REPORT

of

COMMITTEE ON EXAMINATION

This is to certify that we the undersigned, as a Committee of the Graduate School, have given Olaf Sverrer Aamodt final oral examination for the degree of Master of Science. We recommend that the degree of Master of Science be conferred upon the candidate.

Minneapolis, Minnesota

March 23rd 1922

H. K. Hayes
Chairman

E. C. Stakman

Henry F. Nachtrieb

THE UNIVERSITY OF MINNESOTA

GRADUATE SCHOOL

Report

of

Committee on Thesis

The undersigned, acting as a Committee of the Graduate School, have read the accompanying thesis submitted by Olaf Sverrer Aamodt for the degree of Master of Science They approve it as a thesis meeting the requirements of the Graduate School of the University of Minnesota, and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science.

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March 23rd 19~~18~~ 22

THE INHERITANCE OF GROWTH HABIT AND RESISTANCE TO STEM RUST IN A CROSS BETWEEN TWO VARIETIES OF COMMON WHEAT

A thesis presented to the Faculty of the
Graduate School of the University of
Minnesota in partial fulfillment
of the requirements for the
Degree of Master of
Science

By

Olaf S. Aamodt

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INTRODUCTION

The black stem rust, Puccinia graminis tritici, (Eriks. & Henn.), is one of the most important factors in lowering the yield of wheat. It has caused enormous losses, especially in the hard red spring wheat area, in the past five years. The eradication of the common barberry, now progressing over a wide area, undoubtedly will reduce losses caused by stem rust. But it is probable that rust will not be eliminated entirely by this means, and the development of resistant varieties with high milling ability and other necessary agronomic characters, therefore, is very desirable.

The purpose of this paper is to present facts regarding the mode of inheritance of rust resistance in relation to the inheritance of (winter versus spring) growth habit in a cross between Kanred and Marquis wheats. The results were obtained in the course of cooperative investigations between the Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture, and the Department of Agriculture, of the University of Minnesota.

Review of Literature.

Biffin (1) and Nilsson-Ehle (10) have shown that it is possible by hybridization to develop varieties of wheat resistant to Puccinia glumarum (Eriks. & Henn.). Resistance and susceptibility were found by Biffin to segregate in a simple Mendelian ratio, with susceptibility dominant; while Nilsson-Ehle obtained definite proof of the inheritance of rust resistance but found that the results could be explained only by assuming that several factors were present.

The production of varieties of wheat resistant to stem rust, however, is a complex problem. It was generally supposed that only one form of stem rust caused the epidemics on wheat although some of the early workers believed the parasitic capabilities of the rust to be modified easily (2). Stakman and Piemeisel (15) followed by others (9) (8) (13), have proved the existence of many biologic forms of stem rust.

This discovery explained why the same variety of wheat may be resistant when grown in one locality and susceptible when grown in another, or why a wheat variety may be resistant in the same locality one year and susceptible the next year. It is then very evident that if a wheat is to be resistant in the field it must be resistant to all of the biologic forms present in the locality in which it is to be grown.

Recently Hayes, Parker and Kurtzweil (7) studied resistance and susceptibility to a single biologic form in crosses between common and durum wheats and common and emmer wheats. It was shown that the inheritance of resistance and susceptibility to this form of rust was not the same in different crosses. In the durum common cross susceptibility appeared to be dominant to resistance. In the emmer common cross the F_1 was resistant, but not as resistant as the emmer parent. There was some linkage in transmission between the emmer and durum types and resistance to stem rust. Resistant emmer and durum types were very common while it was quite difficult to obtain resistant common wheat.

During the past year Puttick (11) has reported the results of a study on the reaction of the F_2 plants of a cross between two varieties of wheat which react reciprocally to two biologic forms of stem rust. Many gradations in reaction appeared, varying from complete susceptibility and immunity to both forms of rust.

Extensive rust surveys have been made during the last few years. The prevalence, distribution and virulence of the various biologic forms of Puccinia graminis tritici are now being ascertained and the parasitic effect on the hosts seems to be constant (14) for all practical purposes. The breeder now has a definite basic foundation for the development of varieties resistant to attacks of stem rust.

Twenty-one biologic *forms of rust have been found in the upper half of the Mississippi Valley. The winter wheat, Kanred, is resistant to two of these forms and is immune to eleven of them. The value of this variety in breeding a rust resistant spring wheat is apparent. If a spring wheat could be isolated from the progeny of a Kanred x Marquis cross, which would be resistant to some or all of the forms to which the winter parent is resistant, then at least one step would be added to the many which will be needed to produce a generally resistant variety.

