SOME FACTORS INVOLVED IN THE FORMATION OF TELIAL SORI BY *PUCCINIA RECONDITA* F. SP. *TRITICI*

By

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INTRODUCTION

The foundation for studies of sexual recombination in the rust fungi was established by Craigie (3) with the discovery of the function of the pycnial stage in the rusts. Subsequent genetic studies have served to elucidate many heritable properties of these fungi. Knowledge concerning the inheritance of genes for virulence or avirulence has proven to be especially valuable in selecting resistant host genes for use in breeding programs.

Certain exotic species of the genus Thalictrum were shown to be alternate hosts for the wheat leaf rust fungus by Jackson and Mains (6) in 1921. Young, Saari, and Curtis (17) reported that several species of Thalictrum native to the United States may serve as alternate hosts for the wheat leaf rust fungus, Puccinia recondita Rob. ex. Desm. f. sp. tritici Erikss. and that T. dasycarpum, at least, may function to a limited extent in nature as an alternate host in the Rocky Mountain area of the United States. They indicated that this species did not function significantly as an inoculum reservoir, but that it may present a potential hybridization site for the fungus in nature.

P. recondita f. sp. tritici appears to have a highly variable pathogenic potential on wheat. Studies elucidating the source of specific genes for pathogenicity, which may appear as the result of sexual recombination of the fungus, would be helpful in breeding leaf rust resistant lines of wheat. The specific source of new virulence gene combinations

appearing in the leaf rust population can be only determined by observing the progenies resulting from hybridization and/or selfing of known combinations of virulences of the fungus on the alternate host.

Before such genetic studies can be successfully initiated, a reliable method of inducing teliospore formation of pure leaf rust cultures in the laboratory needs to be developed. With this objective in mind, the studies reported here were made to determine some of the factors involved in teliospore formation by the wheat leaf rust fungus.

REVIEW OF LITERATURE

Many investigators (8, 10, 11, 16) have reported that the wheat leaf rust fungus does not consistently produce abundant telia in the greenhouse or laboratory. Furthermore, teliospore formation in most cereal rusts has been associated with maturation and senescence of the host plant.

Raines (11) indicated that telial production by P. recondita f. sp. tritici was more abundant on older wheat plants than on plants in younger stages. He postulated that the vegetation vigor of the host was inversely correlated with teliospore production.

Johnson (7) concluded that maturation of plant tissues had a direct effect on teliospore production by Puccinia graminis Pers. f. sp. tritici Erikss. & E. Henn. He noted that the most succulent parts of the wheat plant were the last to produce telia and that those parts of the plant which had a large proportion of vascular tissue were the first to produce telia.

Davis (4) was successful in obtaining teliospores of two races of wheat leaf rust on two varieties of spring wheat in the greenhouse. The plants were inoculated at the age of 2 months and spores from previous infections were spread and reincubated every 7-14 days afterwards. When the plants were 3 months old, the temperature was lowered from 76 F to 68 F and held at that level until telia appeared 2 weeks later.

Placing infected detached leaves in nutrient solutions has been reported to aid in inducing teliospore formation in certain cereal rusts.

Waters (16) was able to induce teliospore formation on wheat leaf rust infected plants by floating detached infected leaves on a sucrose solution. Just prior to uredial rupture, leaves were detached, placed on distilled water for 3 days, and subsequently placed on a 7% sucrose solution. An abundance of teliospores was formed on the leaves after 5 days in the sucrose solution. The telial sori were linear in shape and separate from the uredial sori, although some teliospores were found to be interspersed with urediospores in uredial lesions. Many of the teliospores were abnormal one- or two-celled spores with spines; however, typical smooth, two-celled teliospores were also present.

Hooker and Yarwood (5) have recently reported teliospore production by Puccinia sorghi Schw. on detached leaf sections floated on 5% sucrose solution containing 20 ppm kinetin. They stated that teliospores developed on many occasions when leaf sections were floated on the solution for 14-16 days without supplemental light. Teliospores also developed on leaf sections that were floated for 10 days on water containing 20 ppm kinetin when supplemental light was used. Several biotypes of the fungus produced telia on numerous host varieties.

Young, Keeling, and Samborski (Personal communication) all have stated that P. recondita tritici occasionally forms teliospores on wheat leaves that have been detached from the plant just prior to inoculation and floated on benzimidazole solution. Uredia normally rupture after 7-9 days and telial sori are sometimes found after 18 days especially on moderately resistant varieties.

Some reports have indicated that teliospore formation may be dependent to some extent on the host variety. Waters (16) subjected rusted wheat plants of the variety Golden Wave to darkness, low temperatures

and dessication, and was unable to induce teliospore formation on this variety.

Prasada (10) stated that teliospores of the wheat leaf rust fungus were never found on wheat varieties planted in experimental plots near Simla, India. However, a susceptible wheat variety, IP 144, was found on which abundant telia were formed. This variety was later extensively used for the production of teliospores for routine laboratory testing. Prasada indicated that teliospore formation on this variety was difficult to explain when teliospores did not develop in the same plots on other varieties which were equally susceptible to the uredial stage. Therefore, the host variety appears to play an integral role, at least in India, in teliospore formation.

