

THE INHERITANCE OF LEAF RUST RESISTANCE
IN TWO SIMPLE WHEAT CROSSES

by

VAL WADDOUPS WOODWARD

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INTRODUCTION

Leaf rust, Puccinia triticina, Eriks., is one of the most severe diseases of wheat, one of the world's most important food crops. Permanent resistance to this pathogenic fungus lies only in the germ plasm of varieties possessing the ability to repel the disease. It therefore seems reasonable that the mode of inheritance of this ability to repel, called resistance, be thoroughly studied. A knowledge of the genetics of inheritance will greatly reduce the empiricism involved in a practical breeding program and hasten the production of resistant varieties.

That the problem is important is seen by the fact that the annual loss caused by leaf rust averages \$10,000,000 with losses of 50 to 97 percent in localized areas not being uncommon (Chester, 1946). This fungus is found everywhere in the world where wheat is grown; therefore all wheat producing areas are concerned with this widespread disease.

The objective of this study concerns the inheritance of leaf rust resistance in two simple wheat crosses; this comprises a part of an organized genetic study under way at Kansas State College. If a wheat variety possesses seedling resistance to certain physiologic races of rust, it will also possess mature plant resistance to the same races of rust (Kale, 1938, 1939), therefore, seedling resistance only is being studied.

There remains much to be done in this field of study and before we can confidently claim a victory over this common pest the genetics of the host and of the pathogen will have to be

more fully understood.

REVIEW OF LITERATURE

The Pathogen

The importance of leaf rust has for many years been underestimated because of the fact that the losses caused by this pathogen are difficult to descry. Losses are due to a failure of the head to produce the normal number of kernels and the size of the kernels produced is reduced (Johnson, 1931; Johnston and Miller, 1934). Until the present century there has been confusion among farmers and research men as to which disease, leaf rust or stem rust, was responsible for the devastating damage of wheat.

The history of cereal rust dates back to early Biblical time. Levine in 1919, according to Chester, 1946, quotes Biblical references indicating that rusts were known at the time of Moses and other early prophets. Aristotle (384-322 B.C.) noted that rust was more severe in some years than in others; he attributed it to warmth and moisture. Several other quasihistorical writers that made mention of leaf rust were quoted by the same author.

Chester (1946) further states that reliable information indicates the origin of rust to be in Southwest Asia, the probable location of the inception of its host, wheat. The earliest record of leaf rust in this country dates back to a short time after the introduction of wheat in 1528, and has gradually increased in importance since that time until it has become one of the most important diseases of wheat.

Due to the fact that this disease is important and causes many millions of dollars damage per year, a world wide cooperative breeding program is required to successfully combat this disease. The first step in such a program would logically be a study of the morphological, physiological, and cytogenetical characteristics of the pathogen.

Macroscopically the disease may be identified by the production of orange pustules, called uredia, during the photosynthetically active stage of the wheat. These uredia usually occur on the upper surface of the leaf and occasionally on the leaf sheath, and they are numerous and small, whereas, stem rust pustules may occur on any part of the plant including the inflorescence, and are not usually as numerous. Leaf rust pustules may also be distinguished by their ellipsoid shape, small size, and their orange red color as compared to a linear shape, comparatively large size, and brownish-red color characteristic of stem rust. The same pustules later in the season become telia, which contain teliospores. The telia of leaf rust differ from those of stem rust in that they are smaller and more spherical, rather than large and linear. Also, they are not rumpant, but have a thin epidermal layer over the pustule causing a glossy, smooth surface. These are the only two stages of leaf rust commonly seen in America; its alternate host, Thalictrum, being highly resistant prevents the completion of the life cycle. This is important in another regard; the pathogen seldom hybridizes due to the fact that haplois occurs on Thalictrum and this part of the life cycle does not occur in

this country; therefore mutations are probably the only means of the origin of new physiological races of leaf rust (Chester, 1946).

The life cycle of leaf rust is reviewed very well by many authors (Chester, 1946; Johnston et al., 1935, etc.). The red spore, or uredial stage can develop on any stage of a physiologically active wheat plant. Damage to the host occurs when heavy infection has occurred before blooming time. The wheat plant may contact the urediospores in two ways; by over wintering urediospores, and by urediospores that blow in from the South in spring and from the North in autumn. The wheat develops at succeeding later dates from Mexico, north into Canada, and the rust follows this development with the prevailing winds. The first infection of rust within a given area is called the primary infection, and after the primary infection secondary and tertiary cycles may occur in ten to twelve days intervals, depending upon the environment, thus increasing the number of asexual spores manyfold. The number of asexual cycles depends upon the environment and this determines the severity of the disease.

The teliospores develop as the grain matures in the same pustule that previously held the urediospores. Transition stages may be observed when both kinds of spores occupy the same pustule. The production of teliospores is not serious because they must produce basidiospores, the spores which infect Thalictrum; and Thalictrum is resistant in this country. The production of urediospores is serious however, and the only means of stopping this never ending migration of spores is to produce and grow resistant

varieties of wheat.

Microscopically, leaf rust differs from stem rust in that the urediospores are spherical and small instead of oblong and large. The urediospores of stem rust have four conspicuous equatorial germ pores while in leaf rust urediospores there are four to six scattered germ pores that are not easily seen. The teliospores of leaf rust are more compact and not as linear as those of stem rust.

Mains (1927) described the losses caused by leaf rust as being due directly to a reduction in tillering if attacked in the seedling stage, and a failure of the florets to mature grain, if attacked in the mature stage. This loss is caused by the parasite using essential plant food elements, increased transpiration rate of the plant, reduced photosynthetic activity, and an increase in susceptibility of the wheat plant to winter injury. Leaf rust causes a more consistent loss yearly than stem rust, but is not as spectacular in damaging wheat as is stem rust. This consistency is due in part to its regularity of occurrence and in part to its ability to overwinter in the uredial stage farther north and in more diversified climates than stem rust.

