$^{=}$-2

[a]Foot candles.

Red light

Seedlings of Clinton were inoculated with culture 102 of race 11A and after removal from the moist chamber the plants were kept in the same room with the incandescent experiment (Fig. 13). A Cinemoid number 6 plastic sheet limited radiation to the primary red (625-700 mu). Transmission was rated at 17%. Infrared radiation was avoided

again by using a container of distilled water in the system. The intensity was kept at 3,000 ft-c throughout the experiment. First flecks were visible four days after inoculation, and sporulation began two days later. Full uredial development was observed nine days after inoculation. Abundant secondary sporulation was present (Fig. 11); this was similar to that of incandescent light. The average uredial size was about half of that of uredia which developed under incandescent light, and the infection type was 2-2^{+}.

Blue light

The Cinemoid number 20 plastic sheet supplied the inoculated seedlings with a wavelength of 400 to 500 mu with a peak at 450 mu. Transmission was rated at 0.5%. Early flecks on Clinton were visible six days after inoculation. Secondary sporulation was sparse and the uredia, in general, were circular in shape. The infection type was 2$^{=}$-2 (Fig. 11 and Table 3).

The peripheral chlorotic ring associated with uredia which developed in the blue, red, and incandescent light treatments was very similar to that which developed in the fluorescent low light intensity treatment. Experiments conducted with light intensities lower than 500 ft-c and blue, red, or green filters resulted in poor development of both host and pathogen. Leaf tips became scalded in appearance and the infection types were of a range from 0; to 2$^{=}$.

Spore germination tests were run using the method of Hobbs (1958). The results are shown in Table 4. The data show that germination was excellent for spores borne under fluorescent light at both light intensities. The germination of spores borne under incandescent light decreased in direct relation to the increase in light intensity. The effect was the same on Pg-1, pg-8 and Kyto varieties, but on the last the reduction was more severe. Reduction in germination was present also in spores borne under blue and red light.

Table 4. Percentage germination of uredospores of Puccinia graminis avenae race 11A culture 102 borne under different conditions of light quality and intensity

Light quality and intensity in ft-c	Temperature °C	Host variety and percentage germination[a]		
		Clinton	C.I. 8111	Kyto
Fluorescent	20			
1,000		98	99	99
3,000		100	100	100
Incandescent	28			
1,000		84	87	67
3,000		39	66	29
Red	28			
3,000		63	—	—
Blue	28			
3,000		73	—	—

[a]Average of 250 spores in each of 2 replications.

Carbon Dioxide and Light Interaction

After being removed from the moist chamber, infected seedlings of Clinton, Eagle x C.I. 4023, Richland, Jostrain and Kyto varieties were kept in biological atmospheres of three different levels of CO_2 in air: 100, 300, and 3,000 ppm. The varieties were inoculated with culture 102 of race 11A and culture 105 of race 6AF. Each chamber (Fig. 14) held 10 pots, one of each variety inoculated with each of the rust cultures. A thermometer was suspended in the air space between pots. One experiment was run with a temperature of 28° ± 1.5°C and another one at 20° ± 1.5°C. The small chambers were kept in a growth chamber and plants in them received 3,000 ft-c of light. Compressed air was forced into each chamber continuously and it was exhausted thru a glass tube. The humidity was 100% in the small chambers. Data were taken and spore germinations were made 15 days after inoculation.

Data on infection type, temperature effect, and spore germination are presented in Tables 5, 6, and 7. Flecks appeared on all varieties four days after inoculation at both 300 and 3,000 ppm of CO_2. At 100 ppm flecks were present on Kyto and Jostrain five days after inoculation, but Clinton and Eagle x C.I. 4023 needed seven days. Erumpent uredia were observed eight and nine days after inoculation at 300 and 3,000 ppm, respectively. Sporulation was abundant on all varieties. The development of the infection type 2

Table 5. Response to temperature and CO_2 concentration of 5 oat varieties inoculated with Puccinia graminis avenae culture 102 of race 11A and culture 105 of race 6AF, light intensity 3,000 ft-c.

Variety or Cross	28°C				20°C					
	100 ppm		3,000 ppm		100 ppm		300 ppm		3,000 ppm	
	10A	6AF	10A	6AF	10A	6AF	10A	6AF	10A	6AF
Clinton	$2^{=}$	4	$3^{\pm}$	4	$2^{=}$	4	$3^{\pm}$	4	3^{++}	4
Eagle x C.I. 4023	$1^{-},2^{=}$	4	3^{+}	4	$1^{-}2^{=}$	4	$3^{\pm}$	4	3^{++}	4
Jostrain	X^{++}	4	X^{++}	4	$0;-1^{+}$	4	$0;-1^{+}$	4	$0;-1^{+}$	4
Kyto-2	4	4	4	4	$0;-1^{+}$	$0;-1^{+}$	$0;-1^{+}$	$0;-1^{+}$	$0;-1^{+}$	$0;-1^{+}$
Richland	4	4	4	4	4	4	4	4	4	4

