INHERITANCE OF RESISTANCE TO BUNT AND OTHER CHARACTERS IN THE WHEAT CROSS, ORO X TENMARQ

by

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INTRODUCTION

Producing varieties of wheat resistant to bunt or stinking smut was one of the successes of William Farrer (1901), the well-known pioneer Australian plant breeder. In recent years a large number of crosses have been made in the United States and other countries in an attempt to secure a variety of wheat which is resistant to bunt, and which has the characters necessary to make it popular with both the farmer and the miller. Gaines and others in the Pacific Northwest have been very active in this work because of the serious losses produced by bunt and the failure of seed treatment to control the disease, due to soil infestation.

The cross Oro X Tenmarq was made by Dr. John H. Parker, of the Agronomy Department, Kansas State College. The purpose of this cross was to combine the desirable characters of Tenmarq; namely, excellent quality, high yield, and earliness, with the bunt resistance and winter hardiness of Oro. Both varieties have stiff straw.

The superior quality of Tenmarq wheat is displayed in loaf volume, texture, and color. Tests made by the Department of Milling Industry, Kansas State College, have shown that this variety produces a loaf of greater volume, which is lighter and more desirable than bread produced by the hard red winter wheats commonly grown in Kansas such as Blackhull, Turkey, and Kanred. Yield tests during an eleven-year period show that Tenmarq is distinctly higher yielding than these varieties.

Tenmarq is several days earlier than Oro. Pearson (1927), using the varieties Blackhull, Superhard, Kanred, and Tenmarq, secured data which suggested that ordinarily the variety which heads and ripens first will produce more bushels per acre than a variety which ripens a few days later.

Bunt infection of wheat is of considerable economic importance in Kansas. Melchers (1926) estimated that in 1926 bunt caused a loss of about 15 million dollars in Kansas. Since it is difficult to impress the wheat grower with the importance of seed treatment as a method of controlling this disease, the most satisfactory solution of this problem would be to use a resistant variety.

The ultimate object of this investigation is to produce a variety of wheat with a combination of the desirable characteristics listed above, which will be adapted to Kansas conditions. The present objective is to study the mode of inheritance of resistance to bunt.

Since selection for the more desirable agronomic characters has been practiced in the choice of preceding generations of the cross, Oro X Tenmarq, it is impossible to determine any Mendelian ratios or to present a specific factorial hypothesis. Results are presented which show that resistance to bunt is not inherited in a simple Mendelian manner, but rather that reaction to bunt is probably a "size" or quantitative character, governed by several factors.

Data are also presented which show the lack of correlation or association among any of the agronomic and pathologic characters studied.

REVIEW OF LITERATURE

General and Miscellaneous

No attempt has been made to review all of the literature pertaining to bunt in this paper, as Woolman and Humphrey (1924a) have summarized very well the work in this field previous to this time and have listed 404 references.

Bunt Species. Two species of bunt or stinking smut of wheat are known to attack wheat in the United States. These are *Tilletia tritici* (Bjerk.) Wint. and *Tilletia levis* Kühn.

Mitra (1931) in India found a species of bunt which seemed to differ from *T. tritici* and *T. levis* and has proposed *T. indica* n. sp. as a name for this new smut.

Distribution of Bunt Species. Potter and Coons (1918) report that *T. tritici* is rarely found in the Upper Mississippi Valley and

Great Plains states and most of the eastern states, although it is widely distributed.

Stephens and Woolman (1922) were of the opinion that _T. levis_ was the predominant species east of the Rocky Mountains and that _T. tritici_ was by far the most prevalent west of this range. They observed that both species occurred in western Washington and in Michigan, but at this time _T. levis_ had not been found in eastern Oregon, Washington, and in northern Idaho.

Heald and Gaines (1930) found as the result of an investigation that _T. tritici_ remains as the dominant species of bunt in eastern Washington. They observed, however, that _T. levis_ is now present in all the principal wheat growing sections of this area, and that this species is often the only one to be found in fields of Turkey, Albit, and Ridit wheat.

Bressman (1931) obtained 94 collections of the _Tilletia_ spp. representing nearly all sections of the United States. These indicated that _T. levis_ is the predominant species east of the Rocky Mountains and _T. tritici_ the predominant species west of this area. However, collections of both species were secured from coast to coast.

Hanna and Popp (1930) reported that _T. tritici_ and _T. levis_ were both widely distributed in western Canada.

<u>Seriousness of Bunt.</u> Heald and Woolman (1915), Heald (1918), Hungerford (1922) and Kienholz and Heald (1930) state that in the Pacific Northwest bunt is without doubt the most important disease of wheat.

Stephens and Woolman (1922) state that bunt or stinking smut of wheat has undoubtedly been the cause of a greater aggregate loss to the world than any other crop pest. In addition to the direct loss in yield, there are the indirect losses due to the befouling of the threshed grain, the expense of treating the seed, and the actual loss of seed due to the effect of the fungicide on the viability of the seed.

Reed (1924) reported that the bunt disease is found world-wide with the cultivation of wheat and is acknowledged as being one of the most serious diseases of this crop in all the principal wheat-growing areas.

The effects of varying percentages of smutted heads in the crop on the yield of several varieties were compared by Flor, Gaines, and Smith (1932) in tests conducted at Pullman, Washington, in 1929 and 1930. They observed that the effect of the percentage of bunt on yield varied for different varieties. They found in the case of Hybrid 128 that an average of 16.2 per cent of bunt resulted in a reduction of 20.5 per cent in yield. Bunt infection of 30.3 per cent in Turkey wheat caused a loss of 23.1 per cent in yield, while the yield of Ridit with only 1.13 per cent of bunted heads was reduced 11.3 per cent.

Factors Affecting Bunt Infection

Gaines (1918a) cited three factors which operate in determining the amount of bunt infection that may occur in any given field:

1. Number of viable smut spores in the immediate vicinity of the seed when planted.

2. Date of seeding.

3. Resistance of the wheat plant itself to the smut fungus.

Spore Load. Heald (1921) and Heald and Boyle (1923) state that a gradual reduction in the per cent of bunt infected plants occurs with a reduced spore load, with the exception of certain fluctuations which might be expected. Heald interprets the relation of the spore load to the per cent of bunt infection in a crop as implying either that multiple infection occurs or that there is a chemical mass effect due to numbers of spores.

Temperature. Hungerford (1922) in some greenhouse experiments found that temperatures ranging from 9° to 12° C. (48 to 54° F.), and a 22 per cent soil moisture content and a moisture equivalent of 20.7 were optimal for high bunt infection.

Faris (1924a) in a series of experiments observed that *T. levis* caused maximal losses in Dawson and Red Fife wheat when the soil temperature was 5° C. In Marquis wheat, for both *T. tritici* and *T. levis*, the more favorable temperature for the development of the bunt organisms was 10° C. He states that it is quite significant to find that the relative susceptibility of two wheat varieties to bunt may be quite different when each is exposed at different temperatures to the same combination of other environmental influences.

Woolman and Humphrey (1924b) state that the optimum temperature for bunt infection, according to their results, was 18° to 20° C.

Johnston (1924) reports that bunt infections occur at a soil temperature of 40° F. and that the percentage of infection increases with a decrease in temperature to approximately 27° F. He states that soil moisture content is also responsible for variations in bunt infection, a moist soil favoring infection.

Tisdale et al. (1927) report that plentiful infection may be obtained with either species of bunt when the temperature range is between 5° and 15° C.

Bonne (1931) of Germany states that soil temperatures prevailing during the germination of the wheat are responsible for varying percentages of infection for different dates of planting. He observed that the optimum temperatures for the germination of _T. caries_ is 15° to 20° C.

Varietal Resistance. As early as 1901, Farrer (1901, 1904) of Australia obtained results which suggested that in many instances, plants of a cross which was segregating, differed widely in their susceptibility to bunt. He also noticed that when such a segregating generation was allowed to become infected with smut a much higher average of bunt-resistance could be secured in succeeding generations. In 1904 he wrote of crossing varieties to produce wheats resistant to _T. foetens_.

Sutton (1908) reports Florence and Genoa as the successful products of the efforts made by Farrer in 1901 to secure varieties so resistant to bunt that seed treatment would be unnecessary. These varieties originated from the same crosses; White Naples, Improved Fife, Hornblende, and an Indian wheat were used in their production.

Pye (1909) of Australia found Florence and Genoa highly resistant to but not immune from bunt infection. Medeah, a durum wheat, was the only commonly grown wheat which his tests showed to be entirely free from the disease. He tested several crosses but none were obtained which remained free from infection over a period of several years.

Darnell-Smith (1910) of Australia after numerous experiments concluded that immunity from bunt was correlated with certain kernel characteristics. He mentions Cedar, Florence, and Medeah as being resistant and states that kernels of these varieties have little brush and a horny endosperm.

McAlpine (1910) of Australia reported the variety, Ohio, highly resistant and Genoa immune to bunt infection. He, however, reported that Medeah, which was bunt free at Dookie in 1908, showed 46.6 per cent bunt in 1909.

Gaines (1918a, 1918b) found that Turkey was the only highly resistant wheat of commercial importance in the State of Washington. Alaska, a variety of _Triticum turgidum_, was also distinctly resistant. Later (1923) he reported Florence as being highly resistant.

Gaines and Smith (1929) made a study of the resistance of a large number of varieties and strains of wheat to a form of _T. levis_ collected in eastern Washington. More than a hundred winter wheats proved susceptible to this form, although they had previously been selected for immunity from another form. Ridit, Hohenheimer, Turkey selections, and four hybrids containing Ridit "blood" were smut-free. Marquis was the only resistant spring wheat of commercial value.

Donkins (1921) of South Africa conducted experiments to determine the relative bunt resistance of 20 varieties of wheat. He included in his experiments, 3 varieties of durum wheat, 3 of polish, 2 of poulard, 1 of club, and 11 of common wheat. The common wheats were the only varieties which showed susceptibility to bunt. Of the latter, the variety Rieti produced an average of 3 per cent bunt as compared with 14-36 per cent for the other common wheat varieties.

Stephens and Woolman (1922) found as a result of inoculating 800 varieties and strains of wheat with bunt that the following were very resistant or completely immune: Turkey C.I. 3055, Crimean C.I. 4430, Turkey C.I. 1571C, White Odessa C.I. 4655, Martin Amber C.I. 4463, Red Hussar C.I. 4843, and Turkey X Florence, a selection of the same cross from which Ridit was derived.

Coons (1924) from a test of 40 varieties of wheat, found that with the exception of Fultz, those varieties which showed the most resistance to both _T. levis_ and _T. tritici_ are Turkey wheats or selections from crosses with this type.

Stakman, Lambert, and Flor (1924) from a test of about 870 spring wheat varieties and selections grown for a period of two years found that in general the vulgare group seemed to be susceptible while the dicoccum and monococcum groups seemed to be resistant to _T. levis._

Tisdale et al. (1925) classified the four commercial classes of common wheat in regard to resistance and susceptibility to bunt. They found the hard red winter wheats the most resistant, while the white wheats are usually the most susceptible, although Florence and four selections of this class were immune or highly resistant. Hussar, Sherman, and Ridit of the hard red winter class were found to be resistant as were also the following selections from Turkey: C.I. Nos. 1558-A, 7367, 7363, 7366, 2576-A, and 2903-5. They classed the hard red spring and the soft red winter classes as being somewhat intermediate in susceptibility. Of the soft red winter group, Banner Berkeley was found to be highly resistant. The hard red spring and durum classes were not found to contain any outstanding resistant varieties.