Peturson et al. (1948) gave added information concerning the effect of leaf rust on yield, grade, and quality of wheat. The effects of leaf rust on kernel weight, bushel weight, and yield were more pronounced than those on quality and grade. Leaf rust apparently has a marked effect on the cartinoid content of the grain. The rust did, however, favorably modify protein quality.

Moderately light infections (22 percent) caused appreciable reductions in yield.

Some of the control methods for leaf rust are: control by competition with other fungi, by Darlica filum, by hyperparasitic fungi, by predatory insects, snails and slugs, planting date, planting rate, planting depth, eradication of wild hosts, fungicides, (sulfur being the most widely used), and by growing rust resistant varieties of wheat. The latter is the only means of control that will prove practical or permanent (Chester, 1946). The resistance accrued in this way can be expressed in several ways by different varieties: evasion, pseudoresistance, tolerance, and resistance.

Physiologic Races

Breeding for leaf rust resistance is complicated by the fact that new physiologic races of rust are constantly and consistently appearing.

Mains and Jackson (1920) were the first to record any physiological difference in "two cultures" of rust by their ability or inability to infect selections of Malakof and Turkey x Bearded Minnesota hybrids.

Three years later the same authors stated that two hundred varieties of wheat inoculated with cultures of leaf rust from various parts of the United States, showed that leaf rust was not uniform but consisted of at least twelve strains differentiated by their action on several differential varieties of wheat, Malakof,

Mediterranean, Democrat, and four unnamed spring wheats.

Mains and Jackson (1926) stated that twelve forms, called physiologic forms, of leaf rust could be distinguished by their manner of infection on eleven differential strains of wheat. They added that twenty-five strains of wheat were found to be more or less resistant to one or more of these forms. They distinguished the different physiologic forms of rust by the reaction shown by these twenty-five varieties when infected with leaf rust. No form had been found at that time to which all of these varieties were susceptible. On the other hand, other than the variety Vernal emmer, S. D. 293, no variety had been found which, in the seedling stage in the greenhouse, had proved highly resistant to all twelve of these forms.

Johnston and Mains (1928) mentioned that Scheibe described three new forms from collections made in Central Europe and designated them as forms 13, 14, and 15.

Wellensick (1930) accounted for physiologic forms 11, 14, and 15 as being present in Holland. He stated that form 11 was widespread in America and Europe, and wheat varieties in Holland were all found to be moderately to highly susceptible to all three forms found in Holland. He advocated breeding for rust resistance by crossing foreign (American) wheat varieties with Dutch ones.

By May of 1930, Johnston and Mains (1930) accounted for and reported twenty-three physiologic forms of leaf rust.

The origin of new physiologic forms was a matter of much speculation for many years. Newton and Johnson (1927) recorded the occurrence of color mutations in Puccinia graminis Pers.,

which gave rise to the theory of new physiologic forms resulting from mutations. Johnston (1930) implied that the aberrant type (culture 199) of leaf rust may have arisen from a mutation. It differed from all other forms of leaf rust in length of incubation period, color of spores, size of uredinia, and spore dimensions. He had at the time only meagre evidence in favor of the mutation theory.

By 1935, Fisher (1935) accounted for fifty-three physiologic forms of leaf rust by their reaction to a differential set of agronomic varieties of wheat. Thirty-nine of these occurred in North America and were described by Johnston and Mains (1932). In the same report the authors claimed that the distribution and prevalence of physiologic forms in the United States are, as far as is known, independent of the occurrence of species of Thalictrum. Physiologic form 9 was the most prevalent at this time.

Physiologic races of leaf rust were continually being discovered and described. Johnston (1948) summarized the data compiled from 1926 until 1946. During this period a total of 61 physiologic races of leaf rust has been isolated from collections made in the Western half of the United States. Only six or eight races proved abundant during any one year. The author reported seven prevalent races during the year 1946: 5, 9, 15, 37, 44, 126, 128.

In recent years there has been a steady increase in the prevalence of physiologic races which heavily attack such varieties as Kawvale, Comanche, Pawnee, and winter wheat hybrids with Hope in their parentage. Johnston reports that races 44 and 126 are

the most important in this regard, and adds that there is good evidence that the important changes in the prevalence of physiological races have been associated with the distribution and rapid increase of new wheat varieties, such as Austin, in Texas, and Kawvale and Pawnee in Kansas, Nebraska, and Oklahoma. Table 1, from Johnston (1948), shows the percent of important physiologic races of leaf rust of wheat in western United States during the years 1927 through 1946.

Table 1. Percent of total isolates represented by important physiologic races of leaf rust of wheat in western United States.

Race no.	Percent of total isolates			
	1927-1931	1932-1936	1937-1941	1942-1946
5	2.4	3.6	5.4	6.5
9	44.5	46.8	25.5	20.7
11	1.1	.8	2.7	2.2
13	7.2	1.9	3.5	1.8
15	7.3	11.9	10.7	8.0
19	6.2	6.1	7.3	6.8
31	2.1	6.6	3.5	2.0
37	3.4	1.1	2.6	2.8
44	.3	1.9	5.3	9.0
58	---	.3	1.1	2.3
105	---	---	3.8	3.1
126	---	---	4.5	18.2
128	---	---	---	4.0

The third revision of the international register of physiologic races of leaf rust of wheat, Johnston et al. (1942) listed and described one hundred twenty-nine physiologic races of leaf rust. New races will no doubt continue to appear; on this continent by mutation, and in Europe and other places by both mutation and hybridization.

Nature of Leaf Rust Resistance

The several forms of resistance, mentioned earlier, must be taken into account when breeding for disease resistance. Chester (1946) points out that the use of "rust escaping" varieties has been known to be effective in reducing the loss caused by leaf rust; the early maturing varieties have less rust infection than the late maturing varieties. This type of resistance may be classified as one type of klendusity, or rust-escaping resistance. Resistance may also be based upon different properties of the plant, morphological, chemical, and physiological. Chester makes it clear that the nature of leaf rust resistance is of value. For example, a few plants of a highly resistant variety growing in the midst of many susceptible plants may be materially injured by the many tiny necrotic lesions produced by the spores from neighboring plants; but if the resistant variety occupies many acres there is no local rust reproduction and the necrotic lesions are rare, hence the plants remain essentially free from rust damage.