Table 6. Effect of different CO_2 concentrations and light intensities on rust reactions of five oat varieties inoculated with Puccinia graminis avenae race 11A culture 102, temperature 20°C

CO_2 Level ppm	Light Intensity ft-c	Host varieties and rust reactions				
		Clinton	Richland	Jostrain	C.I. 8111	Kyto
100	3,000	2-[a]	4-[a]	0;1[a]	2=[a]	0;-1
300	"	3+	4	X=	3±	0;-1+
500	"	3+	4+	X±	3	0;-1+
3,000	"	3+	4+	X-	3	0;-1+
500	1,000	2	4	0;-1	2±	0;-1+

[a]Delayed sporulation.

Table 7. Percentage germination of uredospores of Puccinia graminis avenae race 11A culture 102 borne at 20°C under different conditions of CO_2 concentration and light intensity

CO_2 Level ppm	Light Intensity ft-c	Host variety and percentage germination[a]				
		Clinton	Richland	Jostrain	C.I. 8111	Kyto
100	3,000	100	100	100	100	100
300	"	100	99	100	100	100
500	"	100	99	100	99	100
3,000	"	100	100	98	100	99
500	1,000	99	98	99	99	99

[a]Average of 250 spores in each of 2 replications.

on lines with genes Pg-1 and pg-8, and the reaction of Richland with Pg-2, was slow at 100 ppm; however, pustules characteristic of those varieties developed by 17 days after inoculation.

Eagle x C.I. 4023 and Clinton showed a high sensitivity to CO_2 concentration and the infection types increased with the CO_2 level (Fig. 15, 16, 17, 18). A sharp difference was obtained between 100 and 300 ppm but a slight increase was observed from 300 to 500 ppm (the average concentration of CO_2 in the growth chambers as determined by gas chromatography was 500 ppm). The reaction of varieties with genes Pg-1, Pg-2 and pg-8 was the same from 500 ppm to 3,000 ppm and the unique difference was the early maturation of the oat leaves at 3,000 ppm.

The infection types of Kyto (Fig. 18) and Jostrain were not affected by the CO_2 level; they gave a reaction 0;-1 to 2" to culture 102 of race 11A at 20°C. The same varieties gave an infection type 4 for all CO_2 levels at 28°C, indicating they are temperature sensitive. Richland, a variety known to be insensitive to light and temperature (Browning et al., 1967) gave the same infection type 4 under all CO_2 concentrations; however the latent period of infection was longer at 100 ppm.

Results of the spore germination test are shown in Table 7. The influence of CO_2 concentration was not detected on the fresh spore material as germination was excellent in all cases.