Growth habit, as used in this paper, is meant to indicate that general difference which exists between true spring and winter varieties in their ability to produce heads normally when planted in the spring of the year. (See Plate 1.) Kanred is a true winter wheat which, when planted in the spring, at University Farm, St. Paul, Minnesota, produces only an occasional head late in the season and does not set seed. Marquis is a true spring wheat which, when planted in the

*Unpublished data by E. C. Stakman, and M. N. Levine.

fall, seldom, if ever, lives through the winter.

Apparently few investigations have been made on the inheritance of growth habit. Innumerable observations have been reported in literature on the differences in heading period and maturity between varieties in both spring and winter grains. These differences, while they may be of the same general nature as winter habit, are comparatively very minute. These differences in growth habit are constant as was shown by Fruwirth (4) in 1918. A single head of wheat was selected and divided into two parts. One half of this seed was constantly sown in the fall and the other half in the spring. This process was continued for eight years. The two lots of seed were then planted together in both the fall and spring and the growth habits compared. The period of blossoming and ripening was the same for all plots; showing that selection within a pure line was of no value.

The nature of the processes involved in bringing about the heading period has been a matter of speculation for some time. The climatic units which control these processes and permit winter grains to produce seed are finely interwoven. Although temperature and moisture are very important factors in the growth and maturing of plants it is quite evident from the plant life about us that the time of flowering and fruiting of most plants is definitely connected in some way with the advance of the season. Garner and Allard (6) have clearly demonstrated this third factor to be the change in length of day and night. They found that certain plants which ordinarily required a short day for flowering and fruiting could be induced to flower and fruit in the middle of the summer by shortening the length of day to that which was normal for the regular flowering season. This was done by placing the plants in a dark-house for a certain number of hours each day.

In contrast to this group of plants which required a short day for flowering and fruiting is that group of plants which require a long day of light. These plants flower regularly in the late spring or early summer. Garner and Allard place our small grains in this group.

As regards the inheritance of the growth habit character, the results reported by previous workers do not at first appear to be in full agreement. Spillman (12) in 1909 reports that the winter character was dominant over the spring character in a cross between a common winter wheat and a club spring wheat.

Fruwirth (3), in 1910, cites Tschermak as having reported that the winter type was dominant over the spring type. The first generation of hybrids, when sown in the fall, wintered over somewhat better than the true winter forms; but when sown in the spring, they remained dormant nearly throughout the whole summer. Single shoots appeared and began to blossom but produced no seed.

Gaines (5), in 1917, reports a cross between two spring varieties of barley, Rice and Beardless, from which he obtained a segregation of spring and winter types. The F1 when planted in the spring headed normally. In the F_2 there was a ratio of three winter plants to thirteen spring plants. The plants in the third generation bred fairly close to expected retios. He found that seasonal variations influenced the heading periods and consequently the ratios. The segregation in the F_2, however, indicates a dominance of the spring type over the winter type.

A detailed and complete study on the genetic nature of growth habit in wheat varieties has recently been presented by Vavilov and Kouznetzova (16). They crossed a common winter wheat with a spring club wheat and found a clear dominance of the spring character over the winter character. There was a complicated segregation in the F_2 and some of the segregates, including many intermediates, were homozygous in the F_3. Of the 552 F_2 plants 500 were early or late spring plants and 52 were typical winter plants. The results obtained by the writer on the inheritance of spring and winter habit are quite in accord with those of Vavilov and Kouznetzova.

Materials and Experimental Methods.

In the summer of 1918, Marquis, a high quality hard common spring wheat, was crossed with Kanred, a high quality hard red selection from Crimean winter wheat. The latter is immune to several different biologic forms of stem rust.

The seed was planted in the fall of the same year. There were eighty plants, two of which were winter-killed and five of which were not crosses. The remainder of the plants were harvested individually and planted in the spring of 1920.

In the second generation a population of approximately 5,000 plants was grown. In order to facilitate the study of the individual plants, the seed, when planted, was spaced to three inches in the row and the rows placed one foot apart. The date of emergence of the first head on each plant was noted. There was a continuous series for date of head emergance in the hybrids, varying all the way from those which did not emerge at all, and thus resembled the winter parent. (See plate 2.) The time of heading was divided into weekly periods. One week from the day that the first plant headed, tags were placed on plants on which one or more heads had emerged. These comprised the first class. All of the Marquis check plants headed during the same period as did those plants included in the first class. One week later tags were attached to all plants which had headed since those of class I. These constitute the second class. String tags of a different color or size were used for each period. This process was continued for eight weeks, after which period no more plants headed. The plants which did not head were classed as true winter types. The winter parent checks did not head, and fell into the same class as the winter hybrids.