Kargapolova (1937) states that rust resistance shows two tendencies; the first of them consists of the comparative study of the anatomic-morphological structure of resistance and susceptible forms from the point of view of their correlation with resistance. The second consists of the study of the physiological and chemical reaction of the inner cell structure. He states that the works of Henning, Errikson, Biffen, and Vavilov treating of the anatomic-morphological structures of wheat could establish no definite dependence of rust resistance on the anatomic-morphological

characters; and that the cytological investigations of Allen, Gibson, and Stakman have shown that rust enters the cells of resistant forms just the same as those of susceptible forms. However after some time the affected tissues die off and the parasite perishes. These investigations are very interesting, confirming that in its essence, plant immunity is based on specific inner reactions of the cell to the intrusion of the fungus hyphae.

Kargapolova's studies showed a positive correlation between the content of phenolic compounds of the acetic-ethyl fraction and the different resistance of the wheat varieties to leaf rust. The resistant species and varieties of wheat showed a high content of phenolic compounds (32 to 39), "the figures show the difference between the standard and the solution tested; and the measuring was made by means of a Dubosque colorimeter," while in susceptible varieties it ranged from 0 to 10. He concludes that his results justified considering this group of phenolic compounds of the acetic-ethyl fraction as one of the fundamental factors of the wheat resistance to leaf rust.

Chester (1946) summarized the importance of mechanical resistance spoken of above by stating that it undoubtedly played some role in determining the resistance of wheat varieties to leaf rust, but that it was a minor role, and that we must seek the principal answers to the complex display of resistance phenomena in the chemistry and physiology of the host plant.

Chester further adds that the physiological-chemical factors of leaf rust resistance have been studied as a result of the inability to explain resistance in a morphological basis. Such

properties as pH of cells, osmotic value, carbohydrates, aromatic organic compounds, and enzymes have failed to shed light on the problem. Chester further states that we are still far from having this explanation, but with the evolution of Gassner's hypothesis of the dependence of rust resistance on specific proteins, and the relation of this to antibody reactions in the rust relationship, "we appear to be making some progress toward an understanding of this basic riddle of parasitism."

Inheritance of Leaf Rust Resistance

Resistance, in general, is inherited in a Mendelian manner; one of the more recent verifications of this is described by Adams (1939). Breeding for resistance, therefore, follows a similar pattern to that of breeding for agronomic characters such as stiffness of straw, yield, quality, etc. Farrer, in Australia, may be called the father of modern breeding for disease resistance; he and his associates bred "rust proof" wheats before the turn of the century. Most of the breeding work, however, has been done since 1926.

Leighty (1926) summarized the facts known about leaf rust inheritance at that time in the 1926 Yearbook of Agriculture. At that time all of the important varieties of wheat grown in the United States were susceptible to one or more forms of leaf rust. Hard Red Winter Wheats, when grown in humid sections were more or less resistant to leaf rust, but they lacked adaptation to humid climates and did not yield as well as the soft wheats which were better adapted to these conditions. The soft wheats were

susceptible to leaf rust, so it was proposed to combine, by crossing, the resistance of one with the adaptability of the other. Experiments were begun in 1920 using several strains of Kanred as the resistant parent, later Malakof and other Hard Red Winter Wheats were used.

Probably the most significant conclusions drawn from this early work was the fact that resistance is definitely inherited; where the Hard Red Winter Malakof was used as the resistant parent about three resistant to one susceptible segregates appeared in F_2 , and when one parent is resistant to one physiologic race of leaf rust and susceptible to another and the other parent exhibits the reverse reaction, the resistance to the two physiologic races are independently inherited.

Mains, Leighty, and Johnston (1926) made many crosses using Malakof and Kanred as the resistant parents; they confirmed the above statements and added that resistant to the various physiologic races of leaf rust is due to different factors, or groups of factors inherited as a unit, all being inherited independently. They recognized that these factors or groups of factors could be brought together by crossing.

Mains (1926) stated that there were ninety-six strains out of 2,515 studied that showed resistance to leaf rust.

The sources of resistance are reviewed very well by Chester (1946). Most of the resistance we have today can be traced back to the fourteen chromosome wheats. Hope, a cross between Triticum dicoccum and Marquis, a spring wheat, made by McFadden in 1915, has been of great importance in recent breeding programs. H44, its

sister selection, is of equal importance; both of these varieties have been crossed with rust susceptible but otherwise desirable wheats to give many commercially desirable varieties. Also species of Aegilops, T. timopheevi, T. timococcum, and several other more primitive types have been utilized as a source of resistance.

McFadden (1949) reported an experiment involving a test of 1,639 varieties and strains of foreign wheats under field conditions to stem and leaf rust. Of these, 43 common wheats gave resistant reactions to stem rust and 13 of the 43 were highly resistant to leaf rust. Hope was among those varieties showing high resistance; some of the varieties have never been used for breeding; but the author indicates there is an abundance of resistant germ plasm for future work.

McFadden (1930) claims that he was able to transfer many desirable characters of Yaroslav emmer to Triticum vulgare, such as stem rust resistance, high resistance to leaf rust and to loose smut, and tough flexible straw. Emmer and Durum wheats have provided present day breeders with an abundance of disease resistant germ plasm.

Other good sources of resistance are the differential wheat varieties used in wheat leaf rust identification; Mediterranean and Malakof are used most in this regard in the United States.

In studies made by Johnston (1929) it was found that 28 out of 200 varieties tested were found to contain resistant strains to physiologic race 9 of leaf rust. He stated that, with but few exceptions, the resistant strains resembled the varieties from which they came morphologically. Most of the varieties in which

resistant strains were found were Soft Red Winter Wheats. His studies have shown that selections within varieties of wheat is a useful method of quickly securing strains which are resistant to a single physiologic race of leaf rust.