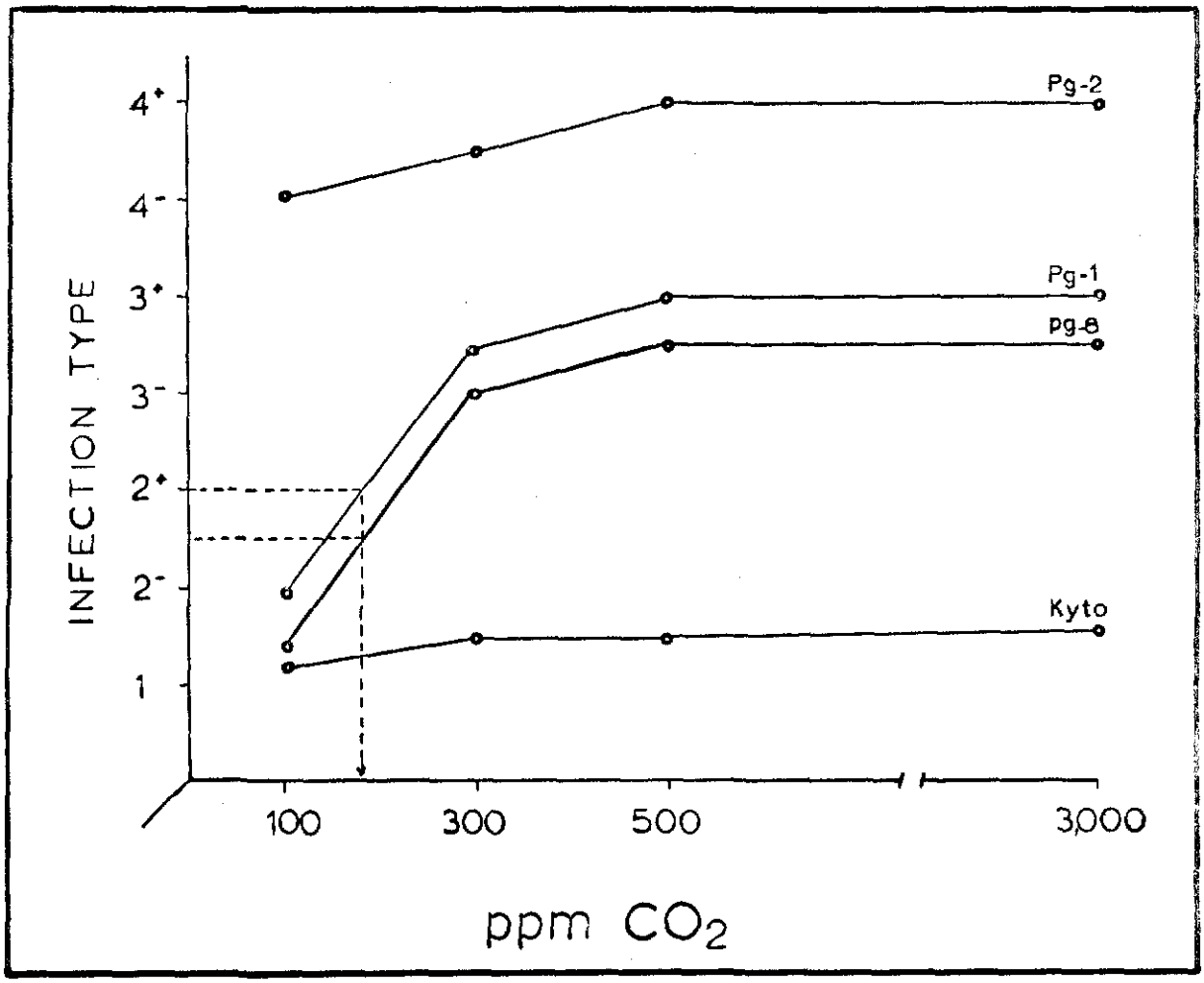
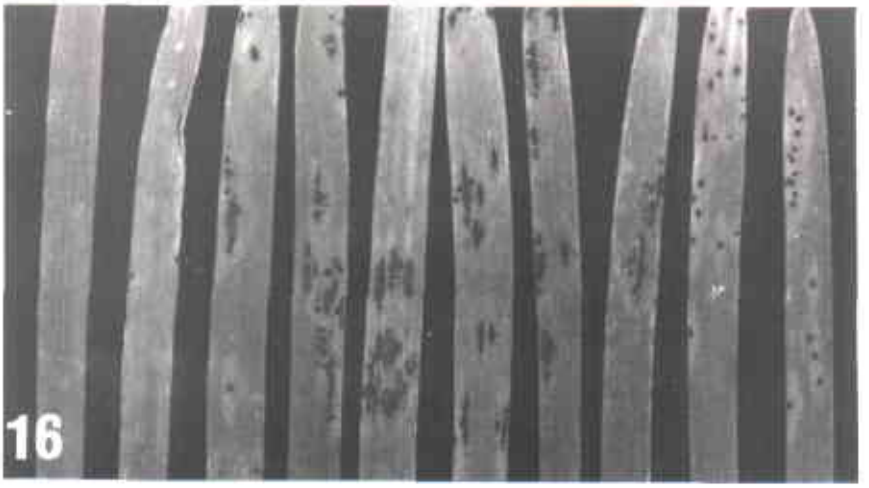
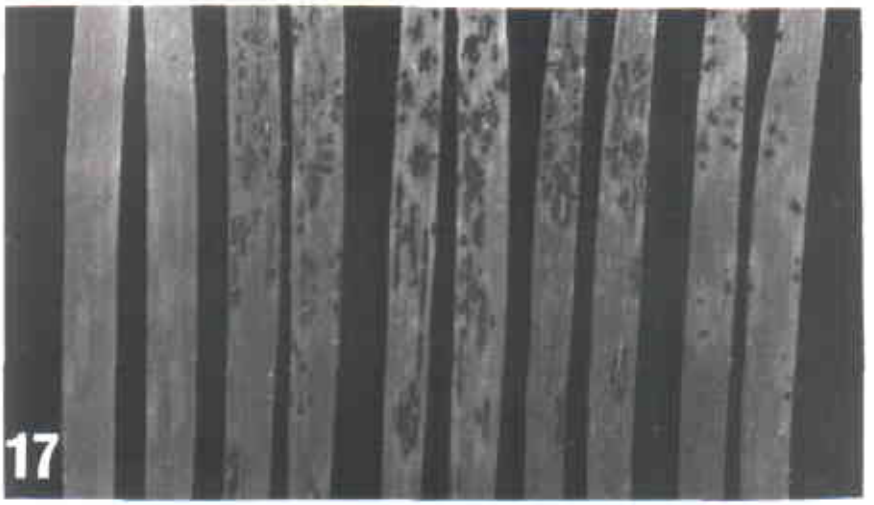