Sixty-five families from the first seven classes in the F_2 were grown in the F_3. The plants from the seventh class produced only a few seeds while those of the eighth class headed so late that no seed was produced at all. The seed, when planted, was again spaced as in the second generation so that a study could be made of the individual plants.

A number of the families were uniform for heading period in the F_3. In those cases the entire plot was simply given a general heading data as in a variety test. A number of the families were heterozygous for date of head emergence. In those plots a final count was made at harvest time of the number of plants which failed to head and the number which produced heads.

The rust studies were made by two general methods. The first consisted of growing the plants in the field under an artificial epidemic produced with several different biologic forms of stem rust. The second consisted of inoculating the plants in the seedling stage under control conditions in the greenhouse with cultures of the various biologic forms.

In the second generation all the plants were grown in the field under an artificial stem rust epidemic, produced by spraying the plants with a suspension of urediniospores of several different biologic forms. Both parents were susceptible to some of the rust forms which were used. All of the hybrid material was as susceptible as either parent under this artificial epidemic and a detailed genetic study of the inheritance of rust resistance under field conditions, therefore, could not be made. Such results would have only a general indicative value.

The genetic studies on the inheritance of resistance and susceptibility to these various biologic forms of rust were made in the greenhouse under controlled conditions. This was done by inoculating the F_3 seedlings with cultures of urediniospores of known biologic forms.

In the greenhouse the seedlings were grown in four-inch pots and when they were one and one-half to two inches in height, they were inoculated with the urediniospores. After inoculation they were placed in a glass-topped chamber and incubated for forty-eight hours. The notes on infection were taken twelve to fourteen days after the date of inoculation. Some of the plants were completely susceptible and the others were immune; there were no intermediate types of infection. The uredinia were large, coalescing and normal in every respect on both the Marquis seedlings and on susceptible hybrid seedlings. The seedlings of Kanred and the resistant hybrids were immune. There were no intermediate types of infection. This fact simplified the problem of recording the rust reaction of the large number of plants tested by necessitating the use of only two classes, immune and susceptible.

An intensive study was made by testing a large number of F_3 plants with a single known biologic form to which one parent (Marquis) is susceptible and the other parent (Kanred) is resistant. The question which then naturally arises is, how is the reaction of the host to all of these biologic forms inherited? Are they all inherited as a single genetic factor, or is each one carried as a single genetic factor? An attempt was made to solve this question by inoculating various F_3 selections which were homozygous in their reaction to the first form studied with twelve other biologic forms of stem rust.

Experimental Results.

The Mode of Inheritance of Growth Habit.

The first generation material was planted in the fall. By the high percentage of spring survival the F_1 plants showed to some extent the influence of the winter parent. Only two plants out of seventy-five were killed during the winter. However, the winter was quite mild, as winter wheat in general was injured but little. Had the winter been severe, it is possible that a large percentage of the first generation plants would have been killed. No F_1 plants were grown from spring sown seed.

All of the seed from the F_1 was sown in the spring of the following year. This gave an F_2 population of 5,250 plants. Of this number 4,308 plants produced heads during the summer, and 442 plants failed to produce heads. Of the former, 980 plants headed at the same time as the spring parent. In the second period 1502 plants headed, which is the greatest number to fall into any one heading period. From the second period on to the eighth period, there was a gradual decrease in the number of plants. In the eighth period there were only 19 plants. The total number of plants for each class is shown in the chart. (See Fig. 1.) From the chart it is very evident that the segregation of the plants for growth habit characters in the F_2 is of a complex nature. All of the plants in the first five classes grew to maturity and produced seed like any ordinary spring wheat variety. It would be quite fair, then, to assume that in general the plants in these first five classes could reasonably well represent the true spring type. If such were the case we would have a proportion of 4,350 plants of the spring type to 900 of the winter type, a ratio of approximately five spring to one winter. If it were assumed that all plants which headed during the summer were spring types we would have a ratio of approximately nine spring to one winter. In either case there is a partial dominance in the cross of the spring habit over the winter habit.

A study was made to ascertain whether there was any correlation between the inheritance of growth habit and awns. 392 plants were tabulated according to their growth habit in relation to the awned character. The awned character was recorded from the F_2 Individual plants and checked by the progeny performance in the F_3. (See Table I.)

Table I. The relation between awns and growth habit in F_2.