In a study of the correlated inheritance of resistance to eight races of wheat leaf rust, powdery mildew, Erysiphe graminis tritici, and glume color, Caldwell and Compton (1947) found that the segregation indicated a monogenic inheritance of resistance to leaf rust. Susceptibility was dominant, and each progeny reacted uniformly to the group of eight races indicating that for all eight races the same gene controlled either the resistant or "X" reaction; also, leaf rust and mildew resistance and chaff color were independently inherited, the deviation from a phenotypic ratio for three factors being insignificant.

Swenson et al. (1947) made a cross between two susceptible varieties of wheat, Thatcher and Triunfo, and obtained lines which were highly resistant to leaf rust. The segregations obtained in F_2 and F_3 were satisfactorily explained by postulating two complementary dominant genes, one from each parent. The authors add that because there was some indication that one or more modifying genes might be present, an alternative hypothesis involving three gene pairs was also suggested. Under this hypothesis, two genes, non-complementary to each other, are contributed by one parent, and these two genes are complementary, either singly or in combination, with one gene contributed by the other parent. Greenhouse studies of seedling reactions revealed that the resistance observed in the field is a mature plant reaction. Seedlings from resistant,

segregating, and susceptible lines all proved to be completely susceptible.

It is evident that more work regarding the inheritance of leaf rust resistance is necessary. The study in the past has been partially neglected, but at the present time, at the Kansas Station, genetic studies of leaf rust resistance are organized and offer promise of adding much to aid the plant breeder in his conquest of this disease.

Breeding for Leaf Rust Resistance

By 1940 the basic methods of breeding for leaf rust resistance were well established. Hayes and Immer (1942) reviewed these methods, and with the exception of a few slight alterations, the methods are used as described by present day breeders. In brief, the methods fall under four headings, 1- the search for resistant materials, 2- the plan of breeding, 3- the artificial production of epiphytotics, and 4- a study of fundamental problems that aid in a logical attack on the breeding problem. The search for resistant material is the logical first step because one cannot breed for resistance without a source of resistance. It is important to learn as much as possible regarding the genetic factors responsible for resistance.

The second step, the artificial production of epiphytotics, is carried on in the following manner with leaf rust of wheat.

1. Increase rust of the races to be used on seedlings in the greenhouse.

2. Plant susceptible varieties as border rows around and

through the fieldrust nursery.

3. Spray the plots with an aqueous suspension of all races usually present in the locality. The plants should be inoculated on a still night when the humidity is high. Seedlings may be inoculated in the field when about eight inches high.

This method is altered by many workers; the spores may be mixed with talc and dusted on the wheat plants, or injected as a spore suspension hypodermically into the whorl of seedling plants.

4. Irrigate, if necessary, to attain proper environmental conditions for the development of rust over a period of time, and to insure two or three cycles of rust.

5. Tag resistant plants, if the lines are segregating. Final selections are made at harvest time from these resistant plants.

The third step, the plan or method of breeding, can be carried on most advantageously by carrying on the studies of disease reaction as a part of the main breeding project, selecting for disease reaction, for quality, and for agronomic characters at the same time, although in some cases in special nurseries. In this way, if selection must be made for several characters, progenies that excel in all these characters may be used as a basis of selection.

The last step, the study of fundamental problems, includes a knowledge of the pathogen, which has been discussed, and the environmental conditions favorable for the development of the disease.

Since 1930, most leaf rust breeding programs have been carried

out in the manner just described, but there have been some modifications and variations in technique. Most of the variations have been along the line of classification of resistance and susceptibility, however. Classification based upon reaction "type" is more likely to give reliable results than percentage readings. Reaction type is dependent upon the host-parasite relationship and is more independent of external environment than rust intensity (Chester, 1946). The reaction "type" is explained in detail under the heading "Material and Methods."

Because of systematization and of cooperation there has been rapid advancement made since 1930. Waterhouse (1930) reviewed the Australian rust studies which were very similar to those being practiced in this country. He made wheat x barley, wheat x rye, and interspecific wheat crosses to try to incorporate disease resistance into an agronomically useful wheat, but without success. They studied vulgare and durum crosses and found a single factor involved in the inheritance of resistance in the crosses: Federation x Arnautka durum, Federation x Mindum durum, Federation x Spelmar durum, and Marquis x Mindum.

The Kansas Station (1930) reported many new rust resistant hybrids, but at the time the hybrids were not tested for agronomic characters. Johnston, who is still working along these lines, made most of the early progress in producing rust resistant wheats at this station. In 1932, he reported several hybrids that were resistant to some of the races of leaf rust. The best of these were F_3 and F_4 progeny from the cross (Kanred x Fulcaster) x Tenmarq. Also crosses of Kanred x Kawvale, Kanred x Fulcaster,

Mediterranean x Webster, and Fulcaster x Marquis showed promise. Johnston (1934) used the variety Kawvale, released by the Kansas Station in 1932, in several crosses, and obtained resistant and agronomically desirable strains. The following crosses proved most promising: Kanred x Kawvale, Kawvale x Blackhull, Kawvale x Tenmarq, and Hard Federation x Kawvale. The author also states that compound crosses such as (Kanred x Fulcaster) x (Kanred x Hard Federation), (Kanred x Fulcaster) x Tenmarq, and (Kanred x Fulcaster) x Iobred continue to exhibit greater resistance than most of the simple crosses. He adds that among the varieties of winter wheat, the highest field resistance continues to be found in the soft wheats. Kawvale, Fultz selections, Mediterranean selections, and Fulcaster selections have continued to show high field susceptibility to leaf rust.

Roussakoff (1937) stated that certain American (Kansas) wheat hybrids, such as Fullhard, and the Kanred x Fulcaster Nos. 266324, 266319, 266313, and more especially 266287, were outstanding in their resistance to brown rust, except in 1931, when one or more hitherto unknown physiological races of the rust made their appearance in the Kuban area, but disappeared later; the hybrids were reported also, to have given high yields.