Of the remaining classes they state that the club wheats as a group are the most susceptible to bunt. The durum, polish, and poulard wheats as well as emmer and spelt in general are somewhat more resistant than the common wheats, except hard red winter which is more resistant than durum and poulard.

Bayles (1927) reported Turkey X Bearded Minn. #48, Minturki X (Beloglina X Buffum) C.I. 8033 (recently named Yogo), Ridit, and Oro were the most resistant of 40 winter wheat varieties and hybrids tested in Montana.

Sampson (1927) observed that Martin and Hussar were immune, and White Odessa, Ridit and Turkey were highly resistant to bunt in Wales. Heils Dickkopf, a resistant variety from Germany, was also found to be relatively resistant.

Tingey (1927) reported that of 260 strains of wheat grown in Utah the varieties Hussar, Martin, Ridit, White Odessa, and Hybrid 128 X White Odessa proved to be highly resistant.

Brentzel and Smith (1929) concluded that durums as a class were more resistant to _T. levis_ and more susceptible to _T. tritici_ than the hard red spring wheats. The reverse was true of hard red spring wheat.

Hanna and Popp (1930) observed that while the hard red spring wheats may become infected by both species, the durums were almost entirely infected with _T. tritici._

Melchers (1930) found from a study of 16 wheat varieties that Minturki, Minturki X (Beloglina X Buffum) C.I. 8033 (recently named Yogo), and Oro were the most resistant. Collections of bunt from Kansas, Nebraska, South Dakota, Minnesota, Colorado, and Montana were used in this experiment.

Heald and Gaines (1930) cited Marquis as being the most resistant of the commonly grown spring wheats. Lutescens, a variety from Russia, was also found to be resistant. Spring wheats which they found to be resistant were Hope and Spring Alaska. However, these varieties were low in yield.

The best white wheat in relation to both resistance and yield was from the cross, Martin X Marquis.

Aamodt (1931) classifies such spring wheat varieties as Marquis, Renfrew, Reliance, Huron, and Kitchener as intermediate in susceptibility, while Garnet and Ruby were fairly resistant.

Bosley (1931) reported Oro, Turkey X Bearded Minnesota #48, and Minturki X (Beloglina X Buffum) C.I. 8033 (recently named Yogo), resistant to all collections of Kansas bunt. Martin, Ridit, Hussar, White Odessa, Banner Berkeley, Regal, and Cooperatorka showed resistance to most forms of bunt.

Nieves (1931) of Argentine obtained very susceptible to highly resistant strains in a local variety, Kansas, which he thought to be the same as Crimean C.I. 1435, of the U. S. D. A. He found certain strains of Hungarian winter wheats highly resistant to bunt.

Smith, W. (1932a) found Hope spring wheat resistant to bunt when planted in the spring but moderately susceptible when planted in the fall. He carried on tests in which Hope and Jenkin were compared as to their relative reaction to bunt for different temperatures at different stages of growth. He observed that plants of Hope were resistant if grown at relatively low temperatures until they emerged from the soil and were then subjected to a higher temperature, although continued cool temperature caused the plants to be susceptible. Jenkin was always susceptible when grown under similar conditions.

Bressman (1931) states that Turkey X Bearded Minn. No. 48 is the only variety, so far tested, that is highly resistant to all forms of bunt used. Varieties such as Martin, White Odessa, Albit, Regal, Hussar, Banner Berkeley, and Ridit that have commonly been called resistant or immune are found to be quite susceptible to one or more forms.

Dillon-Weston (1929) by inoculating Sherman, a variety resistant to bunt in Oregon, with its own bunt obtained 85.7 per cent infection. This same method has since been used in producing susceptibility in other wheats such as Ridit, Turkey, Hussar, and Berkeley Rock which were known to be resistant to _T. tritici._

He concludes, in the same way that the plant breeder may select a unit from a population of a variety for resistance to a certain pathogen, so the destructive mycologist may select a pathogen from an analogous population to which a given host is susceptible.

In a later paper, Dillon-Weston (1932) states that the general trend of hybridization experiments between resistant and susceptible wheat varieties indicates that several so-called immune or highly resistant varieties are susceptible when they are contaminated with bunt spores produced on those varieties. It is thought that resistance depends not on one single factor but on at least three: namely, the physiologic forms of the parasite, its environment, and the strain of the host and its environment.

Physiologic Forms. The existence of physiologic forms in the smut fungi was proved by Faris (1924b) for covered smut of barley. He expressed the opinion that other smut species should also be studied to determine the presence or absence of races in them.

Reed (1924) in reviewing the results obtained by other investigators believes that forms may exist within the species of *Tilletia* and that such races may be responsible for the different results obtained by various workers.

Gaines (1926) made the statement that unlike many other parasitic fungi, bunt is not known to exist in more than one biologic form. Sampson (1927) states that *T. tritici* is not a fungus with many highly specialized biologic species.

Rodenhiser and Stakman (1927) tested collections of *T. levis* from Minnesota, Italy, Egypt, and from two localities in Hungary, and collections of *T. tritici* from New Zealand, Hungary, Norway, Sweden, Canada, and from Minnesota, California, and Washington in the United States. They identified three forms of *T. levis* and two forms of *T. tritici*. They state that it seems likely that with the proper differential hosts, numerous forms of both species of bunt can be distinguished.

Gaines (1928) found that wheats formerly resistant to bunt later became badly smutted, due probably to the presence of new forms of *Tilletia.*

Reed (1928) reports 4 races of *T. levis* and 6 races of *T. tritici* as differentiated by the use of the varieties Kanred, Turkey, Hussar, Martin, and Odessa.

Holton (1930) found 3 forms of *T. tritici,* one form of which was very virulent on durum wheats.

Later Holton (1931) reported further observations in which he noted that a physiologic form of *T. tritici* previously not prevalent was responsible for epiphytotics of bunt in durum wheats. He also observed that a physiologic form of *T. levis* which had not before been described was the cause of outbreaks of bunt in Marquis.

Melchers (1930) in a study of Kansas bunt collections found an indication of the existence of several forms of bunt in Kansas when tested on 16 varieties of wheat.

Bosley (1931) identified 6 physiologic forms of *T. levis* by their reaction on the varieties Turkey, Martin, Hussar, White Odessa, and Banner Berkeley.

Bressman (1931) reports that there are at least 10 forms of bunt, 6 of _T. levis_ and 4 of _T. tritici._ These have been identified by their reaction on the varieties Albit, Hussar, Ridit, and Oro.

Smith, W. (1932b) showed that three forms of _T. tritici_ could be distinguished by their reaction on Martin. Martin was smut free when inoculated with T. 1, intermediately susceptible to T. 2, and very susceptible to T. 3, while Hybrid 128 was uniformly susceptible to each of these forms. T. 2 could also be differentiated from T. 3 by the presence of bunted spikes in the second form (T. 2).

Inheritance of Resistance to Bunt

Several investigators have studied wheat hybrids to determine as nearly as possible the mode of the inheritance of resistance to bunt.

Briggs (1926) studied the inheritance of resistance to bunt in F_1, F_2, and F_3 crosses.

He used the following combinations in his crosses: (1) susceptible X susceptible; (2) resistant X resistant; and (3) resistant X susceptible, in which Hard Federation, Baart, and White Federation were used as the susceptible and Martin and Hussar as the resistant parents. A slight difference was observed in the susceptibility of Hard Federation and Baart to bunt which was believed to be due to modifying factors. The difference between Martin and Hard Federation was explained on the basis of one dominant factor for resistance. Hussar is thought to differ from Baart and Hard Federation in two dominant factors, one of which is the same as that found in Martin. The exact behavior of the second factor was not determined at this time. Later (1930a) Briggs secured a selection, No. 1418, in which the second Hussar factor was present, but in which the dominant factor common to Martin and Hussar was absent. This second Hussar factor permits about 50 per cent of the heterozygous plants to become infected. He designated the factor for resistance in Martin MM and the second Hussar factor as HH.

Briggs (1929) suggested that variations of bunt percentages for heterozygous and homozygous susceptible F_3 rows may be explained on the basis of modifying factors.

Briggs (1930b, 1931) presented data which indicate that White Odessa and Banner Berkeley each contain a main dominant factor for resistance similar to the factor in Martin. He believes there may be other factors for resistance in these varieties which would become evident if they were tested with other physiologic forms of bunt.

Briggs (1932) reported results which showed that Turkey C.I. 1558 and Turkey C.I. 3055 each contains one main factor for resistance to bunt which is similar to the second Hussar factor.

Churchward (1931) working with the cross Florence X Hard Federation obtained evidence which seemed to show the presence of a one-factor difference for resistance to bunt in which susceptibility was dominant.

Gaines has made extensive studies of the genetics of bunt resistance in wheat. His studies differed from those of Briggs mainly in that he used a composite of smut forms and several individual collections, instead of one form, as in the California experiments. Gaines (1920) reported studies of the resistance of bunt in the crosses Turkey X Hybrid 128, and Turkey X Florence. From a study of these crosses, he believes that the greater number of factors for resistance are recessive and that Florence and Turkey each contains separate factors for resistance.

Gaines reaches the following conclusions:

(1) Bunt resistance in wheat is not a simple Mendelian unit character.

(2) Resistance, if Mendelian is composed of multiple factors, for a continuous series of forms ranging from complete immunity to complete susceptibility has been obtained.

(3) Different wheat varieties possess different kinds of resistance.

(4) Linkage between resistance and morphological characteristics is not sufficient to prevent the selection of a resistant strain of any morphologic type desired.

Gaines (1923) found different factors for resistance in the highly resistant varieties Turkey, Florence, and Alaska. Hybrids from crosses between these varieties ranged from immune to those completely susceptible to bunt.

Gaines (1925) did not find any heritable factors for resistance to bunt in Hybrid 128, Winter Fife, and Velvet Node. He further observed that the amount of bunt could be reduced 10 to 20 per cent by using Fortyfold and Red Russian, and 70 to 75 per cent with Turkey, Alaska, or Florence as compared with susceptible varieties as parents. Marquis shows resistance when spring sown but is susceptible when sown in the fall.

Gaines and Singleton (1926) reported transgressive segregation in F_3 hybrids of Marquis X Turkey, whether fall or spring sown. They state that resistance in this cross is apparently caused by two factors, the one carried by Turkey being more 'prepotent' than the one carried by Marquis.

Bressman (1931) found the deviation too great in the cross Hybrid 128 X Martin to explain the resistance of Martin to three collections of smut on a one factor basis. He states that the existence of physiologic forms of bunt makes the breeding program for the production of bunt resistant varieties much more complex. To undertake such a program, the breeder must have a rather thorough knowledge of the number and distribution of the physiologic forms of bunt.

Aamodt (1931) obtained transgressive segregation in a number of F_3 lines beyond the range shown by both parents in each of nine crosses. He concludes that multiple factors, the exact nature of which has not yet been determined, govern the reaction of bunt to wheat.