Although the effect of temperature has not been explored completely, there are indications that temperature may affect the formation of teliospores by the wheat leaf rust fungus. Shifman (13), in a preliminary study, concluded that 59-68 F was the optimum temperature of teliospore formation by P. recondita. Davis (4) followed Shifman's recommendation with respect to temperature and successfully induced teliospore formation on adult plants.

Prasada (10) noted that the telial stage of P. recondita seldom occurs in India. This stage was sometimes found in the plains but never in the hills on planted wheat. However, teliospores were sometimes observed on volunteer plants suffering from moisture stress. He postulated that such teliospore formation may have been induced by gradual loss of water at low temperatures.

Teliospores of P. recondita have only rarely been reported on plants in the seedling stage. Mains (8) indicated that he had never

seen telia of the wheat leaf rust fungus on seedling plants in the greenhouse. Young, Browder, Saari and Samborski (Personal communication) have stated that telia are only rarely seen on seedling plants during routine leaf rust race identification studies.

On the other hand, Takahashi, Yamada, and Takahashi (14) have reported that the majority of the wheat leaf rust isolates found in Japan formed teliospores on the first leaf of young wheat seedlings rather readily. The authors inoculated the primary leaf of many wheat varieties when the plants were at the 1 1/2 leaf stage. Teliospores normally were formed 18-24 days after inoculation at least on certain varieties. They found the degree of teliospore formation was not related to the physiologic race of the fungus, but varied according to isolates and wheat varieties. They indicated that the difficulties other workers had in obtaining teliospores on seedling plants probably was due to the improper combination of the leaf rust biotype and wheat variety.

MATERIALS AND METHODS

Adult Plant Studies:

A study of the influence of rust culture and wheat variety on teliospore formation was made using the spring wheat varieties Carina, Kenya Farmer, Loros, Selkirk, Thatcher, and Webster and one culture each of races 2, 9, and 13 of P. recondita tritici. In all cases in this study race numbers used are those of Basile (2). Twenty seeds of a wheat variety were planted in each of eight 6 inch pots and subsequently placed in a greenhouse where the temperatures varied between 65 and 80 F. In a few instances, however, temperatures as high as 95 F were recorded for brief periods on hot days.

The plants were inoculated at the age of 2 months by dusting them with a mixture of 1 cc of urediospores of each race together with 30 cc of talc.

After the plants were inoculated, they were sprayed with water containing a surfactant (Tween 20, two-four drops in each 1000 ml. of water), placed in a moist chamber overnight and then returned to the greenhouse. The plants were reinoculated every 2 weeks by placing them in a moist chamber and spraying them with water and a surfactant.

An experiment was designed to determine the effect of gibberellic acid and/or N^6 benzyladenine on teliospore formation. Twenty seeds of one of the varieties, Carina, Kenya Farmer, Loros, and Webster were planted in each of sixteen 4 inch pots. The test was divided into four

treatments and four pots of each variety were used for each treatment. The plants were grown in a greenhouse similar to the one previously described for a period of 10 weeks, at which time the plants in treatment I were sprayed with a 500 ppm solution of gibberellic acid. Those plants in treatment II were sprayed with a 500 ppm solution of N^6 benzyladenine and those in treatment III were sprayed with distilled water. Two weeks after application of these treatments the plants were reinoculated with the same mixture of leaf rust races and in the same manner as previously described. The plants were inoculated every 2 weeks for the duration of the experiment.

Plants of the variety Kenya Farmer were subjected to water stress prior to and after infection in order to observe the effects of wilting on teliospore formation. Eight 3 inch pots containing 20 plants each were assigned to each of four treatments. The treatments were initiated when the plants were 4 weeks old. The plants in treatment I were allowed to dry sufficiently to produce wilting 2 days prior to inoculation and then watered enough to effect recovery. The plants were then inoculated with a mixture of races 2, 9, and 13 as previously described and placed in a moist chamber overnight. The plants in treatments II and III were allowed to dry so that wilting was produced 1 day and 4 days after inoculation, respectively. The plants in treatment IV were not subjected to moisture stress during the test. The treatment procedure was repeated at 14-day intervals throughout the testing period.

Seedling Studies:

The varieties which comprise the wheat leaf rust International Standard Differential series (Malakof, Carina, Brevit, Webster, Loros,

Mediterranean, Hussar, and Democrat) were used to study telial production on detached leaves with the cut ends immersed in solutions of benzimidazole. Each variety was planted in a 3 inch pot and inoculated with race 9 when the seedlings were at the 1 1/2 leaf stage. Primary leaves were detached daily for 6 days after inoculation and placed in small vials containing benzimidazole solutions of 20, 40, and 60 ppm. Detached leaves were held in three controlled temperature rooms at 40, 50, and 70 F where approximately 700 ft -c of fluorescent and incandescent light were supplied 12 hours daily.