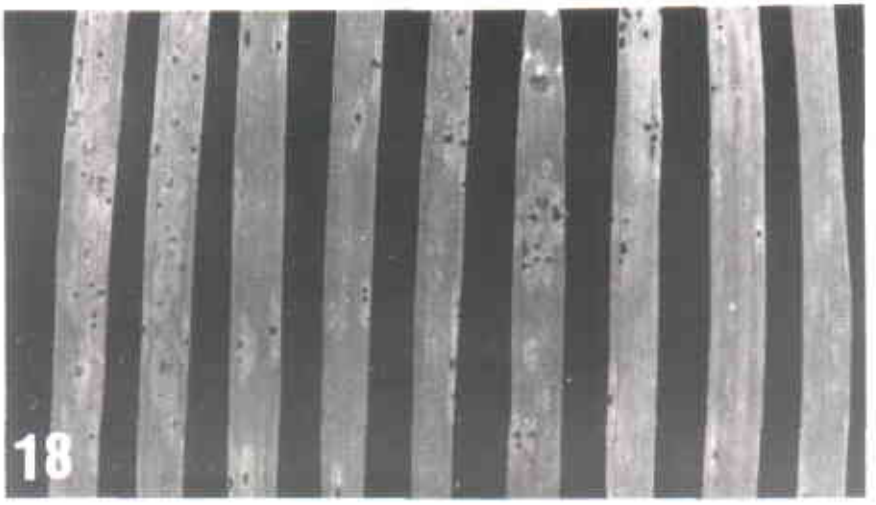
Fig. 15. Increase in infection type with increasing CO_2 level of four oat varieties inoculated with a culture of race 11A of Puccinia graminis avenae. Dotted arrow points out the theoretical CO_2 level used at low light intensity by Pg-1 and pg-8 variety. Light intensity 3,000 ft-c and temperature 20°.

Fig. 16 and 17. Response of seedling oat leaves to Culture 102 of *Puccinia graminis avenae* at different CO_2 concentrations. From left to right each leaf pair received, respectively, 100, 300, 3,000, and 500 ppm at 3,000 ft-c of light. The righthand pair of leaves received 500 ppm of CO_2 at 1,000 ft-c. Fig. 16 shows leaves of 'Eagle x C.I. 4023', and Fig. 17, 'Clinton'.

Fig. 18. Response of seedling leaves of the oat variety 'Kyto' to Culture 102 of *Puccinia graminis avenae* at 100 ppm of CO_2 (left 3 leaves), 300 ppm (center 3 leaves) and 3,000 ppm (right 3 leaves). Light intensity was 3,000 ft-c, temperature 20°C, photoperiod 14 hr. The photograph was taken 15 days after inoculation.


16


17


18

Since tests of spore germination were not made later, data are not available on spore vigor after a period of storage.

DISCUSSION

The infection type 3± is the only reaction normally produced in the Colombian highlands on varieties containing genes Pg-1 and pg-8 by races of *Puccinia graminis avenae* with intermediate virulence for these varieties. By reducing light intensity this infection type could be restricted to a 2±, considered normal for varieties with these genes at the Iowa Agricultural Experiment Station, or it could be increased to 4 or even 4+ at 3,500 ft-c in plant growth chambers (Browning et al., 1967). To see whether this was a phenomenon peculiar to Colombian races, I selected several isolates of North American races of the oat stem rust fungus, and several varieties with genes Pg-1 and pg-8 and tested these in all combinations under conditions we had found successful in breaking resistance in Colombia.

These tests showed that with North American races as with Colombian, races which produce a 2± reaction on varieties with genes Pg-1 and pg-8, develop in more or less direct proportion to the amount of light incident on the leaf. Therefore, my study showed that there is no apparent difference between pathogenecity genes present in Colombian and North American races as measured by rust development on varieties with genes Pg-1 and pg-8 at different light intensities.

Varieties with genes Pg-2, Pg-3, and Pg-4 appeared to

be insensitive to light, except that the latent period of infection is longer, by at least two days, at low light intensity.

Studies previous to those of Browning, et al. (1967) on the effect of light intensity did not detect the breakdown of resistance in intense light. The main reasons were the use of rust races and host varieties with genes not sensitive to intense light or the use of insufficient light (Gregory, 1966; Melander, 1935). Observations made by Shukla (1954) on wheat stem rust showed that the light effect was secondary to temperature. He found that low intensities (100 ft-c) were sufficient for extensive growth of mycelium but there was very poor sporulation. He said that a light intensity of 3,500 ft-c or higher intensified the primary and secondary sporulation. Emge (1958) found that the infection-type structures of Puccinia graminis tritici developed on artificial substrates only under these environmental conditions: A light intensity of 2,000-5,000 ft-c and a temperature of 25°C to 28°C. With light-sensitive oat varieties, it is clear that a level of 3,500 ft-c is sufficient to break down resistance and the temperature level (within, say 15°-30°C) has no influence.