Vavilov (1937) said that the greatest promise of adaptibility to Russian conditions is apparently offered among the spring wheats by Thatcher, a Minnesota cross between the Kanred x Marquis and Marquis x Iumillo hybrids; by the Canadian varieties Apex and Renown, and the relatively older Canadian Kitchenes, Marquis, and Garnet wheats; among the winter forms the most promising results

have so far been obtained with the Kansas wheats Illini Chief, Fullhard, and the Kanred x Marquis 214211 hybrid.

In Kansas, Johnston (1938) reported that none of the commercial varieties of true hard red winter wheat exhibited strong resistance to leaf rust in the rust nursery. Kawvale, a semi-hard variety, continued to exhibit marked resistance, however. He found strong resistance in certain soft red winter varieties, and also selections from soft red winter hybrids. Mediterranean was among the varieties studied and some selections from it were highly resistant to certain races. The spring wheats were used to incorporate rust resistance into the winter wheats because the latter usually lack strong resistance; selections from the Mediterranean x Hope cross were crossed with promising winter wheat hybrid selections resulting in compound hybrid lines showing marked resistance.

Kostov (1938) considers Triticum timococcum highly resistant to almost all fungous diseases that attack wheat. Kostov, reporting on Vavilov's work, described the origin of T. timopheevi (N = 14) as being highly resistant to almost all fungous diseases that attack wheat plants. Most of the varieties of T. monococcum (N = 7) were also highly resistant to rust; but the best varieties of the cultivated wheats, T. vulgare, (N = 21) are susceptible to a series of fungous diseases. Crosses between common wheat varieties and T. timopheevi and (or) T. monococcum are difficult to make, and the hybrids obtained usually are self sterile, therefore the transfer of resistance of the latter two species on the background of T. vulgare is a difficult task. The most promising

resistant segregates obtained were derived from the composite crosses: T. dicoecum x T. monococcum and T. compactum x T. timopheevi x T. vulgare. Vavilov produced the amphidiploid of T. timopheevi x T. monococcum which gave a wheat with 21 pairs of chromosomes, the same as T. vulgare. It was called T. timococcum. This amphidiploid wheat combines the resistance of T. timopheevi and T. monococcum into one plant.

In a cytological study of resistance to leaf rust in interspecific and intergeneric hybrids of wheat, Guard (1938) found that in twenty-four lines from crosses between Chinese wheat and Vernal emmer, seven lines had a haploid chromosome number of 14, while in seventeen lines the haploid number was 21. All lines with the lower chromosome number were resistant to leaf rust, physiologic race 65, in the seedling stage. Six of the lines with twenty-one chromosomes were susceptible and eleven were resistant. The wheat-rye hybrid studied, an amphidiploid, was very resistant to physiologic race 65. Fifteen F_1 hybrids between Chinese wheat and Secale montanum were very resistant to the same race of leaf rust.

Sharids (1941) reported the successful transfer of Triticum timopheevi resistance, which includes resistance to many fungus diseases, to common winter wheat.

In Australia, Waterhouse (1930, 1938) used the differential variety Webster, in a cross with Federation to produce a variety, Fedweb, resistant to all known races of leaf rust in that country.

The tendency in modern plant breeding is to select strains of

wheat for resistance to the definite races of the rust or rusts occurring in a given country (Kale, 1938, 1939). This fact is very important because, as Kale states, it has brought about a close cooperation between the plant pathologist, the geneticist, and the plant breeder. Though the total number of biological races discovered is fairly large, the number of races which really dominant in a given locality or country may be manageably small.

This recent trend of breeding may be further complicated by the fact that wheat varieties susceptible to leaf rust in the seedling stage may develop resistance in later growth stages to the same races of rust, Newton and Johnson (1943). As early as 1929 Johnston and Melchers showed that a number of varieties of wheat susceptible in the seedling stage to physiologic race 9 were highly resistant at heading to that same race. Newton and Johnson (1943) concluded from their experiments that seedling reactions are by no means reliable indices to the leaf rust reactions of the adult plants, at least when the seedling reaction is of a susceptible type. On the other hand, they indicated that when the seedling reaction is of a resistant type, it is a satisfactory guide to the reaction of the adult plant. It is evident that many wheat varieties that are susceptible in the seedling stage become progressively less susceptible as they mature.

Watson and Baker (1943) reported that resistance to race 1 of Erysiphe graminis tritici and to race 95 of Puccinia triticina is controlled by either closely linked genes or pleiotropic genes in the varieties Thew and Kenya 744. The gene in Kenya 744 is allelic to the gene in Thew.

Chester (1947) states that Pawnee wheat (C.I. 11669), released in 1943 and described as having moderate leaf rust resistance, has declined in leaf rust resistance due to a shift in the race populations of the rust from a predominance of race group 9, to which Pawnee is resistant, to other races to which Pawnee is susceptible.

MATERIALS AND METHODS

The manner of inheritance of seedling resistance to three physiologic races of leaf rust was studied in two simple wheat crosses. The parents used in the two crosses, Malakof, Democrat, and Mediterranean, comprise three of the eight differential varieties used to test race reaction in leaf rust. The original crosses, made at Manhattan, Kansas, were Malakof x Democrat and Democrat x Mediterranean. F_3 seed, harvested from individual F_2 plants, was used in the leaf rust inheritance studies.

The seed from each individual F_2 plant was divided into three groups of twenty-five seeds each. Each hybrid plant progeny was then tested to three different physiologic races of leaf rust. The reaction of the parents to the physiologic races studied are shown below (C. O. Johnston, 1946).