A similar study was also made in a greenhouse where the temperature varied between 65 and 75 F and no supplemental light was used.

A study of teliospore formation on attached primary leaves in the seedling stage in the greenhouse was made using 60 leaf rust cultures collected in a state-wide leaf rust survey and 16 differential wheat varieties (Malakof, Carina, Brevit, Webster, Loros, Mediterranean, Hussar, Democrat, Dular, Lee, Waban, Sinvalocho, Exchange, Westar, Wesel, and Lerma Rojo). The plants of each variety were inoculated with each culture at the 1 1/2 leaf stage and treated in the same manner as plants used in routine leaf rust race identification. That is, the plants were inoculated by brushing with infected plants, sprayed with water containing a dilute surfactant and held in a moist chamber overnight. These infected plants, however, were not discarded once uredial reactions were recorded but were held for observation of teliospore formation until death of the infected leaves. Observations and descriptions of telial sori were normally recorded about 30 days after inoculation. The temperature in the greenhouse where these plants were held varied from 60-80 F with occasional temperatures as high as 90 F on hot days.

RESULTS

Adult Plant Studies:

The combinations of varieties and rust cultures used, or the conditions under which the plants were grown, apparently were not conducive to telial formation. Only three telial sori developed on the plants in the variety test; all were located on the dorsal surface of leaves in three separate pots of the variety Carina. These sori developed when the plants were 3 1/2 months old and were found on upper leaves which, at that time, were chlorotic. The plants were thick in the pots under these conditions and growth was rank. This had been done purposely in an attempt to hasten the exhaustion of soil nutrients and thereby, perhaps, hasten maturity and senescence. However, under these conditions powdery mildew (Erysiphe graminis DC.) became a rather serious contaminant problem and may have had an influence on telial formation.

Similarly, in the study involving the effect of gibberellic acid and N^6 benzyladenine only two telial sori developed. These sori also developed when the plants were 3 1/2 months old and on the variety Carina. One sorus appeared on a plant sprayed with gibberellic acid and the other on a control plant.

In the study which involved wilting of the leaves, it was difficult to bring about wilting at desired periods. Considerable experience needed to be acquired before water could be withheld at a time which would induce the wilting of leaves at the proper time. Eventually,

the entire wilting study was made twice. The first time the experiment was made no telia developed on any of the treatments. During the second attempt, 10 telial sori developed, all of them on control plants not subjected to wilting. It was noted in the course of both tests that when leaves became fairly heavily infected with uredial lesions (± 20 percent Modified Cobb Scale) and were subjected to wilting, they died rather rapidly and no telial sori developed.

Seedling Studies:

When seedling wheat leaves were inoculated with race 9, detached, and the cut ends immersed in benzimidazole solutions and held at constant temperatures of 40, 50, and 70 F, teliospores failed to develop. When similar leaves were held in the greenhouse at temperatures varying between 65-75 F, however, teliospores were observed to develop on certain varieties (Table I).

More telial lesions were formed on Carina and Brevit than any of the other varieties tested. Race 9 did not form any telial lesions at all on the resistant varieties Mediterranean and Democrat nor on the variety Hussar. Over twice as many telial lesions were found on leaves detached within 3 days of inoculation as were found on those detached between 3 and 6 days. There appeared to be no correlation between the appearance of telial lesions and the concentration of benzimidazole into which the leaves were placed. This test was repeated five times, and no telial lesions were observed on detached leaves in any of the last four trials.

The plants remaining after the necessary leaves had been detached were held in the same greenhouse as the detached leaves. It was noted

TABLE I

PRODUCTION OF TELIAL SORI OF PUCCINIA RECONDITA TRITICI RACE 9 THIRTY DAYS AFTER INOCULATION ON DETACHED WHEAT LEAVES WITH THE CUT ENDS IMMERSED IN SOLUTIONS OF BENZIMIDAZOLE

Variety	Benzimidazole Concentration	Time of leaf detachment (days after inoculation)					
		1	2	3	4	5	6
Malakof	20 ppm	+ [a]	+	-	-	-	-
	40 ppm	-	-	+	-	-	-
	60 ppm	-	+	-	-	-	-
Carina	20 ppm	+	+	-	-	+	-
	40 ppm	+	+	+	-	+	-
	60 ppm	+	+	-	+	+	+
Brevit	20 ppm	+	+	+	-	+	-
	40 ppm	+	-	+	-	-	-
	60 ppm	-	+	+	-	-	-
Webster	20 ppm	-	-	+	-	-	-
	40 ppm	-	-	+	-	-	-
	60 ppm	-	-	-	-	-	-
Loros	20 ppm	+	-	-	+	-	-
	40 ppm	-	-	-	-	-	+
	60 ppm	-	-	-	-	+	-
Mediterranean	20 ppm	-	-	-	-	-	-
	40 ppm	-	-	-	-	-	-
	60 ppm	-	-	-	-	-	-
Hussar	20 ppm	-	-	-	-	-	-
	40 ppm	-	-	-	-	-	-
	60 ppm	-	-	-	-	-	-
Democrat	20 ppm	-	-	-	-	-	-
	40 ppm	-	-	-	-	-	-
	60 ppm	-	-	-	-	-	-

[a] + Indicates telial sori
- Indicates no telial sori formed

that telial sori began to form between the 18th and 25th day after inoculation on these attached leaves. The sori developed more abundantly on leaves that had become somewhat chlorotic but were also observed to form on some leaves that were still green. The data on teliospore formation on attached leaves in all five trials are given in Table II.