The resistance breakdown increased after flecking and it was sharp in the period between the opening of uredia (8 days after inoculation) and full sporulation (11 days after inoculation). Many physiological changes have been found to

occur during this critical period. Kiraly and Farkas (1962), working with wheat stem rust, found marked differences in the rate of phenol accumulation by the time of appearance of chlorotic spots (5 to 6 days after inoculation). The big difference consisted of a more rapid accumulation of phenols in resistant plants with a peak on the 7th day after inoculation, and a subsequent decrease in the phenolic concentration. Susceptible varieties increased the phenolic concentration after flecks appeared without a reduction in phenolic accumulation 9 days after inoculation. Doodson (1965), studying the influence of stripe rust development on wheat, found that during the first week only small differences in translocation were observed between infected and control plants. However, a rapid decrease in translocation in infected plants was observed after 8 days and this appeared to be caused by the increased conversion of alcohol-soluble to alcohol-insoluble compounds. Absolute translocation, when infection was well developed, was only 0.87% of that from the control. Battacharya et al. (1965), working with wheat stem rust, found that RNA increased to a maximum six days after infection and declined slowly after 12 days. They considered that the increase in RNA and acidic protein is related with the activation of particular genes in the nuclei of affected host cells. The alterations in the specific metabolic pathways in the host determined the infection type and the success or failure of the infection.

Shaw (1963:282) stated that, "Since genes control the production of enzyme protein and since there is a gene-for-gene relationship in host-parasite systems, susceptibility to rust depends upon the controlled formation of induced enzymes -- in other words upon an ordered aberration of synthetic processes in the host cell." Thus, it is probable that a mechanism like that suggested by Shaw (1963) is working in varieties containing genes Pg-1 and pg-8, but not in those containing Pg-2, Pg-3, Pg-4 and Kyto as a response to light.

Light intensity experiments suggested that intense light may be the direct cause of resistance breakdown. However, certain wave lengths may be involved differentially or, the effect of intense light may be only on the total photosynthate. Therefore, light quality and CO_2 experiments were conducted to further elucidate these points. Cool Beam incandescent and red light at an intensity of 3,000 ft-c produced a latent period of infection shorter than that produced in blue light and also abundant secondary sporulation; however, there was no breakdown of resistance. Fluorescent light at 3,000 ft-c resulted in the same latent period of infection as that from incandescent; however, there was no secondary sporulation but a clear resistance breakdown was observed. Daly (1964) found that in wheat the use of fluorescent lights enhances sporulation by the stem rust fungus in comparison with the use of fluorescent plus

incandescent lights. My results also suggest that an adequate ratio of blue-red light more than the individual action of either is the cause of the resistance breakdown on Pg-1 and pg-8 genes. On this assumption, a ratio B:R higher than one is necessary to obtain the change in rust infection types.

It is clear that a potentially satisfactory B:R ratio will not work alone if light intensity is limiting. This could be the difference between 1,000 ft-c and 3,000 ft-c in fluorescent light. Andreeva and Korozheva (1964) found that low light intensity is the cause of the absence of difference between blue and red light on quantitative amino-acid composition. Under high light, however, it was found that the type of light not only influences the total rate of amino-acid formation, but also changes the direction of amino-acid synthesis. These results supported the idea that the highly energetic "blue-far red" system composition is the key for conversion of primary products of photosynthesis along one pathway or another. The addition of 4% blue radiation to the red light source exerted the same effect on the distribution of C^{14} among the synthesized amino-acids as illumination by blue light alone.

Field observations of Pg-1 varieties in Colombia and Iowa established a clear difference in rust reaction. A "small pustule trait" which covered all the plant was the common field reaction in Colombia (Krull et al., 1965). Pg-1 varieties, however, presented rust-free panicles and a

slight rust attack at the base of the internode in Iowa (Dr. J. Artie Browning, personal communication). Climatic conditions also differ between Iowa and Colombia. Iowa has long, cloud-free days during the rust season (June-July), while Colombia has short and variable cloudy to bright days. Intensity readings indicate a higher maximum light intensity (to 19,000 ft-c) in Colombia than in Iowa (maximum about 14,000 ft-c); however, a greater total insolation is present in Iowa. The light intensity difference could not be a critical factor knowing that plants will need only one-third to one-fourth of that radiation (Loomis, 1949) but the probable effect of light quality and especially the B:R ratio is important. Observations at different latitudes showed that the B:R ratio naturally varies somewhat depending upon the latitude (Johnson, 1966). His measurements during the day showed a significant decrease in the B:R ratio at sunrise and sunset, an increase under cloudy days and a ratio clearly higher or close to one during sunny days. Since there is a much higher percentage cloud cover in Colombia than in Iowa during the rust season, it follows that the B:R ratio must be higher there and suggests that this rather than intensity per se may be responsible for the "small pustule" reaction of Pg-1 lines.