Smith, R. (1932) by crossing Komar, a rust-resistant, hard red spring wheat, with Hussar, a hard red winter wheat which carried immunity from some forms of smut, obtained seed from 19 families of wheat with spring habit which were smut free. Komar under the same conditions was completely smutty.

Kilduff (1933) from a study of inheritance of resistance to bunt from Kota and Red Bobs obtained evidence of bunt resistant factors, which indicated the presence of several factors governing bunt reaction.

MATERIALS AND METHODS

Hybrid populations of Oro, C.I. 8220, X Tenmarq Sel., Ks. No. 2637, were received from Dr. John H. Parker, Agronomy Department, Kansas State College, and planted in the Plant Pathology field plots, Manhattan, Kansas, in the fall of 1931.

Parental Varieties

Oro is a pure-line selection developed by D. E. Stephens at the Sherman County Branch Station, Moro, Oregon, from a variety labeled Turkey No. 889 and first called Turkey No. 889-5. The selection was made in 1921. The variety Turkey No. 889 was sent to the Oregon Station by A. A. Potter formerly of the U. S. D. A. from whom Mr. Stephens was unable to find where the variety was obtained. This selection was tested and found to be very resistant to bunt.

Pearson (1927) gave a historical account of Tenmarq. This variety is the product of a cross between P1066 and Marquis. The cross was made in 1917 in the Kansas Experiment Station Rust Nursery by M. N. Levine, working under the direction of Professors L. E. Melchers and John H. Parker, while trying to combine the rust resistance of Kanred with the earliness and superior milling quality of Marquis.

This P1066 X Marquis cross produced three kernels in 1915 which were planted that fall in the greenhouse. These three kernels grew into three plants designated as A, B, and C, each of which produced seed.

In the F_2 and succeeding generations, all of the spring type segregates were discarded or sent to the northern stations. Plant number 16 from the original plant A proved to be the best and was selected to become the ancestor of Tenmarq. There were 28 plants produced from this plant known as 16A in 1919-1920. In the summer of 1920, twelve of the most vigorous plants were selected from this row known as 16A and twelve head rows were grown from these plants in 1920-1921.

In the summer of 1921, plant number 16A12-5815-2, later known as Sel. No. 215421, was selected and seed from it was used for triplicate rod rows planted that fall. It was selected by Dr. John H. Parker of the Kansas Agricultural Experiment Station because of its high yield, apparent superior grain quality, stiff straw and freedom from leaf rust.

Laude (1932) reports that Tenmarq is susceptible to Hessian fly. This variety is susceptible to bunt as shown by several years' results (Table 1).

This selection was named Tenmarq and was sown in field plots at the agronomy farm in 1923 for the first time. Tenmarq has been rather widely tested at other experiment stations and has been grown in cooperative experiments on Kansas farms since 1927. In 1932 the Kansas Crop Improvement Association approved Tenmarq as a standard variety of hard red winter wheat for certification and about 520 bushels of seed were distributed to farmers in August, 1932. Tenmarq wheat is adapted to south central Kansas.

A comparison of Oro and Tenmarq in regard to yield, earliness, and bunt resistance is shown in Table 1.

Table 1.--Comparison of Oro and Tenmarq wheats in regard to yield, earliness, and bunt resistance at Manhattan, Kansas.

Variety	1927	1928	1929	1930	1931	1932	4 years 1929-1932	6 years 1927-1932
				Bushels per acre				
Tenmarq	47.5	50.5	24.3	38.9	47.4	53.4		43.7
Oro	25.7	46.4	18.0	32.9	47.2	46.6		36.1
				Date of heading, May				
Tenmarq	19	20	25	19	25	19		21.2
Oro	24	20	30	22	28	22		24.3
				Per cent bunt				
Tenmarq			46.02	26.12	23.3	57.0	38.1	
Oro			1.13	1.80	0.09	5.0	2.0	

Hybrid Populations

Hybrid populations of Oro X Tenmarq used in these studies consisted of two F_2 populations, each from an F_1 plant, 16 F_3 lines and 183 F_4 rows. They are the result of crosses made by Dr. John H. Parker in the agronomy greenhouse in the years 1930, 1929, and 1928, respectively. The F_1 hybrids for the F_2 generation of 1932 were grown in pots in the greenhouse in the winter of 1930-1931. The F_1 hybrids which provided the F_3 and F_4 generations grown in 1932 were grown in the greenhouse in the winters of 1930 and 1929, respectively. Succeeding generations have been grown in the agronomy nursery.

Plant selections of F_2 and F_3 hybrid material were made in the summer of 1931 for the 1932 F_3 and F_4 generations, respectively. Plants were selected on the basis of number and uniformity of tillers, stiffness of straw, weight of heads and apparent vigor. Some early plants which had been tagged in the field were also selected for planting. Thus the plants from each row which showed easily recognizable and desirable agronomic characters were selected. Tillers which were uniform in length, with good head weight, were chosen in preference to those in which the length of straw was not uniform. Lodged plants were discarded.

Each plant was numbered and threshed separately. Notes were taken on the threshed grain and further selection was made on the basis of kernel characters. The seed was selected for planting on the basis of plumpness, weight in grams per plant, corneous texture, and freedom from yellowberry.

The studies of bunt resistance were divided into two parts: (1) In which the F_2, F_3, and F_4 hybrid selections were inoculated with bunt designated as physiologic form 1, from Lincoln County, Kansas; and (2) in which a second series of the F_4 generation was inoculated with a composite of 19 collections of bunt representative of Kansas. This composite included 6 physiologic forms identified by Bosley (1931). Notes were also taken and are presented for several other characters: winter injury, earliness, leaf rust, and grain quality.

For the studies in Part I, the seed was thoroughly blackened with bunt spores of physiologic form 1 which had been propagated on Kanred the previous season. The inoculum was prepared by grinding the bunt in a sterilized food grinder, taking precautions to avoid mixture with any other forms.

All of the F_1 seed from two individual plants was planted in four rod rows one foot apart, with the kernels in each row spaced 3 to 4 inches apart, to produce the F_2 generation for 1932. The F_2

seed for an F_3 generation in 1932 was space planted in two rod rows. Unfortunately the number of selections in the F_3 generation was small. This is the best generation to use in studies of the mode of inheritance of bunt resistance. A larger number of lines were available in the F_4 generation from which resistant plants were selected for testing in F_5. Seed for the first series of an F_4 generation in 1932, inoculated with physiologic form 1, was space planted in rod rows in the fall of 1931.

The nursery was all planted the same day so that soil moisture and soil temperature conditions were very similar for all of the selections. Two soil samples were taken, one from each end of the series of rows. These samples were taken from the row immediately after it was opened at approximately the depth at which the wheat was planted. The percentage of soil moisture was determined in the laboratory. The soil moisture varied from 15.4 per cent at one end of the series of plots to 19.4 per cent moisture at the other end of the nursery.

A soil and air thermograph was placed in the nursery to record soil and air temperatures for a continuous period ranging from before time of planting to several weeks later. The soil temperature for the week following planting varied from 42° to 70° F. with an average of 58.8° F. for this period. The lowest temperatures were recorded during the first few days after planting.

At harvest, the plants in each row were pulled and separated into three lots; (1) those in which the plants were totally bunted, (2) those partially bunted, and (3) those which were bunt free. Gaines (1923) in dealing with partially bunted plants used the formula $ab + c = d$. In this formula, $a =$ the percentage of bunted heads on partly bunted plants, $b =$ the percentage of partly bunted plants in a row, $c =$ the percentage of entirely bunted plants in a row, and $d =$ the total percentage of bunted plants in a row. This gives a satisfactory quantitative measure which he believes important in studying resistance. Briggs (1926), however, criticizes this method on the basis that it does not indicate the nature of segregation.

In the experiments here reported, the refined methods of Gaines were not used. All smutted plants are recorded as totally diseased in calculating the bunt percentages used in the study of the inheritance of bunt resistance.

The second part of the experiment deals with 183 F_4 progenies from individual F_3 plants which were inoculated with a composite of Kansas bunt forms. This series was sown in five-foot rows one foot apart. The soil moisture in this plot at time of planting was 17.7 per cent, while the soil temperature was the same as that for the space planted series.

Since no selections were to be made from this section of the nursery, the rows in this series were cut during June, as soon as all the heads were out of the boot and the diseased heads could be easily identified. Plants in four feet of each row were cut with a sickle, tied in a bundle, and labeled. These bundles were then taken to the field house and the number of bunted heads in each bundle was counted and recorded. A mechanical hand tabulator was used in counting. Plants in one foot of each row were left standing until after natural leaf rust infection occurred. Leaf rust notes were taken by C. O. Johnston and the writer.

Stand counts of the space planted series were made before cold weather and again in the spring after danger of damage from freezing was past. These counts were made to determine the percentage of winter killing.

Heading dates were taken on all of the hybrids. These were taken as nearly as possible when approximately 75 per cent of the heads in a row had emerged from the boot.

General notes were also taken on row characters as seen in the field, such as good, promising, late, etc. "Good" refers to such characters as vigor and uniformity of plants, height, maturity, etc.

In the summer of 1932 individual plant selections were made in about the same way as in the previous seasons. The individual plants were threshed and grain notes were taken. These notes on kernel characters served as a basis for selection. They have also been used for a study of the relationship between kernel characters and plant characters, including resistance to leaf rust and bunt.

In the fall of 1932, individual plants in the most resistant lines within each of the three generations showing desirable grain characters were selected for planting. In addition two plants in rows showing approximately 20, 40, 60, and 80 per cent infection in 1932 were selected from the F_4 material for planting. The behavior of these susceptible lines will determine whether they are breeding true for their characteristic reaction to bunt. These lines were inoculated with a composite of Kansas bunt forms. The results secured in 1933 should be of considerable value in making further advancement toward a bunt resistant wheat with desirable agronomic characters.

EXPERIMENTAL RESULTS

Physiologic Form 1 of Bunt

Parental check rows of Oro have an average of 7 per cent bunt. Tenmarq shows an average of 43 per cent bunt. The distribution for parents and hybrid progenies into 5 per cent classes for bunt infection is shown in Table 2.

These hybrid populations had never previously been infected with bunt, but selection for desirable agronomic characters has been carried on in each generation.

Two F_2 cultures from individual F_1 plants in 1931 had averages of 20 per cent and 13 per cent bunt. These are intermediate between the two parents in bunt infection. It is of interest to note that these hybrids each contain only about 1 per cent of totally smutted plants. Of the parental rows grown immediately adjacent to these F_2 cultures, the resistant parent, Oro, shows 0 per cent, while the susceptible parent, Tenmarq, shows 12.5 per cent of totally smutted plants.

The F_3 population consists of 17 lines from individual F_2 plants grown in 1931. Two of these F_3 lines show 0 per cent bunt and 4 show bunt infection of from 0 to 5 per cent. Two F_3 rows show greater susceptibility than the average of the Tenmarq parent. The distribution of F_3 lines according to bunt percentages in 5 per cent intervals is shown in Figure 1. The greater number of bunt infection percentages are grouped about the mean of the Oro parent. The number of F_3 lines is far too small for genetic analysis.

Table 2.--Distribution of Oro, Tenmarq and their hybrid progenies into 5 per cent classes for infection of bunt, physiologic form 1.