Teliospores were not always formed on all infected plants. Often the leaves were so heavily infected that death of the leaf occurred a few days after uredial rupture. This was particularly true in the second trial in which no telia developed at all. The leaves were so heavily infected that death occurred, even on plants normally moderately resistant, prior to the time usually required for teliospore formation.

Since it was observed that telial formation on seedling leaves occurred more often on attached leaves in the greenhouse than with any of the other conditions, it was decided to hold the trays of plants being used for race identification and observe them for telial development. In this manner 60 leaf rust cultures in six races were observed for the ability to form teliospores on seedling plants of 16 wheat varieties. Teliospores were produced on at least one variety by 59 of these cultures (Tables III and Figure 1). Teliospore formation was most abundant and occurred with the most frequency on the variety Dular. This variety was moderately resistant to the uredial stage of all cultures tested. Telial sori were frequently found also on the varieties Loros, Hussar, Exchange, and Wesel.

Two types of telial sori were observed on seedling plants. Small, round, individual telial sori were occasionally found, particularly on plants very resistant to the uredial infection. Sometimes, however, these small individual sori were present on plants moderately resistant

TABLE II

THE FORMATION OF TELIAL SORI ON SEEDLING LEAVES OF SEVERAL WHEAT VARIETIES INOCULATED WITH RACE 9 OF PUCCINIA RECONDITA TRITICI

Trial Number	Variety							
	Malakof	Carina	Brevit	Webster	Loros	Mediterranean	Hussar	Democrat
1.	0 /a	1	2	2	2	1	1	0
2.	0	0	0	0	0	0	0	0
3.	2	2	2	2	2	1	2	1
4.	0	1	0	1	1	0	0	1
5.	0	1	0	1	2	1	1	0

/a 0 = No telial sori formed
1 = 1 to 10 telial sori on each leaf
2 = More than 10 telial sori on each leaf

TABLE III

THE INFLUENCE OF WHEAT VARIETIES ON THE FORMATION OF TELIAL LESIONS BY VARIOUS RACES OF *PUCCINIA RECONDITA TRITICI* ON SEEDLING LEAVES

Variety	Race 1	2	5	6	9	13	Total
Malakof	0/5[a]	3/25	0/11	1/5	3/8	0/6	7/60
Carina	2/5	1/25	3/11	3/5	3/8	0/6	12/60
Brevit	3/5	6/25	6/11	0/5	2/8	0/6	17/60
Webster	1/5	1/25	4/11	1/5	3/8	1/6	11/60
Loros	4/5	10/25	7/11	1/5	5/8	0/6	27/60
Mediterranean	2/5	3/25	2/11	1/5	4/8	1/6	13/60
Hussar	1/5	4/25	7/11	1/5	7/8	0/6	20/60
Democrat	2/5	3/25	2/11	3/5	2/8	0/6	12/60
Dular	5/5	22/23	11/11	1/1	8/8	6/6	53/54
Lee	0/5	5/23	2/11	0/1	2/8	0/6	9/54
Waban	0/5	2/23	1/11	0/1	5/8	0/6	8/54
Sinvalocho	0/5	6/23	4/11	0/1	0/8	0/6	10/54
Exchange	2/5	7/23	8/11	1/1	2/8	3/6	23/54
Westar	4/5	2/23	3/11	0/1	2/8	0/6	11/54
Wesel	2/5	5/23	5/11	0/1	8/8	1/6	21/54
Lerma Rojo	0/5	1/23	5/11	1/1	5/7	1/6	13/53
Total	28/80	81/384	70/171	14/48	61/127	13/96	

[a] Numerator indicates the number of cultures forming telial lesions and denominator the total number of cultures used to test the variety.