Spores borne under cool white fluorescent light germinated almost 100%. Blue, red, and Cool Beam incandescent, however, affected the germination process adversely. Dillon

Keston (1932) indicated that the decrease in germination rate could be caused by the enzymatic as well as photochemical reactions in the light response. He found that red-yellow light produced complete inhibition of spore germination after 3½ hours; however, when they were returned to visible light a germination of 90% was obtained. In the same experiment blue produced only 63% against 94% germination under visible white light.

The influence of light intensity and quality on the infection type suggested examination of other factors which might be affected by light. Knowing the influence of light on the utilization of CO_2 and the photosynthetic rate, an experiment with different CO_2 levels was performed to analyze the probable relationship of the photosynthetic rate to infection types.

I considered that all the growth chambers would have about the same concentration of CO_2; however, when light was supplied in different intensities apparently CO_2 utilization and concentration varied. The other side of the CO_2-light correlation was obtained using 100, 300, and 3,000 ppm CO_2 levels and a light intensity of 3,000 ft-c. This experiment showed that Pg-1 and pg-8 varieties presented an increase in susceptibility proportional to the CO_2 level (Fig. 15, 16 and 17) until a hypothetical level close to 350 ppm. Infection types on Kyto and Jostrain, both temperature sensitive varieties, were not influenced by the CO_2 level (Fig. 18). Thus,

there appears to exist a close correlation between photosynthetic rate and the development of rust infection types in light sensitive varieties; however, different CO_2 levels did not influence temperature sensitive varieties. The resistant response to a high light intensity (3,000 ft-c) at a low CO_2 level should be similar to that of a low light intensity (1,000 ft-c) with a high CO_2 concentration (500 ppm). The hypothetical value of 180 ppm of CO_2 (Fig. 15) could be considered as the critical CO_2 level to hold the resistant infection types regardless of the light intensity. Also, a value of light intensity lower than 1,000 ft-c should hold the same resistant infection type regardless of the CO_2 level.

The influence of light and CO_2 level was attributed by Gassner and Straib (1929) and Gassner (1930) to changes in metabolism and particularly to the improved assimilation and carbon nutrition of the plants. However, other workers consider as the most important fact, the availability of nutrients at the infection site. The oat selections, C.I. 7908, exposed to $C^{14}O_2$ in the dark nine days after inoculation with Puccinia graminis avenae race 6AF showed a high level of radioactivity at the infection site (Mirocha and Zaki, 1965). The uredial area was the highest in radioactivity, but radioactivity was common where mycelium was present. The importance of the dark fixation of CO_2 was not observed until sporulation occurred (Daly and Livne, 1966).

However, the dark CO_2 fixation was considered a function of host metabolism and it was regulated by normal host functions.

The flow rate of CO_2, 20 liters/hour, was very low. This factor further decreased the original CO_2 concentrations of 100 and 300 ppm. The CO_2 level of 3,000 ppm decreased also but it would not have become limiting. Thus, the air movement system of the regular growth chambers supplied a high and nearly constant CO_2 level but this aerodynamic process was not possible in the small growth chamber due to the low flow rate. Some workers considered that CO_2 experiments should be made with single leaves (Bjorkman and Holmgre, 1963) and others said that 5 liters/hour was enough in a chamber of 1,500 cc holding 30 oat seedlings (Harrison, 1965). A more sophisticated method could be adapted to keep a constant concentration of CO_2 (Goldworthy, 1965); however, the way in which the experiment was conducted was accurate enough for its purpose.

The comparison between incandescent and fluorescent light influence (Fig. 11) was made with the limitations of differential sensitivity of the Weston meter. Further, it was used in a position perpendicular to the light axis while the oat leaves were oriented parallel to the light axis (Fig. 12 and 13). Light was diffuse and better distributed in the growth chambers. However, the comparison between the two incandescent light intensity levels did not show any difference on the host-pathogen response.

Some environmental components such as moisture and, especially, temperature were not analyzed critically for their possible influence on infection type. However, because of the difficulty of measuring leaf temperatures accurately, temperature-sensitive biological entities were used. Kyto and Jostrain varieties responded to temperature differences as little as 4°C. These varieties were used in all critical experiments to sense and "record biologically" undesirably high temperatures.

SUMMARY

Light intensity experiments indicated that seedlings of oat varieties containing genes Pg-1 and pg-8 lose their resistance at high light intensity to Puccinia graminis avenae races 10A, 8A, and 11A to which they give moderate resistance at low light intensity.