Per cent bunt	Parents: Oro	Parents: Tenmarq	Hybrids: F_2	Hybrids: F_3	Hybrids: F_4
0	1			2	66
0-4.9	2			4	17
5-9.9	5			1	11
10-14.9	3		1	4	8
15-19.9	1			2	13
20-24.9		1	1	1	18
25-29.9		2		1	5
30-34.9		3			5
35-39.9		1			4
40-44.9		5			5
45-49.9				1	7
50-54.9		1			2
55-59.9				1	6
60-64.9		1			6
65-69.9					6
70-74.9					1
75-79.9					2
Ave. per cent	7	43	16.8	15.0	18.2
Total No. rows	12*	14	2	17	182*

* Percentage bunt for 1 row was not recorded.

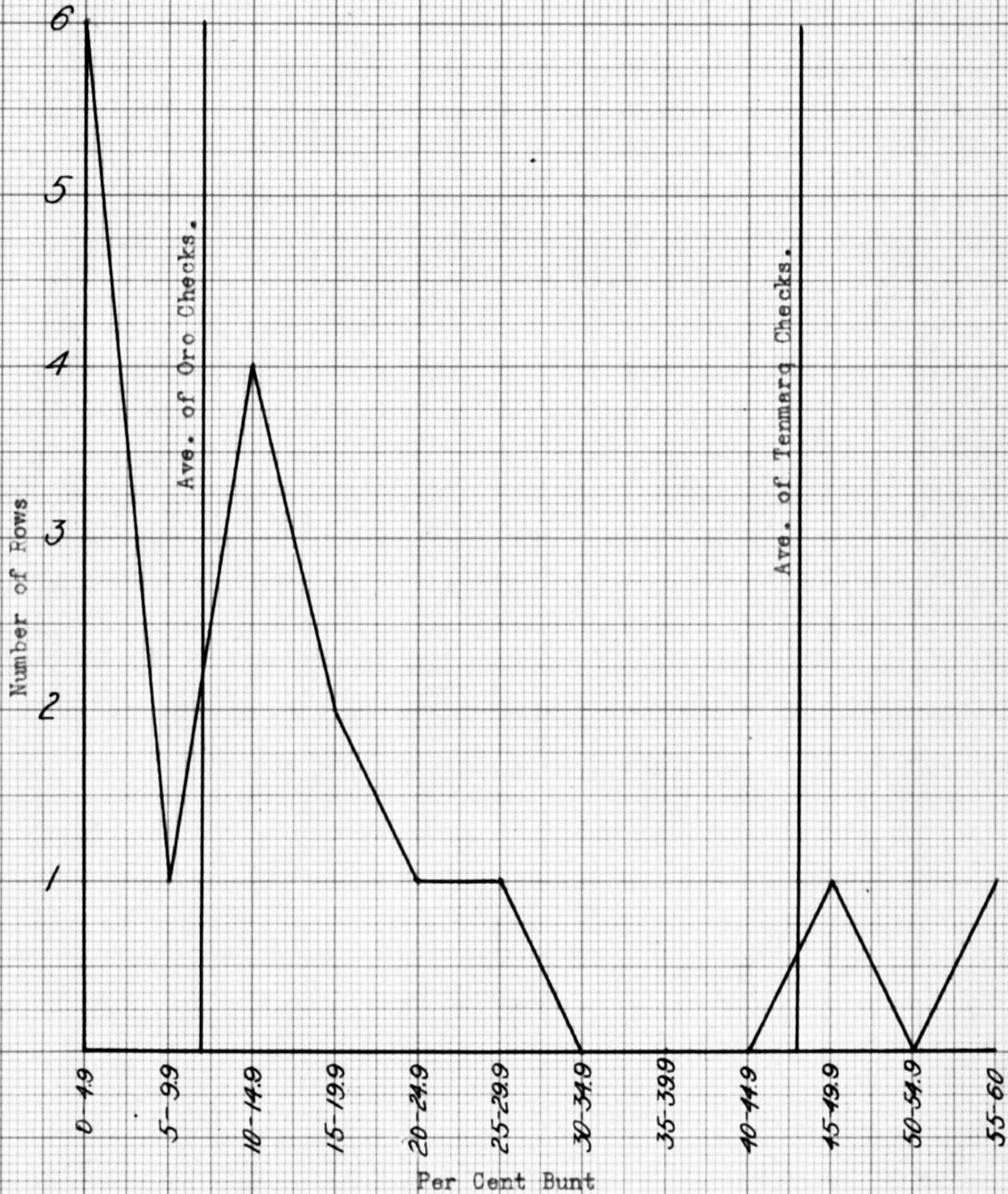

Fig. 1. Distribution of rows of F_3 generation of Oro X Tenmarq, inoculated with bunt, physiologic form I.

The F_4 population is made up of 183 lines from individual plants selected from 23 F_3 lines grown in 1931. Sixty-six rows show 0 per cent bunt, while an additional 17 rows show bunt infection no greater than 0 to 5 per cent. Thirty-one rows show a greater susceptibility than the average of the Tenmarq parent. The distribution of rows according to bunt percentages in 5 per cent intervals is shown in Figure 2. The larger number of bunt infection percentages are grouped near the mean percentage of bunt infection of Oro, the resistant parent.

The distribution of bunt infection percentages of F_4 progenies grouped according to F_3 parental lines, is shown in Figures 3, 4, and 5. The dots on the base line are used to indicate 0 per cent bunt infection. The pedigree numbers show the number of F_4 progenies from each F_3 line designated by the 1931 row numbers. Within each F_3 family, the F_4 progenies are arranged in order from the one with the lowest to the one with the highest average per cent bunt. The average per cent bunt infection of the F_4 lines from each F_3 family is shown by a line designated as such in the figures. The average per cent bunt infection of each of the parents to p. f. 1 is also shown in Figures 4 and 5.

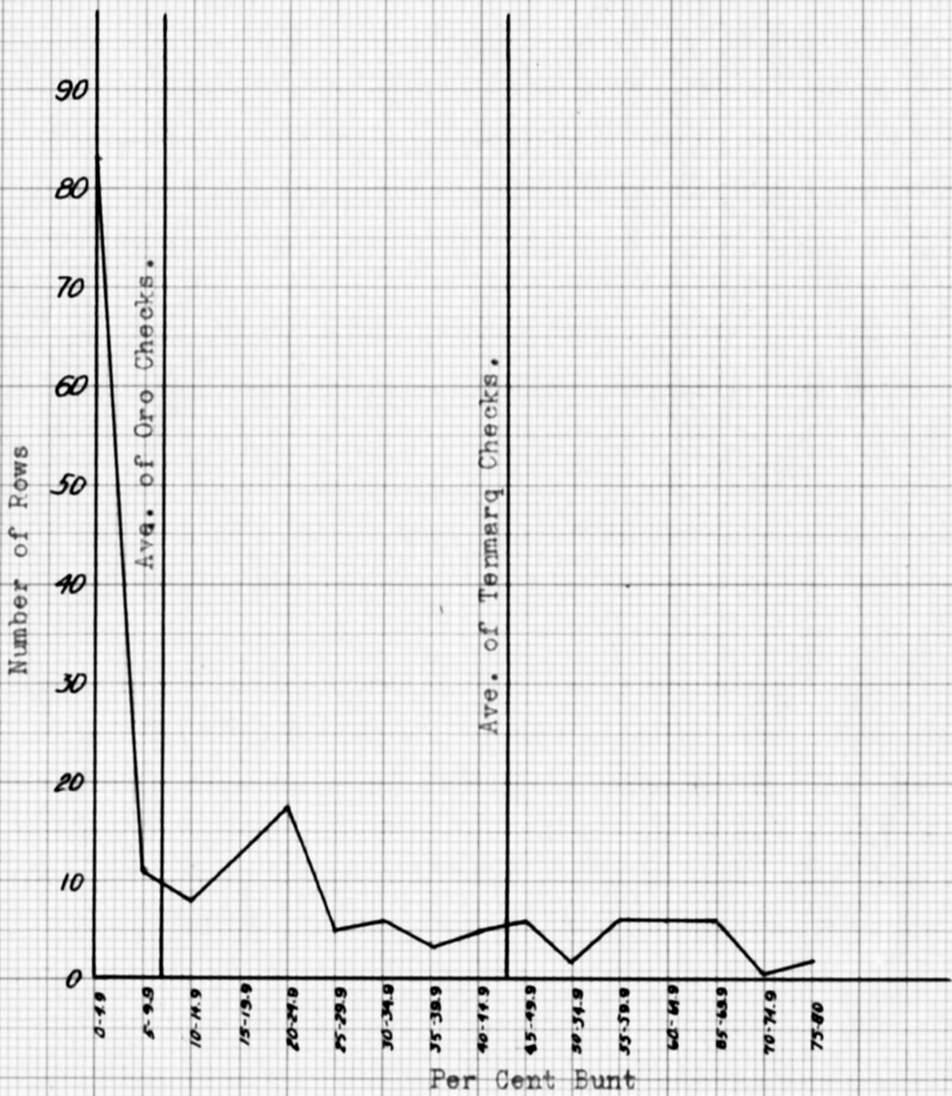

Fig. 2. Distribution of rows of an F_4 generation of Oro X Tenmarq, inoculated with bunt, physiologic form I.

Resistant F_4 progeny rows from 8 F_3 lines which were evidently homozygous for resistance to bunt are included in Figure 3. The F_4 lines from the 8 F_3 families range from an average of 0 per cent bunt to 1.0 per cent bunt infection, with a maximum of 8.5 per cent infection for one F_4 progeny row.

Resistant and susceptible F_4 lines from 12 F_3 lines which were evidently heterozygous for bunt reaction are grouped in Figure 4. The F_4 lines from F_3 lines included in this figure range from an average of 10 per cent to 32 per cent bunt infection. Individual F_4 lines within the F_3 groups range for the most part from zero bunt infection to an infection greater than the average for the susceptible Tenmarq parent. There is unmistakable evidence of clear cut segregation for bunt resistance among the F_4 lines from each of the F_3 lines here represented.

Susceptible F_4 lines from susceptible F_3 lines are represented in Figure 5. These F_3 lines were evidently homozygous for susceptibility, although the number of F_4 lines representing two of the F_3 lines is rather small. The F_4 lines representing F_3 groups show an average bunt infection of 38, 55, and 69 per cent, respectively, for p. f. 1. These lines show a much higher bunt infection when inoculated with the composite of bunt collections (fig. 9).