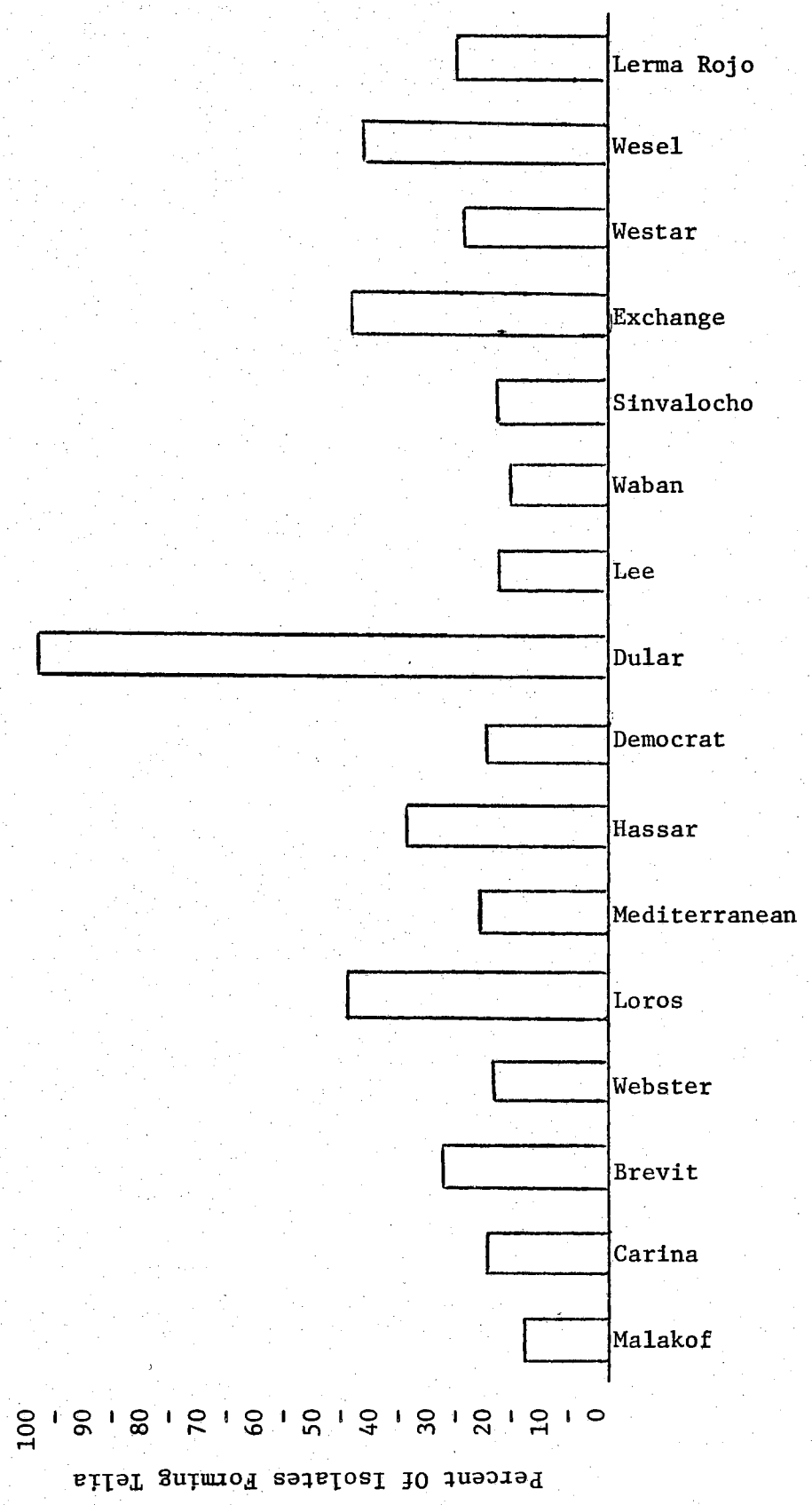

Figure 1. The Percent of Isolates of Puccinia recondita tritici Forming Telial Lesions On Seedling Leaves of Various Wheat Varieties

or susceptible to the uredial stage. Other telial lesions were arc-shaped and formed in an intermittent or continuous ring around a single uredial lesion (Figure 2). In most cases when the uredial infection was light to moderate, secondary uredial sporulation occurred around the primary uredial lesion, usually on the ventral surface of the leaf. The telial sori always formed on the opposite side of the leaf from the secondary uredial sorus, therefore, they were chiefly hypophyllous. The type of telial lesion that formed appeared to be a function of the interaction between the fungus isolate and the variety. For example, the telial sori on Dular were usually the arc-shaped type whereas those that developed on Loros and Exchange were most often the small circular type which were also somewhat limited in number. It was noted that the leaves of Dular remained green longer than many of the other varieties and this may have contributed to the abundance of telial sori produced on this variety.

The frequency of teliospore formation for each race encountered in this study was determined by dividing the number of times each race produced telia on any of the varieties used by the total number of times the race was tested. These data are illustrated in Figure 3. Race 9 formed telia more frequently than any of the other races and on certain varieties produced more abundant telia than the other races. Races 1 and 5 also produced telial sori quite frequently while races 2, 6, and 13 produced telia less frequently on the varieties used in this study. Dular appeared to be the only variety on which these latter three races produced telial sori consistantly and in any appreciable quantity. Telial sori on other varieties infected with these races were quite scanty, often no more than one per leaf.