The reactions at different light intensities of varieties with genes Pg-1, Pg-2, Pg-3, Pg-4, and pg-8, to cultures of Puccinia graminis avenae designated by the Cooperative Rust Laboratory, St. Paul, Minnesota, as of subraces 10A, 8A, and 11A, are the same as reactions to cultures designated by the Instituto Colombiano Agropecurio as of subraces 4B, 6B (or 6C) and 13B, respectively.

Therefore, Colombian races and North American races do not appear to differ in their pathogenecity genes for these varieties.

The critical period of breakdown for lines with gene Pg-1 (i.e. Clinton and Burnett) is about 7-12 days following inoculation. Secondary sporulation after nine days was observed as a response to high light intensity.

Ultraviolet and infrared light do not change the reaction of light sensitive varieties.

Blue and red light experiments did not give a sharp difference in response to rust, but sporulation began two days later with blue light. Light quality experiments with

intensities lower than 500 ft-c resulted in poor development of both the host and the pathogen.

Breakdown is more complete with fluorescent than with incandescent light, but it is not influenced by the distance of the plants from the light source if the intensity is the same.

A ratio of Blue: Red of more than 1 rather than the individual influence of blue or red wavelengths or even of intensity per se is suggested as the cause of the breakdown.

Carbon dioxide experiments showed that the light intensity-photosynthetic rate interaction appears to have the same correlation as photosynthetic rate-rust development. That is, at higher photosynthetic rates, whether caused by intense light or high concentration of CO_2, or both, the attack will approach the infection type 4, and the latent period of infection will be shorter. This is true with light sensitive varieties but not with temperature sensitive varieties, even with high levels of CO_2. Increased photosynthate, therefore, is probably the direct cause of increased rust development on varieties with genes Pg-1 and pg-8.

Kyto is a temperature-sensitive variety. It is resistant in the seedling stage to races 10A, 6F, 6AF and 6AFH below 20°C but it is completely susceptible above 24°C. The infection type and latent period of infection is the same under different CO_2 concentrations unless it is changed by temperature.

Different parasite-host pairs show characteristic reactions to light; this includes a wide range of response within varieties apparently having the same genotype, especially Pg-1 varieties.

LITERATURE CITED

Andreeva, T. F. and G. F. Korozheva.
1964 Influence of the spectral composition of light and its intensity on the formation of aminoacids in leaves. Soviet Plant Physiol. 11: 810-817.

Bailey, D. L.
1925 Physiologic specialization in Puccinia graminis avenae Ericks. and Henn. Minnesota Agr. Exp. Sta. Tech. Bull. 35: 1-33.

Bever, W. M.
1933 Effect of light on the development of the uredial stage of Puccinia glumarum. Phytopathology 24: 507-516.

Bhattacharya, P. K., J. M. Naylor and M. Shaw.
1965 Nucleic acid and protein changes in wheat leaf nuclei during rust infection. Science 150: 1605-1607.

Bjorkman, O. and P. Holmgre.
1963 Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiologia Plantarum 16: 889-914.

Browning, J. A. and E. Bustamante.
1966 Physiologic specialization in Puccinia graminis avenae. Unpublished data. Ames, Iowa. Iowa State University of Science and Technology. Department of Botany and Plant Pathology.

Browning, J. A., E. Bustamante, J. Orjuela and H. D. Thurston.
1967 The sensitivity to intense light of certain stem rust-oat seedling interactions. (To be published in Phytopathology ca. 1967.)

Crowder, L. V., J. Lotero, J. Fransen and C. F. Krull.
1967 Oat forage production in the cool tropics as represented by Colombia. Agr. J. 59: 80-82.

Daly, J. M.
1964 Pre-and postinoculation effects of light quality on infection intensity of stem rust of wheat. Phytopathology 54: 1342-1345.

Daly, J. M. and A. Livne.
1966 Dark fixation of carbon dioxide by healthy and rust-affected leaves of wheat and bean. Phytopathology 56: 164-169.

Dillon Weston, W. A. R.
1932 The reaction of disease organisms to certain wavelengths in the visible and invisible spectrum. II. Reactions of urediniospores to visible light: wave lengths between 400 and 780 mu. Phytopath. Z. 4: 229-246.

Doodson, J. K., J. G. Manner and A. Myers.
1965 Some effects of yellow rust (Puccinia striiformis) on carbon assimilation and translocation in wheat. J. Exptl. Bot. 16: 304-317.

Emge, R. G.
1958 The influence of light and temperature on the formation of infection-type structures of Puccinia graminis var. tritici on artificial substrates. Phytopathology 48: 649-652.

Forsyth, F. R.
1956 Interaction of temperature and light on the seedling reaction of McMurachy wheat to race 15B of stem rust. Can. J. Bot. 34: 745-749.

Gassner, G.
1930 Rust infection as a nutritional physiological problem (Translated title). Angewandte Bot. 9: 541 1927. Abstracted in Biological Abstracts 4: 7212.