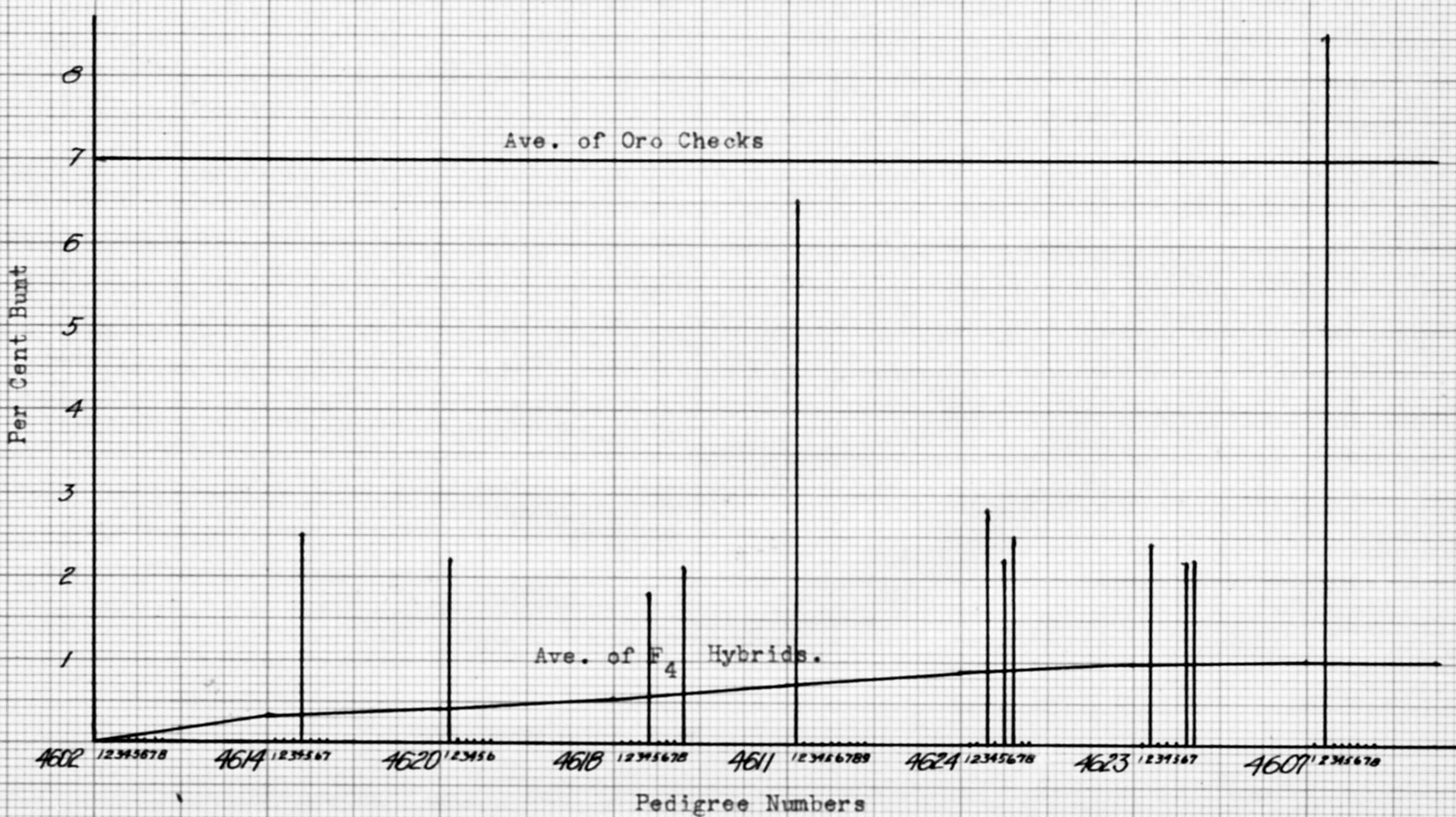

Fig. 3. F_4 lines of Oro X Tenmarq from resistant F_3 lines inoculated with bunt, physiologic form I.

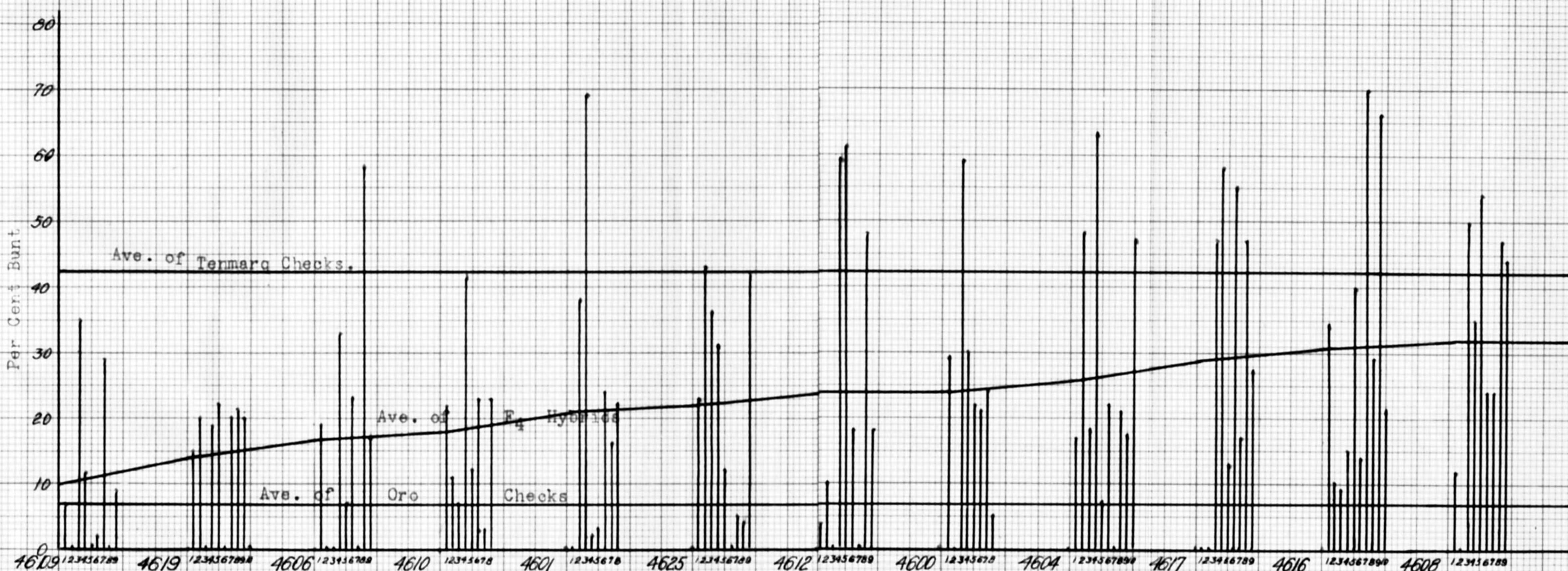

Fig. 4. F_4 lines of Oro X Termarq from F_3 lines heterozygous for bunt resistence, inoculated with bunt, physiologic form 1.

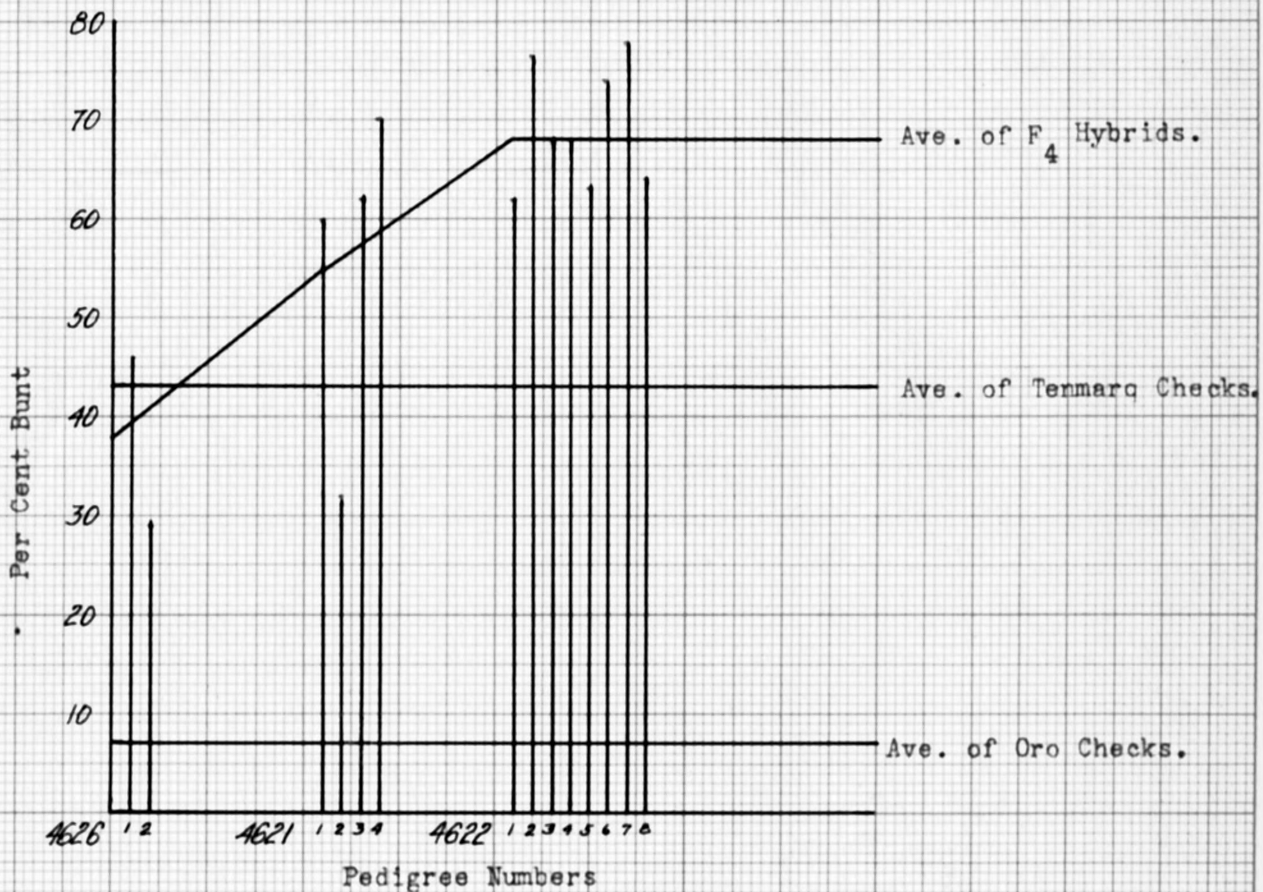

Fig. 5. F_4 lines of Oro X Tenmarq from susceptible F_3 lines inoculated with bunt, physiologic form I.

As shown in these three figures representing F_4 lines, the parental F_3 lines may be classed as homozygous resistant, heterozygous, and homozygous susceptible, in the proportion of 8:12:3, respectively. The number of F_3 lines represented is too small for genetic analysis, though high susceptibility is evidently recessive in this cross.

Composite of Kansas Bunt Collections

When inoculated with a composite of Kansas bunt forms, Oro has an average of 5 per cent and Tenmarq an average of 57 per cent bunt. The distribution of bunt infection percentages for parents and F_4 lines is shown in intervals of 5 per cent bunt infection in Table 3.

Table 3.--Distribution of bunt infection percentages of Oro, Tenmarq and F_4 lines into 5 per cent classes when inoculated with a composite of Kansas bunt forms.

Per cent bunt	Oro	Tenmarq	F_4 hybrids
0			37
0-4.9	6		45
5-9.9	4		6
10-14.9			16
15-19.9			14
20-24.9			9
25-29.9			6
30-34.9			5
35-39.9		2	2
40-44.9		1	3
45-49.9		1	2
50-54.9		2	4
55-59.9		1	4
60-64.9			4
65-69.9			5
70-74.9		1	6
75-79.9		1	6
80-84.9			5
85-89.9			2
90-95		1	1
Ave. per cent bunt	5	57	21.9
Total No. rows	10	10	182*

* No count is recorded for one row.