Figure 2. Arc-shaped telial sori forming an intermittent or continuous ring. Most frequently observed on plants moderately resistant or susceptible to the uredial stage.

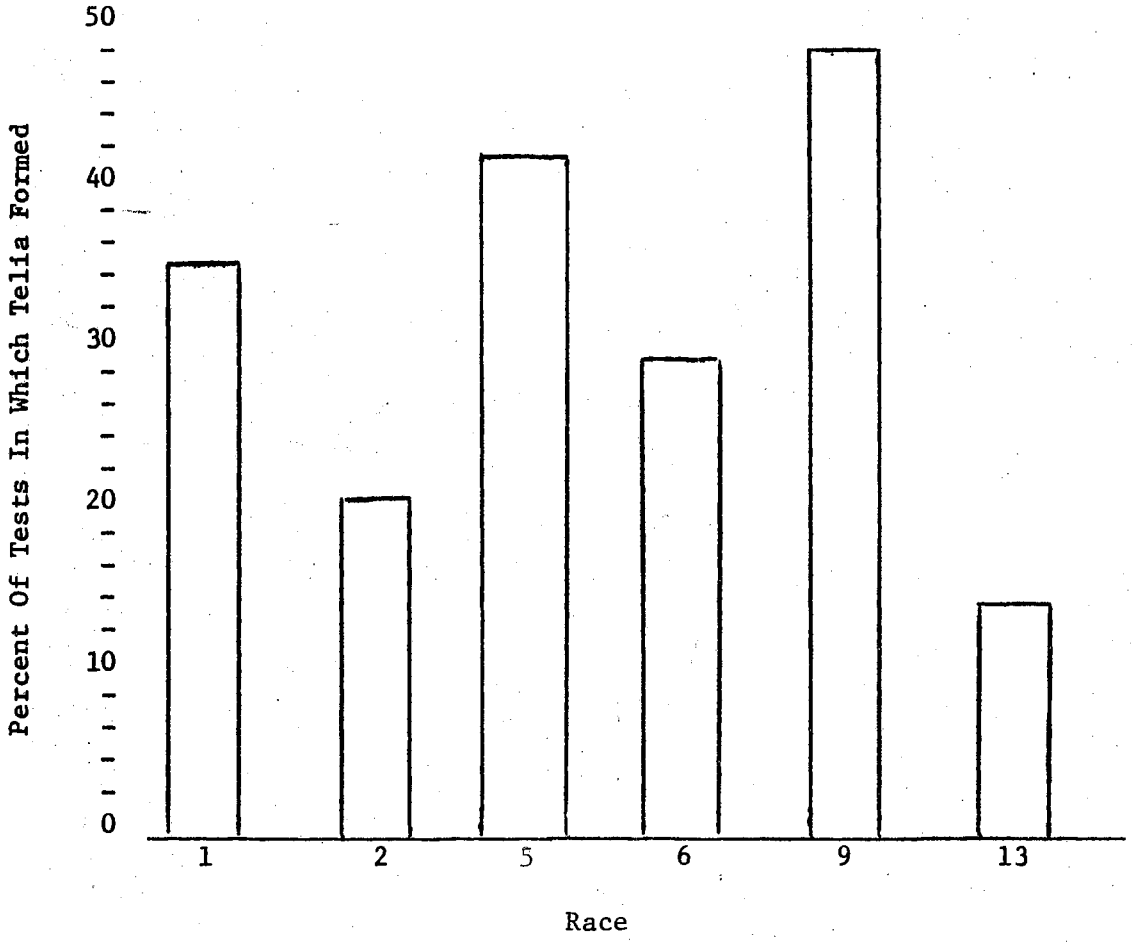

Figure 3. Frequency of Teliospore Formation By Various Races of Puccinia recondita tritici On a Group of 16 Wheat Varieties

Teliospores produced under controlled conditions, to be of value, must be normal in size, shape and viability. Although no tests of viability were made in this study, spores produced in the greenhouse on the variety Dular were compared with those produced on the same variety following natural infection in the field, and with the description of teliospores of this rust given by Arthur (1). He described the teliospores as oblong, clavate or cylindric, 13-24 μ wide by 32-65 μ long or on some hosts 10-18 μ wide by 26-45 μ long. They were rounded or truncate above, narrowed below and usually not constricted at the septum. The spore wall was described as chestnut brown, paler below, 1 μ or less thick at the sides, and 3-7 μ thick above. The pedicel was found to be colored and very short.

The width and length of 500 teliospores from mature plant material of the variety Dular collected in the field and 500 teliospores from seedling plants of the variety Dular in the greenhouse were measured. Teliospores from the mature plants from the field averaged 16.5 μ wide by 41.2 μ long. Teliospores from the seedling leaves in the greenhouse measured 16.0 μ wide by 38.6 μ long. A comparison of the length of spores from these two sources is given in Figure 4. Although the spores from the field averaged somewhat larger than those from the greenhouse, the difference was not statistically significant. Teliospores from both sources fell within the smaller size range reported by Arthur (1). Observations on the shape and color of the spores from both the field and the greenhouse indicated a close fit to the description given by Arthur. However, in this material two types of teliospores were observed on both mature and seedling plants. Typical two-celled teliospores (Figure 5) were by far the most abundant, but single-celled teliospores (Figure 6) quite frequently were observed.