Kanred x Marquis Progeny.

Heading Period	No. of Plants With Awns.	No. of Plants With Intermediate Awns.	No. of Plants Awnless.
I	18	25	14
II	17	29	11
III	14	21	16
IV	21	21	24
V	23	26	16
VI	29	41	38
VII	6	9	11
VIII	1	-	1
TOTAL	129	172	131

The results presented in Table I show that there is a lack of correlation in the inheritance of awns and growth habit characters. While the numbers are not very great for each separate heading period, there is a total number for the first eight periods of 129 bearded plants to 131 beardless plants.

The segregation for growth habit in the F_3 families was in accord with the segregation obtained in the F_2. The breeding habit of the plants belonging to the various F_2 groups are shown in Table II.

Table II. The breeding habit in F_3 of plants belonging to separate F_2 heading groups.

Heading Period.	No. of Families Grown.	No. of Families Homozygous for Spring Habit	No. of Families Heterozygous for Growth Habit	No. of Families Homozygous for Winter Habit
I	10	10	0	0
II	10	6	4	0
III	10	7	3	0
IV	10	5	5	0
V	10	2	8	0
VI	9	0	9	0
VII	6	0	4	2

The plants selected from the first heading period in the second generation were homozygous for the spring habit of growth in the third generation. Beginning with the plants in the second heading period there was a gradual decrease in the number of families which were homozygous for the spring character and a corresponding increase in the number of families heterozygous for this character as one approached the seventh heading period. There was also a gradual change in the ratios of spring to winter types as one progressed from the first to the seventh heading period. In the seventh period there were two families homozygous for winter character. If the plants in the eighth class had produced seed in the second generation there undoubtedly would have been a still larger number of homozygous winter types in proportion to the number of spring types.

One can readily see from the data presented that there is a great difference in degree of heterozygosity of the plants in the various heading periods. In the first heading period all ten of the F_3 families are homozygous for spring type; in the second, six out of ten; in the third, seven out of ten; in the fourth, five out of ten; in the fifth, two out of ten; in the sixth, all nine of the families are heterozygous for growth habit, and in the seventh period four families are heterozygous for growth habit and two of them are homozygous for winter type. With the exception of the sixth heading period homozygous forms were obtained in all classes grown. A number of F_3 families were homozygous spring types which were comparable to our ordinary spring wheat varieties grown in the northwest. Besides these plants which had an early heading period a few families were obtained which were homozygous for a heading period much later than that of the Marquis parent.

From the following table it will be noticed that there is a correlation between the F_2 heading period and the percentage of spring types produced by the various F_3 families.

Table III. Showing the breeding habit of F_2 plants heterozygous for growth habit.

Heading Period.	Total No. of Spring Types.	Total No. of Winter Types.	Percentage Spring Types.
I	all	none	100
II	154	13	92.2
III	121	14	89.6
IV	158	39	81.2
V	236	46	83.7
VI	187	69	73.0
VII	12	6	66.7

With the exception of the very slight increase in the fifth heading period, there is a very regular decrease in the percentage of spring types to winter types as one proceeds from the first to the seventh heading period. Here also there undoubtedly would have been a more complete reversal of the ratios of spring types to winter types in the eighth and ninth periods, if it had been possible to grow these plants in the third generation.

The Mode of Inheritance of Rust Resistance.

The F_1 plants grown in the field during the summer of 1919 were not infected, as no rust developed in the field where they were grown. Consequently no determinations could be made of resistance or susceptibility under field conditions.

The F_2 plants were extremely susceptible when grown in the field under an epidemic produced artificially with several biologic forms.

The Marquis check plants which are completely susceptible to all of the forms used in producing the epidemic had an average rust infection of 87.7 per cent. The hybrids growing under the same conditions had an average rust infection of 80 per cent. This high degree of susceptibility of the hybrids growing in the field was to be expected because both the Marquis parent and the Kanred parent are susceptible to some of the forms used in bringing about this epidemic. These results very clearly demonstrate how a general field epidemic may fail to differentiate the segregation for resistance and susceptibility in the progeny from a given cross. The most accurate and reliable meth-od of determining the resistance and susceptibility of hybrid progeny at the present time to any given number of biologic forms is to grow the plants under controlled conditions and inoculate them with the various known biologic forms.