Of the 183 F_4 progeny rows from 23 F_3 lines, 37 show 0 per cent bunt infection, while an additional 44 fall within the interval 0-5 per cent. Thirty rows show a greater susceptibility than the average of the Tenmarq parent. There are no F_4 lines with a greater susceptibility than that of the highest Tenmarq check.

The distribution of F_4 lines according to bunt percentages in 5 per cent intervals is shown in Figure 6. The largest number of F_4 lines are grouped near the average bunt infection of the checks of the resistant parent, Oro.

The distribution of bunt infection percentages of F_4 lines inoculated with the composite bunt and grouped according to F_3 source is shown in Figures 7, 8, and 9. The F_3 groups are arranged in order from the one with the lowest to the one with the highest average per cent bunt in F_4. The order of the F_4 lines within the F_3 groups is not exactly the same as with p. f. 1 (figs. 3, 4, and 5) though the same F_4 lines remain in their respective F_3 groups.

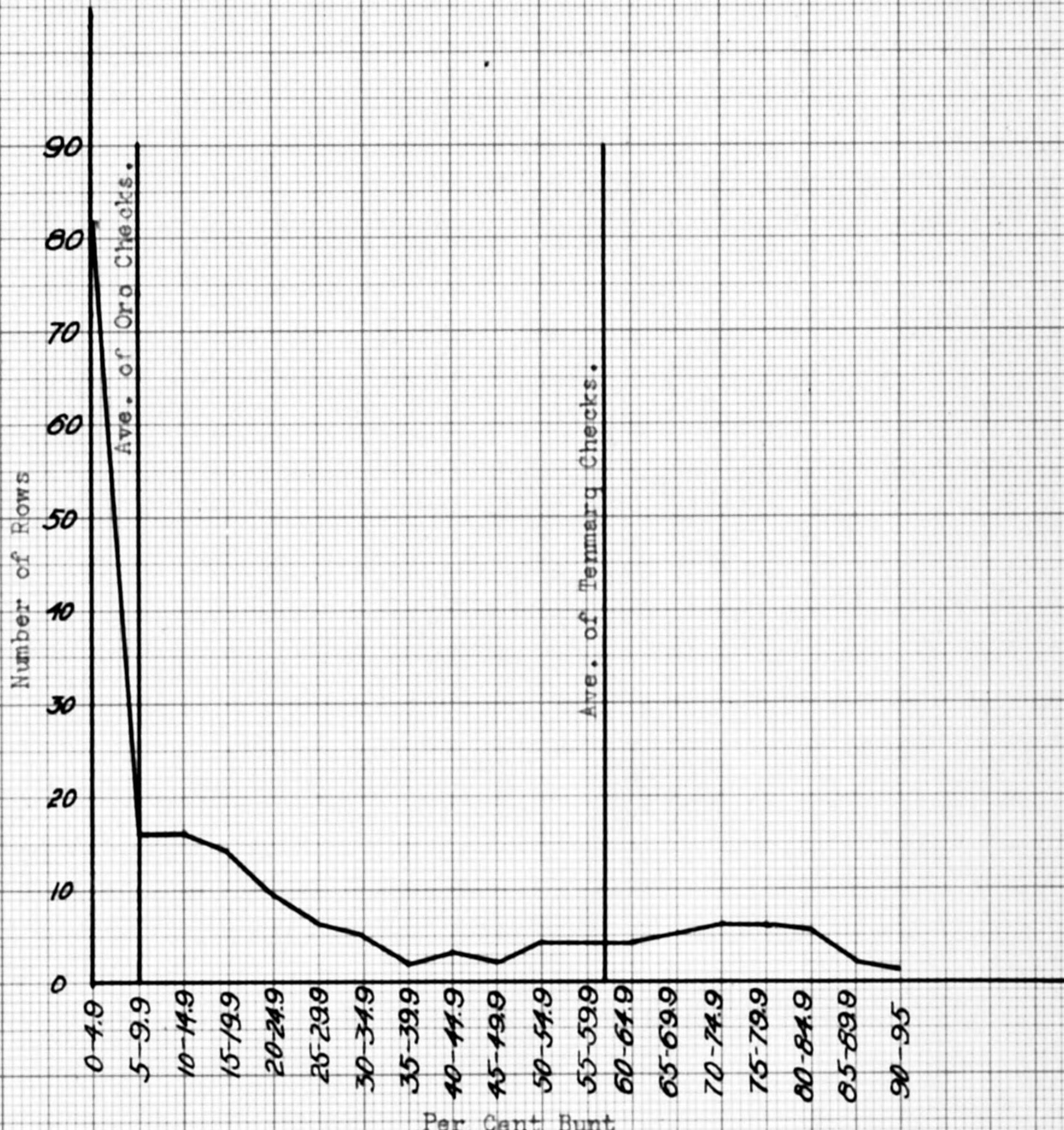

Fig. 8. Distribution of F_4 lines of Oro X Tenmarq, inoculated with a composite of physiologic forms of Kansas bunt.

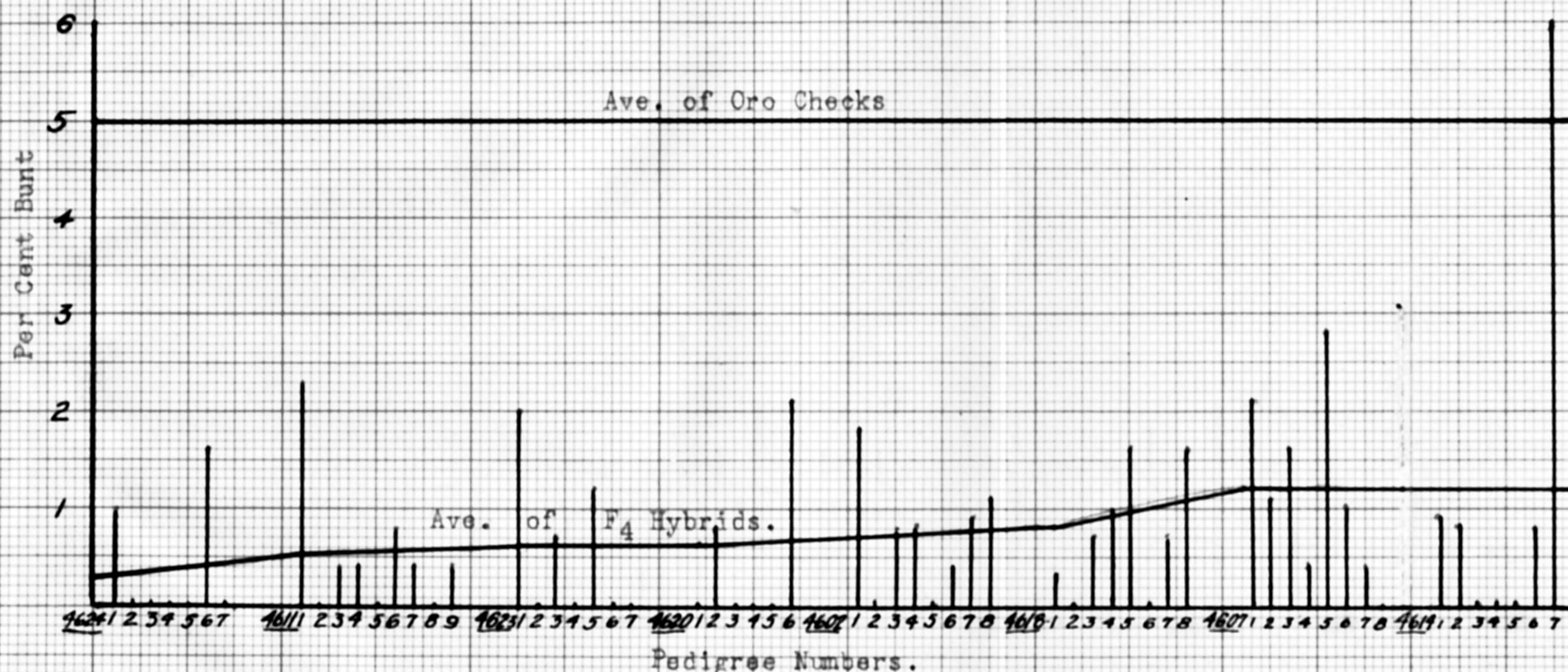

Fig. 7. Resistant F_4 lines of Oro X Tenmarq from resistant F_3 lines, inoculated with a composite of Kansas bunt forms.

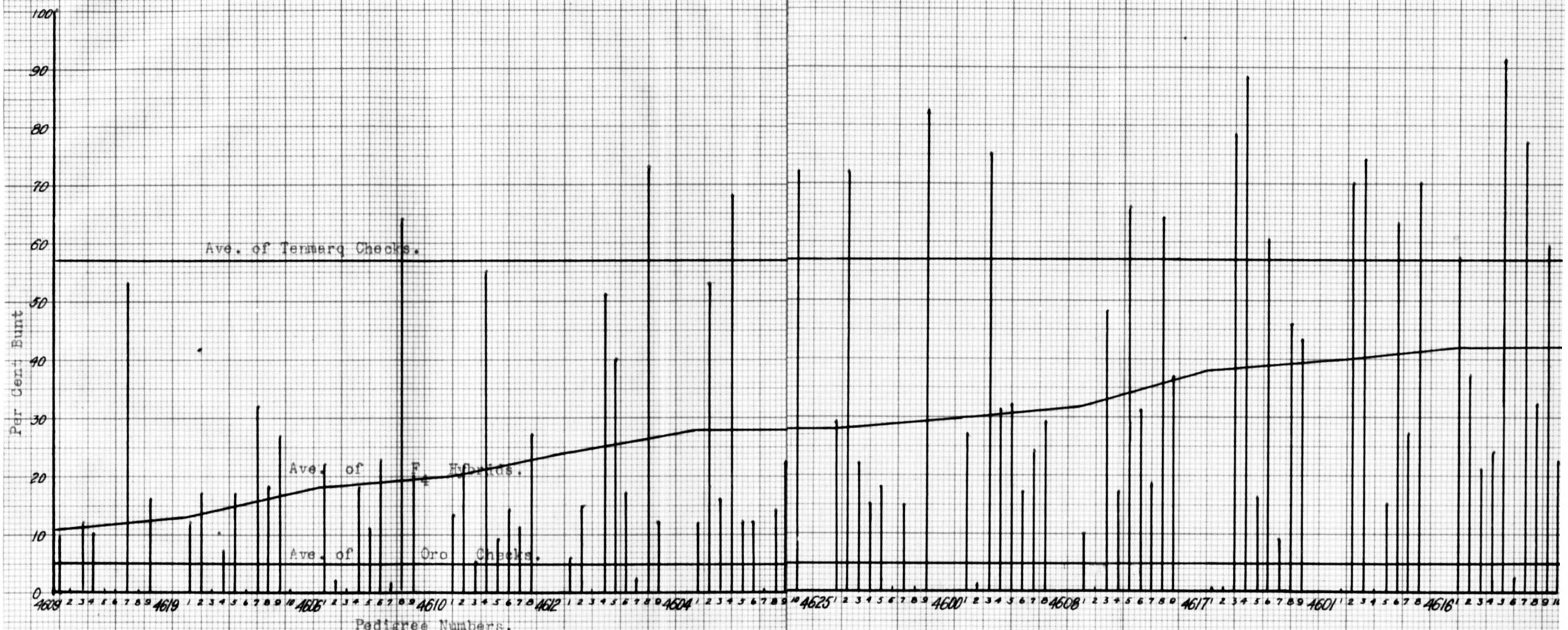

Fig. 8. F_4 lines of Oro X Tenmarq from F_3 lines heterozygous for bunt reaction, inoculated with a composite of physiologic forms of Kansas bunt.