Gassner, G. and W. Straib.
1929 Unterschugen uber die abhangigkeit des infektionsverhaltens der getreiderostpilze vom kohelensauregehalt der luft. Phytopath. Z. 1: 1-30.

Gaumann, E.
1950 Principles of plant infection. Hafner Publishing Co., Inc., New York, New York.

Goldworthy, A.
1965 A simple apparatus for generating an air stream containing a constant concentration of CO_2. J. Exptl. Bot. 17: 147-150.

Gregory, C. F.
1966 Physiological aspects of the reactions of two isogenic oat lines to the stem rust organism. Cornell Agr. Exp. Sta. Memoir 395.

Harrison, L.
1965 Carbon dioxide effect on the extension in length of Avena coleoptiles. Physiologia Plantarum 18: 208-218.

Hart, H. and K. Zapesky.
1935 The effect of light intensity and temperature on infection of Hope wheat by Puccinia graminis tritici. Phytopathology 25: 1041-1064.

Hobbs, E. L.
1958 Environmental factors affecting germinability of urediospores of Puccinia coronata corda. Unpublished M. Sc. Thesis. Library, Iowa State University of Science and Technology. Ames, Iowa.

Johnson, T. B.
1966 Light quality and quantity in the natural environment. Unpublished Ph.D. Thesis. Library, Colorado State University.

Instituto Colombiano Agropecuario P.L. 480.
1964 Project FG-Co-106. Annual Report, 1963-1964.

Kiraly, Z. and G. L. Farkas.
1962 Relation between phenol metabolism and stem rust resistance in wheat. Phytopathology 52: 657-664.

Krull, C. F., R. Reyes, J. Orjuela and E. Bustamante.
1965 Importance of the "small uredia" reaction as an index of partial resistance to oat stem rust in Colombia. Crop Sci. 5: 494-497.

Loomis, W. E.
1949 Photosynthesis. In Frank J. and W. E. Loomis, ed. Photosynthesis in plants. pp 1-17. The Iowa State College Press. Ames, Iowa.

Melander, L. W.
1935 Effect of temperature and light on development of the uredial stage of Puccinia graminis. J. Agr. Res. 50: 861-880.

Mirocha, C. J. and A. I. Zaki
1965 Fixation of CO_2 in the dark by fungus-infected bean, beet, barley and oat plants. Phytopathology 55: 940-941.

Orjuela-R, J., H. D. Thurston and C. F. Krull.
1962 Physiologic specialization of Puccinia graminis avenae in Colombia. Plant Dis. Rptr. 46: 866-871.

Richardson, G. L.
1967 Development of photosynthesis in cotton seedlings, Gossypium hirsutum L. Crop Sci. 7: 6-8.

Roberts, B. J. and M. B. Moore.
1956 The effects of temperature on the resistance to oat stem rust conditioned by the BC genes. Phytopathology 46: 584.

Rosen, H. R. and L. F. Bailey.
1957 Relationship of reaction type in crown rust to the rate of carbohydrate metabolism in oats. Phytopathology 47: 29.

Rowell, J. B.
1957 Oil inoculation of wheat with spores of Puccinia graminis var. tritici. Phytopathology 47: 689-690.

Sempio, C.
1938 Primo contributo alla conoscensa dell azione esercitata da varifattori ambientali su alcune malattie parassitarie di piante cultivate. Riv. Patol. Veg. 28: 241-351.

Shaw, M.
1963 The physiology of host-parasite relations of rust. Annu. Rev. Phytopathol. 1: 259-294.

Shukla, T. N.
1954 Factors affecting variability in cereal rust reactions. II. Variability due to light. Indian Phytopathol. 7: 43-52.

Silverman, W.
1959 The effect of variation in temperature on the necrosis associated with infection type 2 uredia of the wheat stem rust fungus. Phytopathology 49: 827-830.

Simons, M. D.
1954 The relationship of temperature and stage of growth to the crown rust reaction of certain varieties of oats. Phytopathology 44: 221-223.

Simons, M. D., F. J. Zillinsky and N. F. Jensen.
1966 Standardized system of nomenclature for gene characters of oats. U.S.D.A. Crop Research, A.R.S. Series 34-85.

Welsh, J. N.
1937 The synthetic production of oat varieties resistant to race 6 and certain other physiologic races of oat stem rust. Can. J. Res. Sect. C, 15: 58-69.

ACKNOWLEDGEMENTS

The author wishes to express his sincere appreciation for the counsel, encouragement and constructive criticism offered by Dr. J. Artie Browning during the course of this study and in the preparation of the manuscript.

Special debts of gratitude are due to the Rockefeller Foundation and to the Colombian Agricultural Institute (ICA) who made it possible for the author to undertake graduate education abroad, and to Iowa State University for supporting his research at that institution.

Finally, appreciation is due to his mother and his wife whose patience, understanding and assistance during his years of study merit special recognition.