The plants of ten families from each of the first six classes and five families from the seventh class for growth habit (See Figure 1) were tested for their reaction to Biologic Form I. This form is one which has been carried in pure culture since 1916 and has remained constant in its reaction on various host plants throughout this period. Of the sixty-five families tested, twenty-three were pure for resistance to this form of rust, ten were susceptible and thirty-two were heterozygous. With such a small number of families the ratios are not very significant. There is a numerical ratio of 23 resistant families, 32 heterozygous, and 10 susceptible. The ratio of 33 homozygous families to 32 heterozygous is a very close approximation of the expected 1:1 ratio. The inoculation results are given in Table IV.

Table IV. The reaction of Marquis, Kanred and various families of the F_3 cross between Kanred and Marquis to Biologic Form I.

Class	No. Homozygous for Resistance		No. Heterozygous for Resistance.			No. Homozygous for Susceptibility.	
	No. Families	No. Ind.	No. Families	No. Ind. Res.	No. Ind. Sus.	No. Families	No. Ind.
I	3	102	4	96	26	3	82
II	3	75	7	184	54	0	0
III	3	108	4	102	35	3	88
IV	1	21	8	239	59	1	26
V	4	111	4	89	28	2	73
VI	6	140	3	65	18	1	24
VII	3	50	2	23	2	0	0
Total	23	607	32	798	222	10	293
Marquis	-	0	-	0	0	-	83
Kanred.	-	83	-	0	0	0	0

A total of 2,286 individual plants were inoculated. The resistant hybrid plants were just as free from infection lesions as the resistant Kanred parent. The susceptible hybrid plants were completely susceptible, producing large, vigorous, confluent uridinia. This type of infection was like that obtained on the Marquis parent. (See Plate 3.)

In the thirty-two families which were heterozygous in their reaction to Biologic Form I, there were 1,020 individuals. 798 of these plants were free from any apparent infection while 222 plants were clearly susceptible. This gives us an approximate ratio of three

three resistant plants to one susceptible. It is not an uncommon occurrence to find susceptible plants which have been carefully inoculated which fail to become infected. In some cases there were a few plants which failed to become infected in families which, judging from the majority of the plants inoculated, should have reacted as homozygous for susceptibility. Upon reinoculation it was found that the plants really were susceptible and had merely escaped infection. It is quite possible that this has also happened in the case of the heterozygous families and consequently it is not surprising that the number of resistant plants is a little larger than expected, where there apparently should have been a simple ratio of three resistant plants to one susceptible.

From the data just presented it is very evident that the segregation for resistance and susceptibility to this one biologic form of stem rust is of a very simple nature. Many desirable types were obtained in the F_3 which are homozygous for spring habit of growth and immune to Biologic Form I.

Several F_3 selections homozygous in their reaction to Form I were inoculated with twelve other biologic forms. The results obtained were very striking and consistent. (See Table V.)

Table V. The reaction of Marquis, Kanred and F_3 hybrid families of the cross between Kanred and Marquis to thirteen biologic forms of stem rust.

Biol. Form.	Marquis	Kanred	29	30	31	41	42	43	47	48	54	55	60	79	80	205	181
			Variety of Hybrid.														
I	S	I	-	-	I	I	-	-	-	I	I	I	I	I	I	I	S
III	S	S	-	-	-	S	S	S	S	S	-	-	S	S	S	S	S
IX	S	I	I	I	-	I	-	-	-	-	-	I	I	-	I	I	S
XIV	R	I	I	-	-	I	I	I	I	I	-	-	-	-	I	-	-
XVII	S	I	I		I	I		I					I			I	S
XVIII	S	S	S	-	S	S	-	-	-	S	-	-	S	S	S	S	S
XIX	R	I	-	-	I	I	-	-	-	I	-	-	I	I	I	I	-
XXI	S	I	-	-	I	I	I	-	I	I	-	-	I	I	I	I	S
XXIX	S	I	I	I	I	I	-	I	-	I	I	I	I	I	I	-	-
XXXII	S	S	-	-	-	S	-	-	S	S	S	S	S	-	-	-	-
XXXIV	S	S	-	S	-	S	-	-	S	-	S	S	S	S	S	-	-
XXXVI	S	S	-	S	S	S	S	-	S	-	-	-	-	-	-	-	-
XXXVII	S	I	I	-	I	I	-	-	I	I	I	I	I	-	I	-	-

S - Completely susceptible

I - Immune

R - Resistant or an intermediate type of infection between that of S and I

From the above table it will be noticed that as far as the reaction of the two parents is concerned the fifteen biologic forms of rust may be placed into two groups. The first group is typified by Form I, to which Marquis is susceptible and Kanred is immune. All of the hybrid families tested gave reactions which were identical with either the Marquis parent or with the Kanred parent. Family 41, for example, is identical in its rust reaction to that of Kanred with all of the forms used, and family 181 is identical in its rust reaction to that of Marquis.