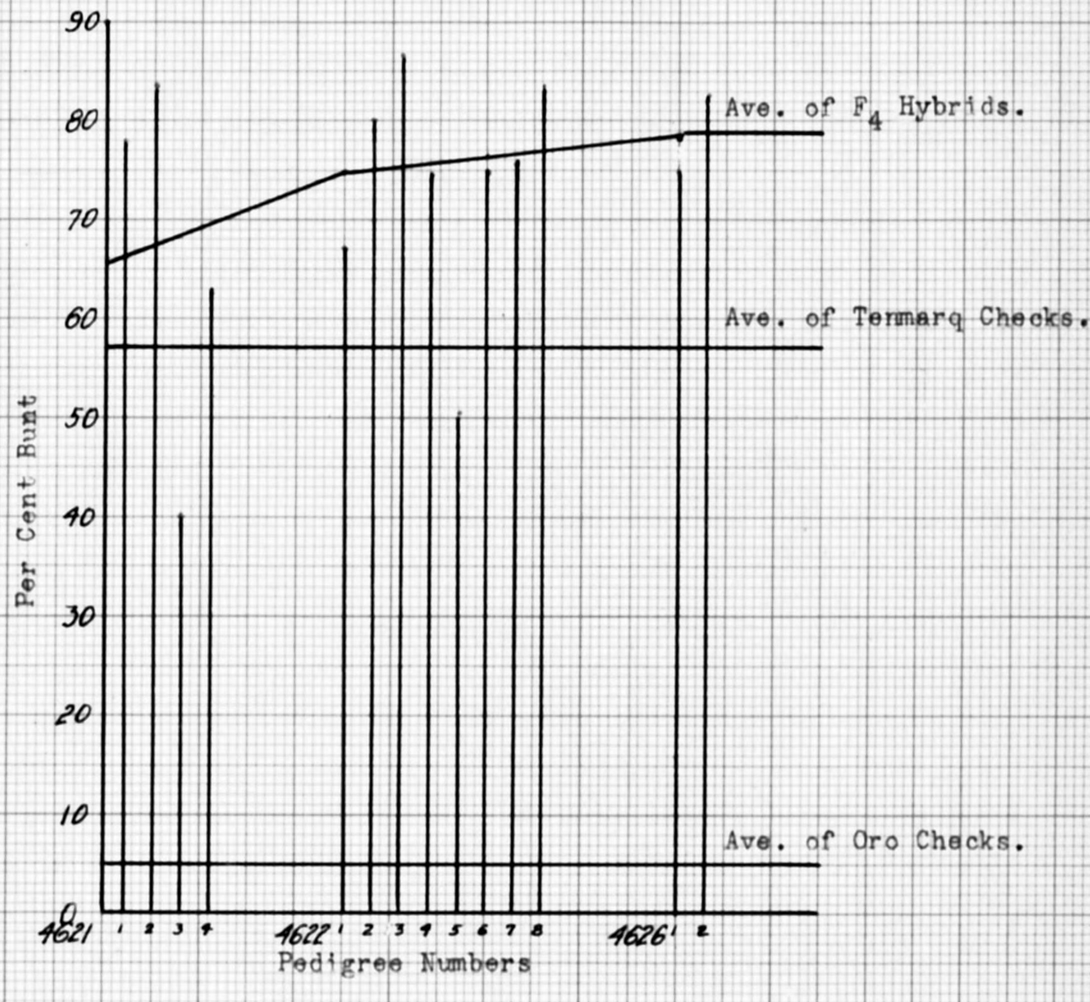

Fig. 9. Susceptible F_4 lines of Oro X Tenmarq from susceptible F_3 lines inoculated with a composite of physiologic forms of Kansas bunt.

The resistant F_4 lines from resistant F_3 lines are shown in Figure 7. The average bunt infection percentages for the various F_4 lines arranged according to F_3 sources, are compared with the average per cent bunt infection for Oro. The average bunt infection of F_4 lines in the F_3 groups ranges from 0.32 to 1.17 per cent. F_4 lines representing 12 F_3 progenies are shown in Figure 8. The bunt reaction of these F_4 lines shows clearly that the F_3 lines from which they were selected were heterozygous for reaction to the composite forms of bunt. The average bunt infection of F_4 lines in the F_3 groups ranges from 11 to 42 per cent.

Susceptible F_4 lines from susceptible F_3 lines inoculated with the composite of bunt forms are shown in Figure 9. The average bunt infection of F_4 lines from these susceptible F_3 lines ranges from 66 to 79 per cent. There is no doubt as to the susceptibility of these F_4 lines which evidently came from homozygous susceptible F_3 lines.

The average bunt infection percentages of the Oro and Tenmarq checks are shown in Figures 8 and 9, for direct comparison with the hybrids.

The average per cent bunt infection for these lines inoculated with a composite of Kansas bunt forms is very similar to that in which p.f. 1 was used, although, as might be expected, the average infections with the composite are slightly higher than those with p. f. 1.

As when p. f. 1 was used, so with the composite bunt, the F_3 lines may be grouped, on the basis of bunt reaction of their F_4 progenies, into homozygous resistant, heterozygous, and homozygous susceptible, in the proportion of 8:12:3, respectively.

In Figures 3 to 5 and 7 to 9, the average percentages of bunt infection of F_4 lines arranged according to F_3 source and inoculated with physiologic form 1 are compared with the bunt percentages when a composite of Kansas bunt forms was used. These figures are very similar. As the F_3 lines are not exactly in the same order within each group, Figures 10 to 15 have been prepared to show the relation of infection of p.f. 1 and the composite of Kansas bunt forms for individual families. The families are arranged in order from that with the lowest per cent infection with p. f. 1 to the highest per cent infection with this form.

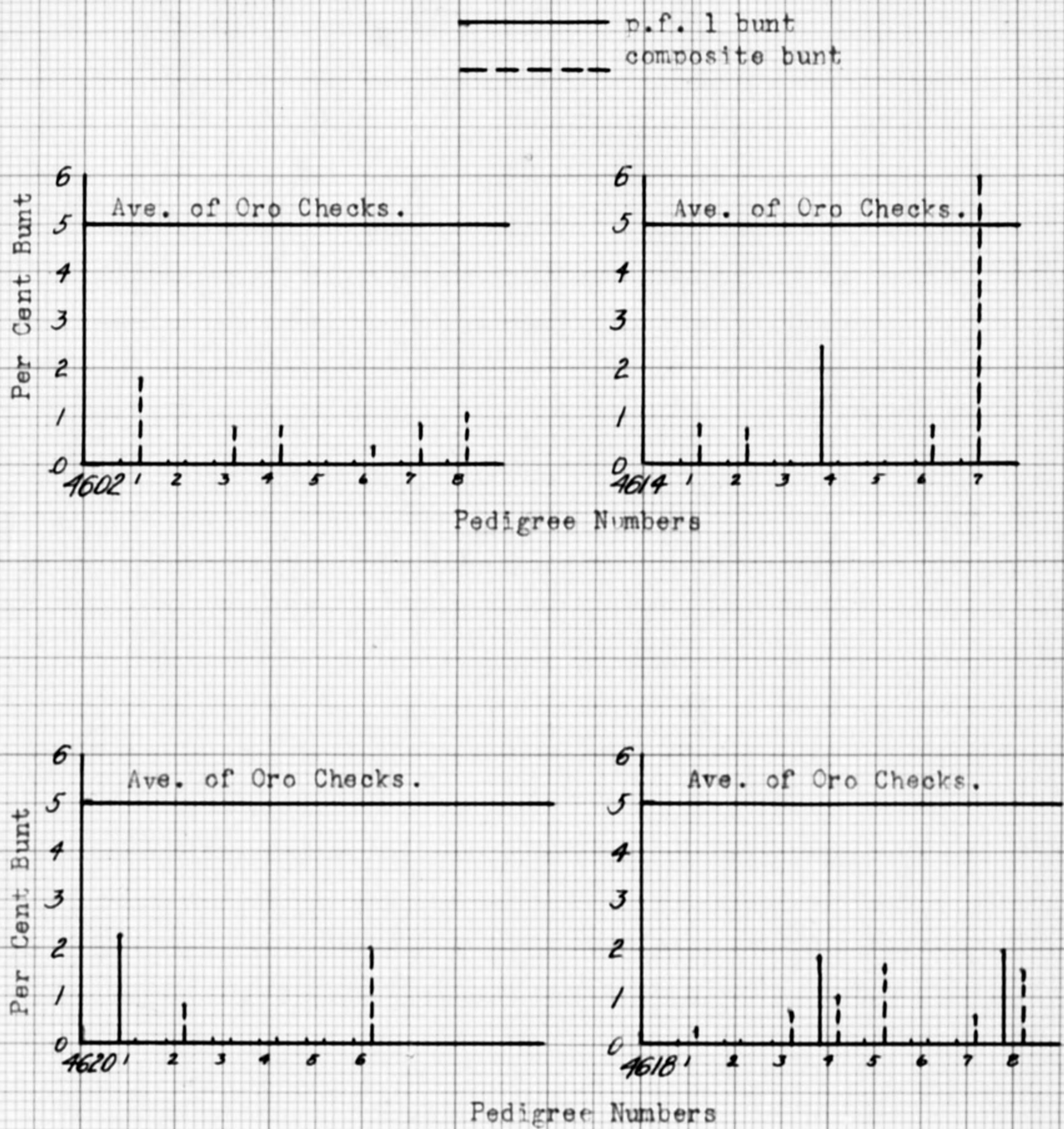

Fig. 10. Comparison of bunt infection percentages of resistant F_4 lines from resistant F_3 lines of Oro X Tenmarq, inoculated with p. f. 1 and a composite of Kansas bunt forms.