	<u>pr. 9</u>	<u>pr. 15</u>	<u>pr. 58</u>
Malakof	4	0	0
Democrat	0	4	4
Mediterranean	0	4	4

The figures used to designate the "type reaction" indicate relative degrees of resistance and (or) susceptibility. The "0" reaction type indicates high resistance, it is recognized either

by chlorotic flecks (0;) or by no visual signs of the pathogen on the seedling leaves. A "1" reaction type indicates resistance and is perceived by tiny pustules surrounded by a chlorotic area, sometimes called a halo. The "2" reaction type is similar to the "1" type and can be differentiated only by the increased size of the pustule; also it indicates less resistance than the "1" type. In addition to the above named types, another type is included in the resistant category, the "X", or more specifically, the mesothetic type. It cannot be placed into any of the above types, but it is a definite reading of resistance that has been observed on many hybrids. It is not universally accepted as a finite type, but it has been used in this study and until more satisfactory evidence is found refuting its use, many researchers will, no doubt, continue to use it. It is recognized by a definite blending of many types of pustules, having "4" types interspersed with "0" fleck chlorosis and others. The "3" reaction type indicates susceptibility and is discerned by small pustules appearing on the leaves with no chlorosis, or halo, around them. The same relationship that holds for the "1" and "2" type differentiation also holds true for the "3" and "4" type differences, i.e. the size of the pustule is the only distinguishing feature, "4" type having the larger pustule (Chester, 1946).

The physiologic races of leaf rust used in this study were 9, 15, and 58. All three races are important in Kansas and surrounding wheat growing areas; however race 9, as shown in Table 1, is the most prevalent, but is decreasing in importance in Kansas while others are becoming more threatening. Race 15

has been quite stable in occurrence since 1927, while race 58 has gradually become more prominent since its discovery in the early 1930's.

Caution was exercised to prevent race mixture in the leaf rust studies by working with one race at a time. All the seedlings to be inoculated with race 9 were inoculated in an isolated section of the greenhouse before another race was introduced. After each race study was completed the greenhouse was thoroughly cleansed.

Pure cultures of each physiologic race of leaf rust were obtained from Mr. C. O. Johnston, Pathologist, United States Department of Agriculture, stationed at Manhattan, Kansas. The infested plants, received from Mr. Johnston, provided a source of inoculum which was further increased on larger pots of Cheyenne wheat. Starting at the time the pure culture inoculations were made and each succeeding day thereafter, six 4 inch pots of Cheyenne wheat were planted. Ten days later the rust pustules, uredia, were developed on the inoculated wheat, and the newly planted seedlings were at the proper stage for inoculation.

To inoculate for increase, the six pots of seedling Cheyenne were placed in a cylindrical, galvanized container about 15 inches in diameter and 12 inches high. Sand was placed in the bottom of the cylinder at a depth of two or three inches; this practice furthered moisture retention. The plants were then exposed to a fine mist of water, applied by a hand atomizer until the droplets began to coalesce, at which time the spores from the infested plants were dusted on the moist leaf surface. A glass cover was placed on the chamber and the plants were allowed to remain in the

moist chamber for twenty-four hours.

The following day one-hundred pots from the first group of the F_3 population were planted in 3 inch pots. After ten days the seedlings had long primary leaves and the secondary leaves were beginning to grow; this was the desirable stage for inoculation; also the rust on the Cheyenne wheat had reached the sporulating stage during the ten day period. A cloth moisture tent was placed over the one-hundred pots of seedling hybrids and the wheat leaves were exposed to a fine mist of water with a special nozzle. When the droplets began to coalesce the spores from the Cheyenne wheat were dusted on; usually twelve pots were used to dust one-hundred pots of seedlings. A cloth cover was placed over the "tent" and it was then moistened sufficiently to remain damp until the following day. Inoculations made in the evening provide a continued cool and humid environment; evaporation is thus reduced to a minimum, a condition favorable for infection.

The following morning the "tent" was again moistened; by this time most of the spores had germinated and entered the stomata (Chester, 1946), but to avoid any chance of non-infection the chamber was again moistened and left undisturbed until evening.

Two days later the same procedure followed with another one-hundred pots of hybrid plants, and this continued until all the hybrids had been tested to all three physiologic races of leaf rust.

After being inoculated the hybrid plants were left alone, except for daily watering, for ten days or so. The time of development of uredia varies with environmental conditions, but usually

in ten days the pustules developed sufficiently well to be classified as to reaction type. As was stated earlier, the reaction type is more accurate than the former percentage method. Some pots, representing an F_2 plant, were homozygous and some were segregating; if the pot of seedlings showed segregation the plants were pulled and classified individually as to their reaction type, if they were homozygous one reading was made for the whole pot of plants. However, in the analysis the segregating plants were counted as one, the same as the homozygous plants, this was done in the determination of the number of factors governing resistance to the physiologic race involved.

With each group of one-hundred pots at least four of the differential varieties were grown to aid in classifying race mixture. All eight differential varieties were grown with at least one group, to further check on the purity of the inoculum being used.

RESULTS

Inheritance Studies in F_3 Progeny of Malakof x Democrat

Seed Color. Democrat is a white seeded wheat variety, Malakof is a red seeded variety. Color of seed produced on F_2 plants segregated in the ratio of 9 white to 175 red. The logical hypothesis to explain this dihybrid segregation, is that two duplicate factors are responsible for kernel color. The above ratio supports the duplicate factor hypothesis that segregation occurs in a 15:1 ratio, having a chi-square of .6 and a P. value

of .4 to .5. Of the nine possible genotypes, only the homozygous recessive one is white. If either or both of the dominant factors from Malakof are present in the heterozygous or homozygous condition, the kernels are red. Therefore, it is concluded that Malakof carries two of the three known dominant genes for kernel color.

Reaction to Physiologic Race 9. Democrat is resistant to physiologic race 9, and Malakof is susceptible. There apparently are two major factors governing leaf rust reaction; i.e. to physiologic race 9, in this cross. The results obtained are as follows:

<u>F₂ progeny observed*</u>	<u>Expected</u>	<u>Dihybrid Ratio</u>	<u>X²</u>	<u>D.F.</u>	<u>P.</u>
Seg. 103	92.0	8	4.3	2	.12-.13
Sus. 75	80.5	7			
Res. 6	11.5	1			

* Seg. = segregating, Sus. = susceptible, Res. = resistant

The hypothesis that the progeny exhibit an 8:7:1 ratio is supported by the above data. Democrat, therefore, is homozygous recessive for leaf rust resistance and the susceptibility carried by Malakof is dominant. The genotypes involved and the reaction type each represents when applying the 8:7:1 hypothesis is shown below.