The second group is represented by Form III to which both Marquis and Kanred are susceptible. Here it will be seen that all of the progeny are as susceptible as either parent and identical in their reaction in this respect.

These results demonstrate very definitely the fact that resistance and susceptibility to several biologic forms of stem rust may be carried either in a single genetic factor or, if in different factors, they are linked in the process of segregation.

With this fact established, it has been possible by inoculating the progeny from this cross with a single biologic form of rust to which the Kanred parent is immune, and by their reaction to this one form, to know that they will react similarly to the other biologic forms to which Kanred is immune. In this manner a large number of F_3 selections have been obtained which are pure spring types and are immune to all of the known biologic forms of stem rust to which the Kanred parent is immune.

Discussion of Results.

The results show very clearly the complicated nature of the genetic difference between a spring and winter variety of wheat. The results could not be explained very well on a simple mono- or di-Hybrid basis. The segregation indicates very minute differences for this character between the individual plants. While the time of heading was divided into weekly periods it was very evident when the work was being done that the differences between the individual plants could be determined to within a few days. For practical purposes and convenience in gathering the data, however, it was decided that heading periods of one week would be sufficient to indicate thoroughly the nature of the segregation for this character.

The results presented in Table IV show that there was no correlation between the growth habit character and reaction to rust. The same numeric relations exist between the susceptible and resistant plants regardless of the time of heading. This transfer of the rust resistance of the winter parent to the progeny having the growth habit character of the spring parent solved the initial objective of the experiment. Several thousand rust resistant families were obtained in the F_3 and F_4 which are being studied and tested for desirable agronomic characters in general.

These results are of particular interest not only in that they contribute to the solution of the general problem of breeding varieties of wheat resistant to rust but also from the biological viewpoint. It is an opinion commonly held that winter forms are more ancient or primitive than spring forms. Vavilov points out that this opinion is based on the fact that so called wild progenitors of our cereals are winter forms. Upon closer investigation of these wild species he discovered the existence of spring forms as well as winter forms among these wild plants. He states, (16) "As a matter of fact spring races in natural conditions have originated as a result of hybridization of different varieties of winter plants, and vice versa spring varieties could give origin to winter varieties. Both kind of plants can be obtained synthetically one from another."

The wide genetic variability which different varieties of wheat may have for growth habit explains why spring characters may be dominant over winter character and vice versa. The segregation which one would expect in a cross depends upon the factors present for the growth habit character in the parental material. One might cross two varieties of winter wheat which from all appearances seemed to be homozygous for winter habit and in the progeny obtain some plants with the spring habit of growth. It has been shown (16) that in the F_2 of such a cross spring types have appeared. Likewise two spring types may be crossed and some progeny obtained which are winter types. This has been shown (5) in the case of two varieties of spring barley, in the F_3 and F_4 of which appeared several winter forms.

In the light of the above facts and the data presented in this paper it is not at all surprising that various workers have drawn different conclusions regarding the dominance of spring and winter characters in wheat and other cereals. The large number of F_3 selections homozygous for heading period and varying all the way from the pure spring character to the pure winter character demonstrates how finely the differences for growth habit may be divided. Each F_3 family (or selection) with a different heading period is of a different genetic nature. And as soon as these types become fixed one ought to be able, by intercrossing the types, to produce varying degrees of dominance of spring and winter characters.

Probably one of the most important principles that this study has helped to mark as being of prime importance in any investigation on the genetics of rust resistance in wheat is that of using pure cultures of rust in the determination of the resistance or susceptibility of any given host. This principle was demonstrated by Hayes, Parker, and Kurtzweil (7) in 1920 and again by Puttick (11) in 1921. It has already been pointed out that previous to the discovery of the existence of biologic forms of stem rust of wheat the breeding of resistant varieties met with failure time and again. Just because a variety of wheat has shown itself to be resistant to the forms of rust in a given locality or for a period of years it is no criterion that it will always be resistant in that locality or any other locality in which it may be grown. And for the same reason one cannot expect to prove conclusively the resistance of any variety in the experimental plot unless all of the rust forms are present which exist in the area in which the variety is expected to be successfully grown later. One can readily see the difficulty of producing an artificial epidemic in the field and being at all certain that a number of forms are present in sufficient quantity to have equal opportunity to attack all plants. Even if this were practically possible it would bring about difficulties in the synthetic production of a resistant variety. This point was clearly demonstrated in the work carried on for the data presented in this paper.