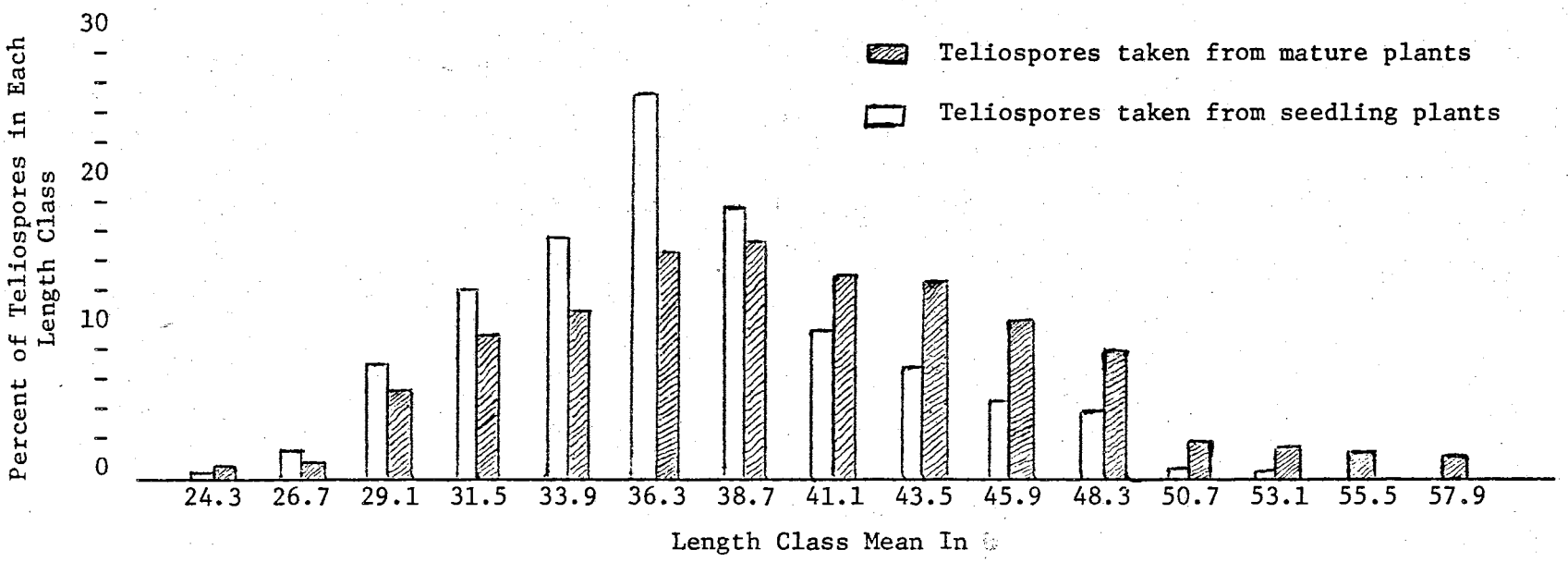

Figure 4. The Relative Length of Teliospores of Puccinia recondita f. sp. tritici From Seedling and Mature Plants of the Wheat Variety Dular

Figure 5. Typical two-celled teliospore of Puccinia recondita f. sp. tritici (X5000)

Figure 6. Single-celled teliospore of Puccinia recondita f. sp. tritici often found interspersed with normal two-celled teliospores (X5000)

DISCUSSION

Normally, telial sori form readily in the field on susceptible varieties as the plants reach maturity. Little or nothing is known of the interaction between host and parasite in the development of telia under these conditions and, although one race may predominate in the uredial stage, the predominant telia may have developed from a race with a lower frequency of uredia.

In this study, varieties known to be resistant, moderately resistant and susceptible were inoculated in the adult plant stage with three of the most predominant races found in the field. It was expected that at least one combination of host and parasite from this group would produce the telial stage. However, telia failed to form and, while this may have been due to improper combinations of rust isolates and wheat variety, it seems more plausible that improper environmental or other conditions were involved. Davis (4) was able to induce limited teliospore formation on susceptible varieties with two races, 2 and 9, both of which were used in the present experiments. However, the environmental conditions under which Davis' tests were made were not identical to those used in this study.