<u>F₂ Genotype</u>	<u>F₂ Reaction*</u>	<u>F₃ Behavior</u>
1 - AABB	4	Breed true
2 - AABb	4	Breed true
1 - AAbb	4	Breed true
2 - AaBB	4	Breed true
4 - AaBb	x	Seg. O; , x, 4
2 - Aabb	x	Seg. O; , 4
1 - aaBB	4	Breed true
2 - aaBb	x	Seg. O; , 4
1 - aabb	O;	Breed true

* 4 = susceptible, x = intermediate, O; = resistant

The 8:7:1 ratio is a modified complementary gene action ratio. Instead of the homozygous recessive individuals being phenotypically like the other eight genotypes, making a 9:7 ratio, it is phenotypically distinct.

The data regarding the progeny of F_2 plants that segregated could not be adequately classified. Therefore no conclusions were made concerning the genotypes of segregating plants, as no F_4 data were obtained.

Reaction to Physiologic Race 15. Resistance to physiologic race 15 of leaf rust came from the Malakof parent. The progeny all showed clear cut reaction types; i.e. they were either completely susceptible or highly resistant. The possibility of misplacing reaction types was nil, however, seed mixtures could have been made while preparing the seed or at the time of threshing. In presenting the analysis this was taken into account, and for each presentation two corrections are shown. If a segregating plant had many resistant plants and only one susceptible plant, the group was classified as homozygous resistant in the first correction. If two susceptible plants were found in a group containing many resistant plants, the F_2 plant was classified as homozygous resistant in the second correction. The same procedure was followed in analyzing the Malakof-Democrat F_3 progeny reactions to physiologic race 58. In both cases the first analysis shows the data as it was recorded.

One factor appears to be responsible for leaf rust resistance to physiologic race 15 in this cross; the resistance carried by Malakof to race 15 is dominant to the susceptibility carried by

Democrat.

The observed data and the corrections made are shown below.

Original data -	Obs.*	Exp.	Ratio	χ^2	D.F.	P.
Sus.	42	42.5	1	9.8	2	less than .01
Seg.	102	85.0	2			
Res.	26	42.5	1			

First correction -						
Sus.	42	42.5	1	4.8	2	.10
Seg.	97	85.0	2			
Res.	31	42.5	1			

Second correction -						
Sus.	42	42.5	1	2.06	2	.38
Seg.	93	85.0	2			
Res.	35	42.5	1			

*Obs. = observed, Exp. = expected.

The heterozygous F_2 plants were analyzed under the three headings above. The original data are shown below.

Original data -	Obs.	Exp.	Ratio	χ^2	D.F.	P.
Res.	1809	1687.5	3	14.6	1	less than .01
Sus.	641	562.5	1			

The value of P. decreases progressively as the two corrections are made. If pots 26 and 45, which read 2 = 0; 20 = 4, and 4 = 0; 16 = 4, respectively, are altered to read homozygous susceptible the results are as follows:

	Obs.	Exp.	Ratio	χ^2	D.F.	P.
Res.	1803	1656	3	6.0	1	greater than .01
Sus.	605	552	1			

The evidence supporting the hypothesis proposed is not conclusive, but no other hypothesis tested will explain the results. To add to the possibility of error, temperature and humidity fluctuations may alter the appearance of the uredia on the seedling wheat plants. Also, if the person making the readings tends to be critical in making classifications, many altered reaction types could have been placed in the wrong reaction group. It is there-

fore believed that these possibilities of error have played a role in making the evidence appear inconclusive.

Reaction to Physiologic Race 58. The evidence that resistance to race 58 is due to one factor hypothesis is apparently the only justifiable one for this data. The inconsistency is apparently due to the same causative factors as for the reaction to physiologic race 15, as can be seen by the following data.

Original data -	Obs.	Exp.	Ratio	χ^2	D.F.	P.
Sus.	37	37	1	9.12	2	.01
Seg.	89	74	2			
Res.	22	37	1			
First correction +						
Sus.	37	37	1	8.8	2	.02-.01
Seg.	88	74	2			
Res.	23	37	1			
Second correction -						
Sus.	37	37	1	1.64	2	.5
Seg.	80	74	2			
Res.	31	37	1			

The progeny of heterozygous F_2 plants give the following results when applying the original data.

	Obs.	Exp.	Ratio	χ^2	D.F.	P.
Res.	1437	1480.5	3	5.112	1	greater than
Sus.	537	493.5	1			.02

When the segregating individuals are tested for the 3:1 hypothesis, using the data of the first and second corrections, the probability values decrease progressively.

Association of Factors. The factors governing leaf rust resistance to physiologic race 9, and those responsible for kernel color are independent in their inheritance. This is shown in Table 2.

Table 2. Test for independence of the inheritance of reaction to physiologic race 9 and seed color.

		Physiologic race 9 reaction			
Seed color		: resistant	: segregating	: susceptible	: no. of individuals
Red Seed	Obs.	5.00	97.00	74.00	176
	Exp.	5.74	98.52	71.74	
White Seed	Obs.	1.00	6.00	1.00	8
	Exp.	0.26	4.47	3.26	
No. of individuals		6	103	75	184
Chi-square = 4.38		D.F. = 2		P = .10	

The factors responsible for kernel color show no association with the factors governing leaf rust resistance to physiologic race 15. The data shown in Table 3 support this statement.

Table 3. Test for independence of the inheritance of reaction to physiologic race 15 and seed color.

		Physiologic race 15 reaction			
Seed color		: resistant	: segregating	: susceptible	: no. of individuals
White Seed	Obs.	3.00	2.00	2.00	7
	Exp.	1.44	3.83	1.73	
Red Seed	Obs.	32.00	91.00	40.00	163
	Exp.	33.55	89.17	40.27	
No. of individuals		35	93	42	170
Chi-square = 2.658		D.F. = 2		P = .50	

The factors governing resistance to race 15 are not associated with the factors governing resistance to race 9. The hypothesis that they are independently inherited is supported by the following test for independence given in Table 4.