The F_2 population was grown in the field under an artificial epidemic produced with several different biologic forms of rust. One of the parents and many of the hybrid plants were resistant to some of these biologic forms, as was proven when inoculated with the pure culture in the greenhouse. But, in the field all of the plants for all practical purposes were equally susceptible. There was no method by which one could differentiate the plants one from another under this general epidemic. If a genetic study was to be made of a given number of biologic forms in their reaction on certain host plants it is evident that the work must be carried on under controlled conditions.

After the susceptible individuals have been eliminated in this manner then the general selection for desirable agronomic characters can be carried on in the field. As soon as this desired agronomic type is obtained, it will be crossed again with other varieties or selections which have shown resistance to other biologic forms. Some of the progeny from this double cross might be expected to carry the resistance of both of the parents, etc., until a desirable agronomic type has been obtained which is resistant to all of the biologic forms of stem rust.

The fact that resistance and susceptibility of the host to several different forms of rust has shown itself to be inherited as a single genetic factor of great value in this cross. K anred is known to be immune to at least eleven different biologic forms of stem rust to date. As far as tested the immune progeny have all of the immunity to rust of the Kanred parent. This fact has further demonstrated that a variety of common wheat may be synthetically produced which is resistand to a large number of the biologic forms of stem rust.

Summary.

(1) The segregation for growth habit characters in the progeny of a cross between a winter and spring wheat is according to Mendelian laws. The results indicate the presence of multiple factors for this character.

(2) Homozygous types for both spring and winter characters were obtained in the F_3. In the F_2 some plants appeared which proved homozygous in F_3 for a heading period which was five weeks later than that of the Marquis parent.

(3) Kanred is an awned common winter wheat while Marquis is an awnless common spring wheat. There was no correlation in the progeny of this cross between awns and growth habit.

(4) The segregation for rust reaction to Biologic Form I in the progeny of a cross between Kanred and Marquis wheats shows a simple Mendelian ratio of approximately three immune plants to one susceptible plant. There is a clear dominance of immunity over susceptibility, there being no intermediate types of infection with this rust form.

(5) When the progeny of this cross were inoculated with several biologic forms of stem rust the results show that the reaction of the host to these several biologic forms is inherited as a single genetic factor.

(6) In the F_3 some of the hybrid families were homozygous for the spring habit of the Marquis parent and the rust resistance of the Kanred parent.

(7) There was no correlation between the inheritance of growth habit and the manner of reaction to stem rust.

(8) These facts further demonstrate that varieties of common wheat may be synthetically produced which are resistant to a large number of biologic forms of stem rust, *Puccinia graminis tritici*.

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Plate 1.
Showing the difference in growth habit when spring sown between Kanred winter wheat (left) and Marquis spring wheat (right) at harvest time.

Plate 2.
Showing the segregation for time of heading
in the Marquis x Kanred F_3 plants
representing F_2 Classes, spring sown.
Left - P 1068 (Kanred)
Center - F_3 Hybrids
Right - Marquis.