Other evidence, however, seems to indicate that teliospore formation on adult plants grown in the greenhouse is dependant upon specific host-parasite combinations. Samborski (Personal communication) observed that more abundant telia were produced on the wheat variety Exchange in the greenhouse than on other varieties he has used. He believed that

this phenomenon might be related to the intermediate reaction type of the uredial stage produced on this variety by most of the races of leaf rust that are predominant in the field. Vakili (15) also found that certain races of P. recondita differed in the earliness of teliospore formation and in the total amount of telia formed on adult plants of certain wheat varieties. He attributed these differences to the interaction of wheat variety and leaf rust isolate. He also found teliospore formation more abundant on plants exhibiting moderate resistance to the uredial stage of a particular isolate. Therefore, it seemed evident that teliospore formation on adult plants, under controlled environmental conditions, was most likely to occur in abundance when the rust culture-variety interaction in the uredial stage produced an intermediate type reaction. It was also evident that environmental or other conditions influenced the development of telia even if the proper rust isolate-variety combination were used.

Teliospore formation by P. recondita has not been reported on seedling plants in North America. However, the common procedure in testing for uredial reactions is to hold the plants only about 12 days after inoculation and then record the reaction and discard the plants. Since telia do not normally appear on seedling plants for at least 18 days after inoculation, the formation of telia on seedling leaves probably has escaped observation simply because in most cases the plants were discarded too soon.

The results presented here indicate that teliospore formation often occurs on leaves of seedling plants held in the greenhouse at 60-80 F for 18-25 days after inoculation.

The production of telial sori on seedling leaves was often correlated with the uredial reaction type produced by the isolate-variety combination. Moderately resistant uredial reactions and abundant telial formation were frequently correlated. For example, all isolates, except one isolate of race 2, formed abundant telial sori on the variety Dular which exhibited an intermediate uredial reaction to all isolates. On the other hand, only small individual telial sori were occasionally encountered on plants highly resistant to the uredial stage. The formation of any appreciable quantity of telial sori on varieties susceptible to the uredial stage was rarely encountered.

These results confirm those reported by Takahashi, Yamada, and Takahashi (14) who found also that the degree of teliospore formation on wheat was correlated with the uredial reaction type exhibited by the variety. They concluded that teliospores were rarely found on highly resistant or susceptible varieties but frequently found on varieties exhibiting moderate resistance or a mesothetic type reaction.

Although teliospore formation and the uredial reaction type were often correlated, other factors were undoubtedly involved. Teliospores were often found on one variety but not on others with a similar intermediate uredial reaction type. Teliospores were also occasionally found in abundance on highly susceptible varieties.

Teliospore formation on leaves of seedling plants appears to be correlated with senescence as it is on leaves of adult, maturing plants. However, moisture stress and other factors, such as high levels of infection, detrimental to plant growth appeared to limit teliospore formation. These factors brought about more rapid deterioration of the leaf and thereby reduced the length of time available for telial formation.

The use of detached leaves would be advantageous because such leaves can be strictly isolated and thereby limit the possibilities of contamination, according to Milholland and Young (9). Detached leaves placed in water rapidly begin senescence, but senescence can be retarded by floating or immersing the cut ends of detached leaves in benzimidazole solution (12). Theoretically then, telial lesions should have ample opportunity to form.

Keeling (Unpublished data) found that telia did form with certain variety-race combinations under the above conditions. However, attempts to reproduce his results in this study were successful in only one trial. All other attempts failed, again indicating that environmental or other factors were operating.

Teliospores formed on the variety Dular in the field and in the greenhouse were comparable in size and shape and fit the description given by Arthur (1). However, both the spores from the greenhouse and from the field were at the small end of the range given by Arthur for this rust.

SUMMARY

1. Several attempts to induce teliospore formation by Puccinia recondita f. sp. tritici on adult wheat plants using various variety-race combinations, applications of N^6 benzyladenine and gibberellic acid, and hastening leaf senescence by wilting were unsuccessful.

2. Limited teliospore formation occurred on detached leaves with the cut ends immersed in benzimidazole solution on one occasion, but attempts to repeat this were unsuccessful.

3. Several leaf rust isolates formed teliospores readily on seedling wheat leaves in the greenhouse. These plants were handled essentially the same as is common with plants used for leaf rust race identification in the uredial stage. Teliospores appeared 18 to 25 days after inoculation of the plants.

4. Teliospore formation was most abundant on varieties exhibiting moderate resistance to the pathogen in the uredial stage. In these studies telial sori of most isolates formed abundantly on the variety Dular which exhibited moderate resistance to all isolates in the uredial stage.

5. The leaf rust races 1, 5, and 9 formed teliospores more frequently than races 2, 6, and 13. This may be related to the fact that more of the varieties used exhibited an intermediate reaction to the uredial stage of races 1, 5, and 9 than to races 2, 6, and 13.

6. Telial sori formed on plants resistant to the uredial stage tended to be small and circular in shape, while the telial sori formed

on plants intermediate or susceptible to the uredial stage tended to be larger, arc-shaped and forming a ring of secondary sporulation around a uredial lesion.

7. Teliospores from leaves of adult plants grown in the field and from leaves of seedling plants grown in the greenhouse appeared to be morphologically indistinguishable. Both 1- and 2-celled teliospores were observed although the normal 2-celled type was found most frequently.

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