Table 4. Test for independence of the inheritance of reaction to physiologic race 15 and physiologic race 9.

Physiologic race : 9 reaction	physiologic race 15 reaction			no. of individuals
	: resistant	: segregating	: susceptible	
Resistant	Obs. 3.00 Exp. 1.18	2.00 3.32	1.00 1.50	6
Segregating	Obs. 18.00 Exp. 18.47	50.00 52.04	26.00 23.50	94
Susceptible	Obs. 12.00 Exp. 13.36	41.00 37.64	15.00 17.00	68
No. of individuals	33	93	42	168
Chi-square = 4.54	D.F. = 4		P. = .30	

Factors governing resistance to physiologic race 58 and the factors governing kernel color are independently inherited. This is indicated by data shown in Table 5.

Table 5. Test for independence of the inheritance of reaction to physiologic race 58 and seed color.

Seed color	Physiologic race of 58 reaction			no. of individuals
	: resistant	: segregating	: susceptible	
White Seed	Obs. 2.00 Exp. 1.25	2.00 3.24	2.00 1.50	6
Red Seed	Obs. 29.00 Exp. 29.74	78.00 76.76	35.00 35.50	142
No. of individuals	31	80	37	148
Chi-square = 1.15	D.F. = 2		P. = .9 - .95	

The chi-square test for independence indicates that factors for resistance to race 58 are inherited independently of factors for resistance to race 9 as summarized in Table 6.

Table 6. Test for independence of inheritance of reaction to physiologic race 58 and physiologic race 9.

Physiologic race : 9 reaction		physiologic race 58 reaction			no. of individuals
		: resistant:	: segregating:	: susceptible:	
Resistant	Obs.	3.00	2.00	1.00	6
	Exp.	1.25	3.24	1.50	
Segregating	Obs.	19.00	43.00	22.00	84
	Exp.	17.60	45.40	21.00	
Susceptible	Obs.	9.00	35.00	14.00	58
	Exp.	12.15	31.08	14.50	
No. of individuals		31	80	37	148
Chi-square = 5.154		D.F. = 4		P = .25 - .30	

The factors for resistance to physiologic race 58 and the factors for resistance to race 15 are not independently inherited, but according to the test for independence, they are definitely associated. The probable explanation is that resistance to both races of rust is due to one gene, carried by the parent, Malakof. The test for independence is shown in Table 7.

Table 7. Test for independence of inheritance of reaction to physiologic race 58 and physiologic race 15.

Physiologic race : 15 reaction		physiologic race 58 reaction			no. of individuals
		: resistant:	: segregating:	: susceptible:	
Resistant	Obs.	22.00	6.00	0.00	28
	Exp.	5.64	14.98	7.19	
Segregating	Obs.	7.00	71.00	2.00	80
	Exp.	16.18	42.78	20.56	
Susceptible	Obs.	0.00	0.00	35.00	35
	Exp.	7.05	18.72	8.99	
No. of individuals		29	77	37	144
Chi-square = 170.52		D.F. = .4		P = less than .001	

Inheritance Studies in F_3 Progeny of Democrat x Mediterranean

Seed Color. The inheritance of kernel color in this cross is best explained by the hypothesis that the variety Mediterranean carries two of the known three dominant factors for red seed. The ratio expected would be 15:1; the data are shown below.

	<u>Obs.</u>	<u>Exp.</u>	<u>χ^2</u>	<u>D.F.</u>	<u>P.</u>
Red	145	143.40	.27	1	.5 - .7
White	8	9.56			

Democrat possesses three homozygous recessive factors for white seed color that was described in the Malakof-Democrat inheritance studies.

Rust Studies. The parents, Democrat and Mediterranean, show identical reactions to the races of leaf rust used in this study. Both are resistant to physiologic race 9, and both are susceptible to races 15 and 58. The progeny all showed the same reactions to

the different races of rust as did the parent varieties. For this reason the F_3 progeny reactions to race 9, 15, and 58 are all discussed under one heading.

The progeny were resistant to race 9 and susceptible to race 15 and 58. There is no indication, from this test as to the number of factors involved in leaf rust resistance to race 9, but from the test of the Malakof-Democrat progeny, it was shown that Democrat carried two recessive factors for resistance to race 9. Mediterranean apparently carries similar factors for resistance to race 9. It is known that the two varieties carry similar reaction types to nearly all of the known races of leaf rust (Johnston, et al., 1942).

SUMMARY

The inheritance of reaction to physiologic races 9, 15, and 58 was studied in two simple wheat crosses, Malakof x Democrat and Democrat x Mediterranean. The parents comprise three of the eight differential wheat varieties used to test reaction type of the 129 different physiologic races of leaf rust.

There are three known factors for kernel color in wheat. Malakof and Mediterranean possess two factors each such that in the two crosses, Malakof x Democrat and Democrat x Mediterranean, the ratio of red seeded progeny to white seeded progeny was 15:1. Democrat is a white seeded variety; it, according to the above observations, therefore, has three homozygous recessive factors for white seed.

Two recessive factors carried by Democrat apparently govern resistance to physiologic race 9 of leaf rust. The F_2 progeny segregated into susceptible, intermediate, and resistant, in the ratio 8:7:1, which is a modified complementary gene action ratio.

Malakof carried one factor for resistance to race 15 and one factor for resistance to race 58. Chi-square tests for independence indicated that resistance of Malakof to race 15 and to race 58 was due to the same factor. Both races are inherited independently of race 9, and of kernel color.

Democrat and Mediterranean carry similar factors for their reaction to the three races of leaf rust. Both parents exhibit identical reactions to the three races, being resistant to race 9, and susceptible to races 15 and 58. All the progeny exhibited reactions identical to that shown by the parents, indicating that the factors for resistance or susceptibility carried by the two parents are the same. The only indication as to the number of factors involved in these inheritance tests, is that Democrat has two recessive factors for resistance to race 9, and this was indicated by testing the Malakof-Democrat progeny.

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