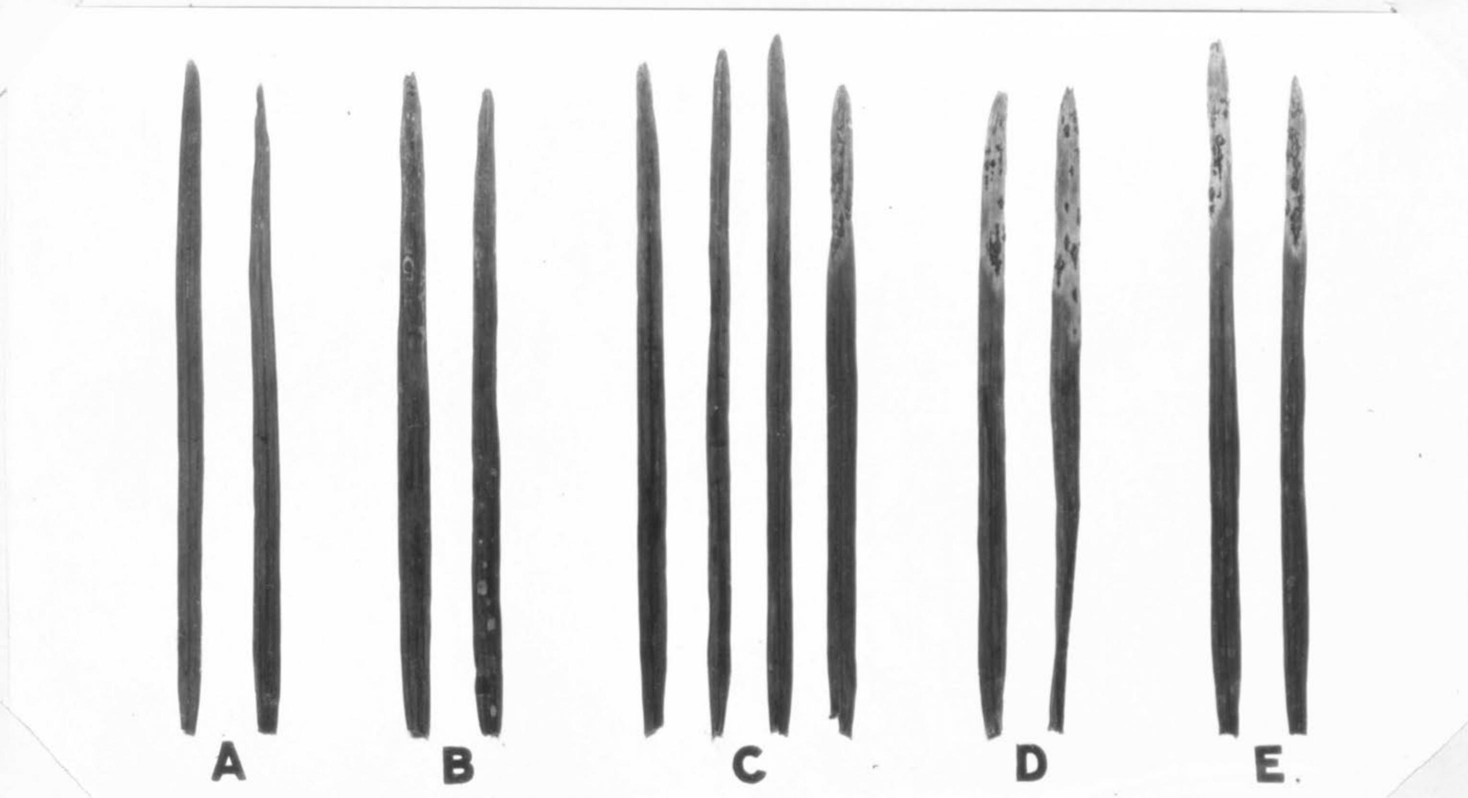

Plate 3. Seedlings of Kanred, Marquis and F_3 families of the cross between Kanred and Marquis inoculated with a rust form to which Kanred is Immune and Marquis is susceptible.

A, Kanred, immune. B, F_3 Kanred x Marquis, immune. C, F_3 Kanred x Marquis, segregating for susceptibility to rust. D, F_3 Kanred x Marquis susceptible. E, Marquis, susceptible.

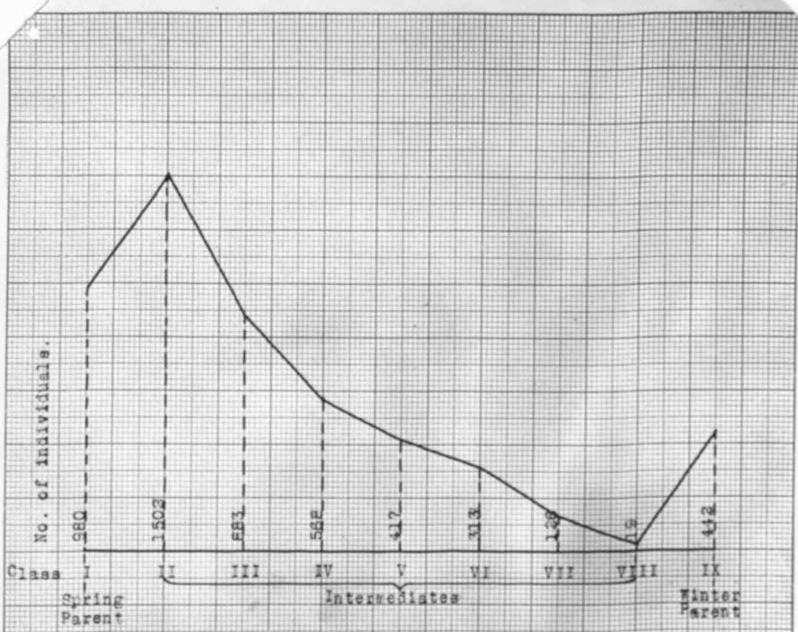

Fig. 1.- Graph showing the segregation for time of heading in the F_2 of Kanred X Marquis.

Figure 1.