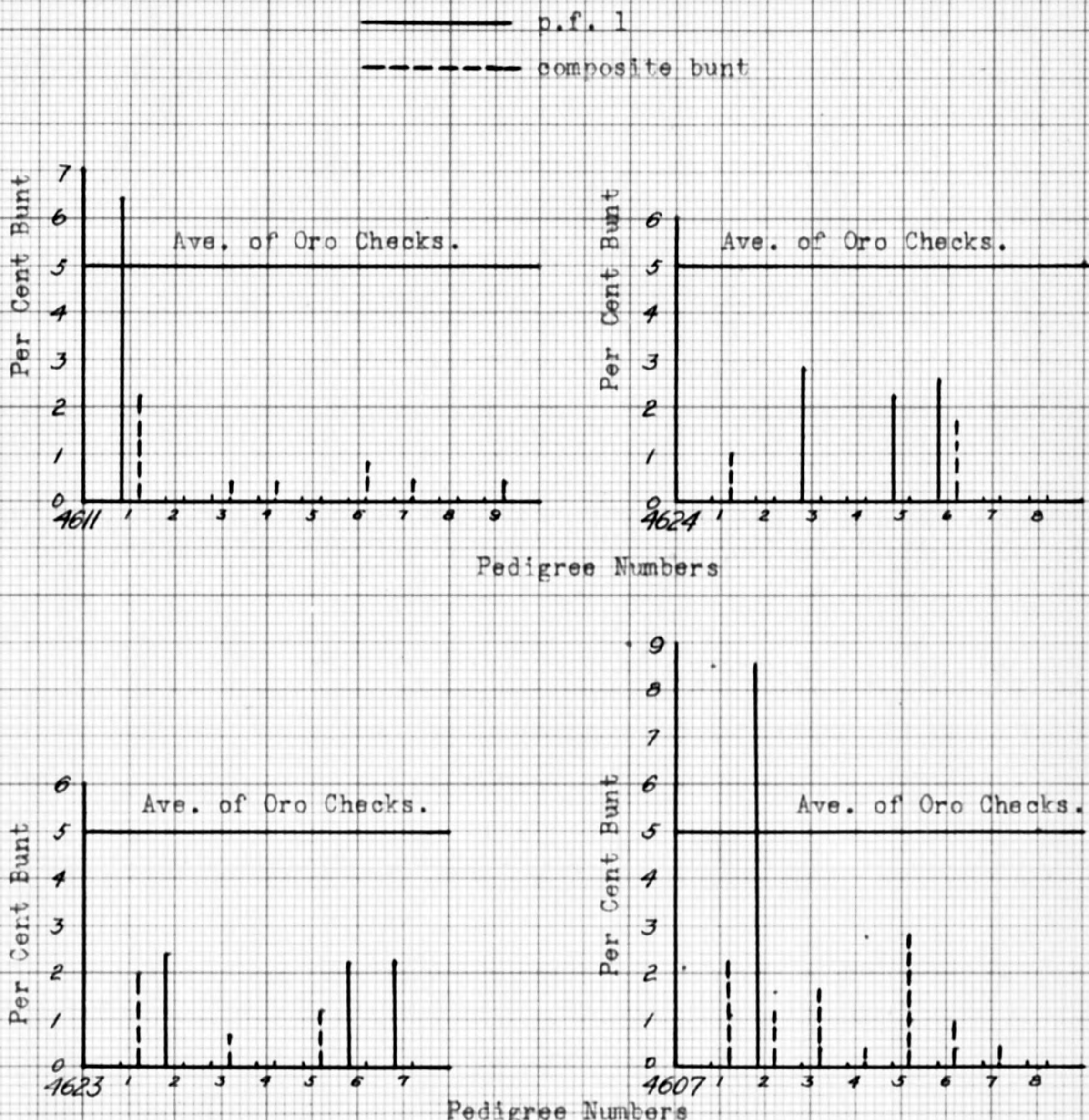

Fig. 11. Comparison of bunt infection percentages of resistant F_4 lines from resistant F_3 lines of Oro X Tenmarq, inoculated with p.f. 1 and a composite of Kansas bunt forms.

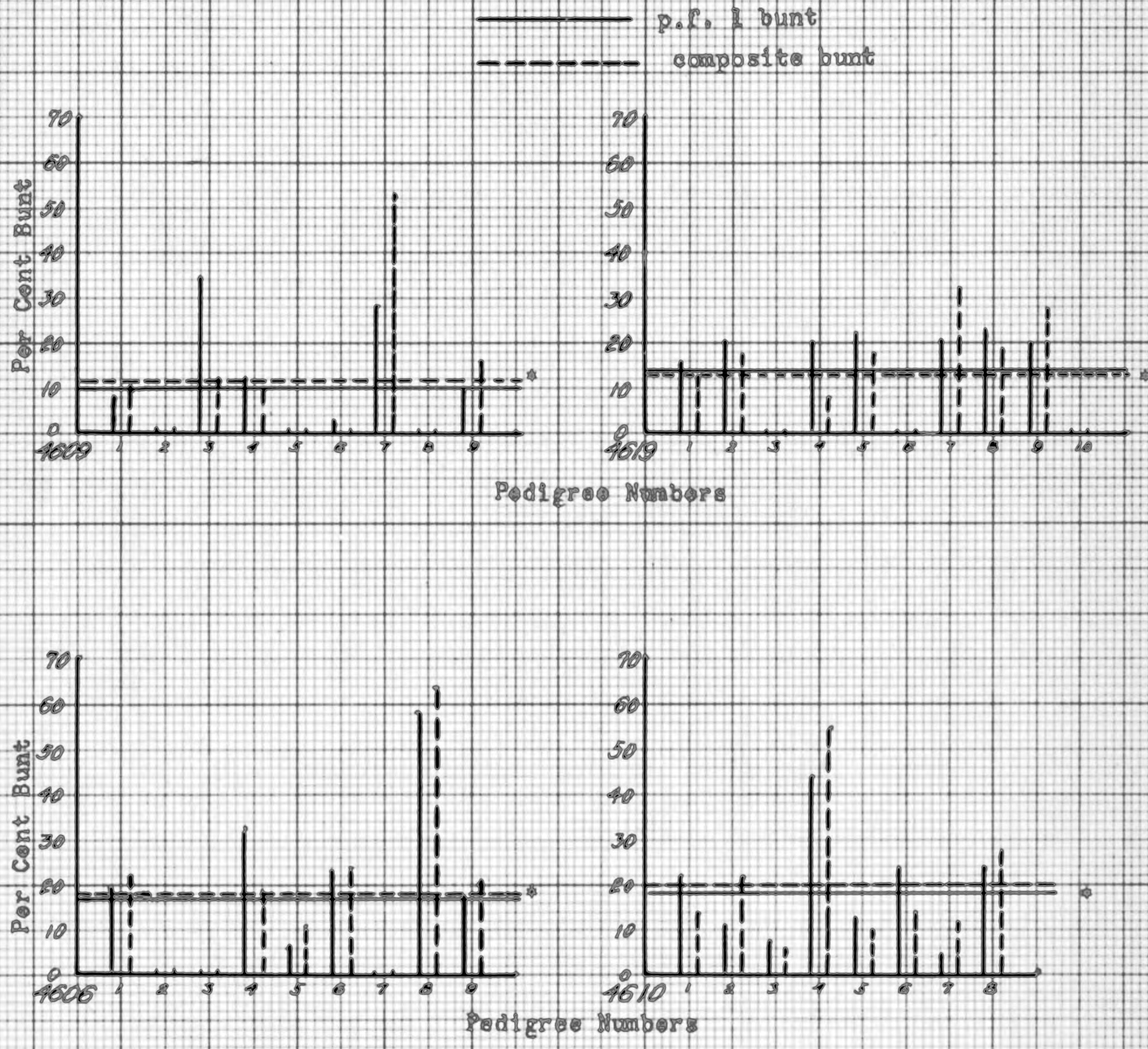

Fig. 12. Comparison of bunt infection percentages of F_4 lines from heterozygous F_3 lines of Oro X Tenmarq inoculated with p.f. 1 and a composite of Kansas bunt forms.

* Average infection for each form of inoculum.

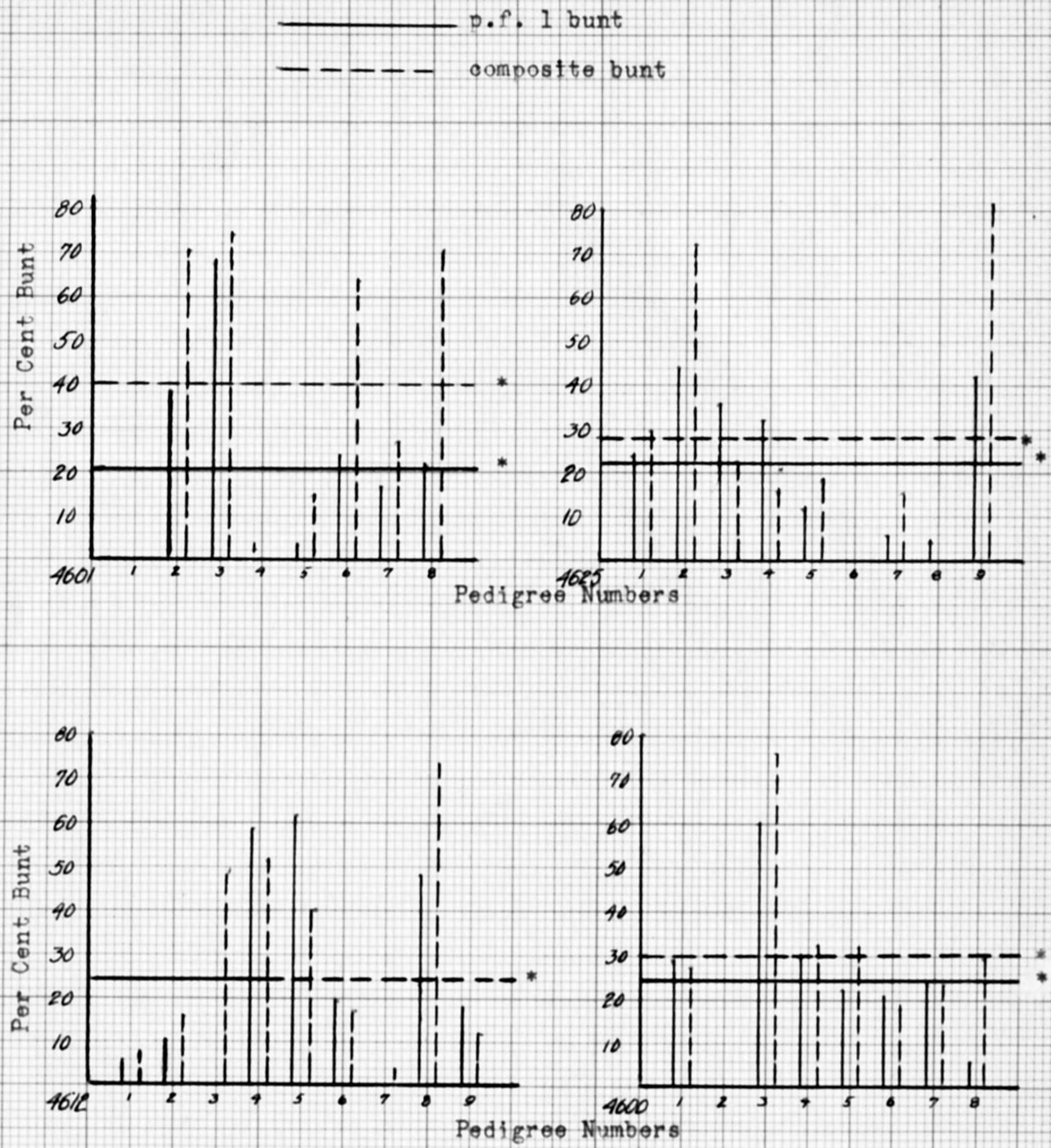

Fig. 13. Comparison of bunt infection percentages of F_4 lines from heterozygous F_3 lines of Oro X Tenmarq, inoculated with p.f. 1 and a composite of Kansas bunt forms.

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* Average infection for each form of inoculum.

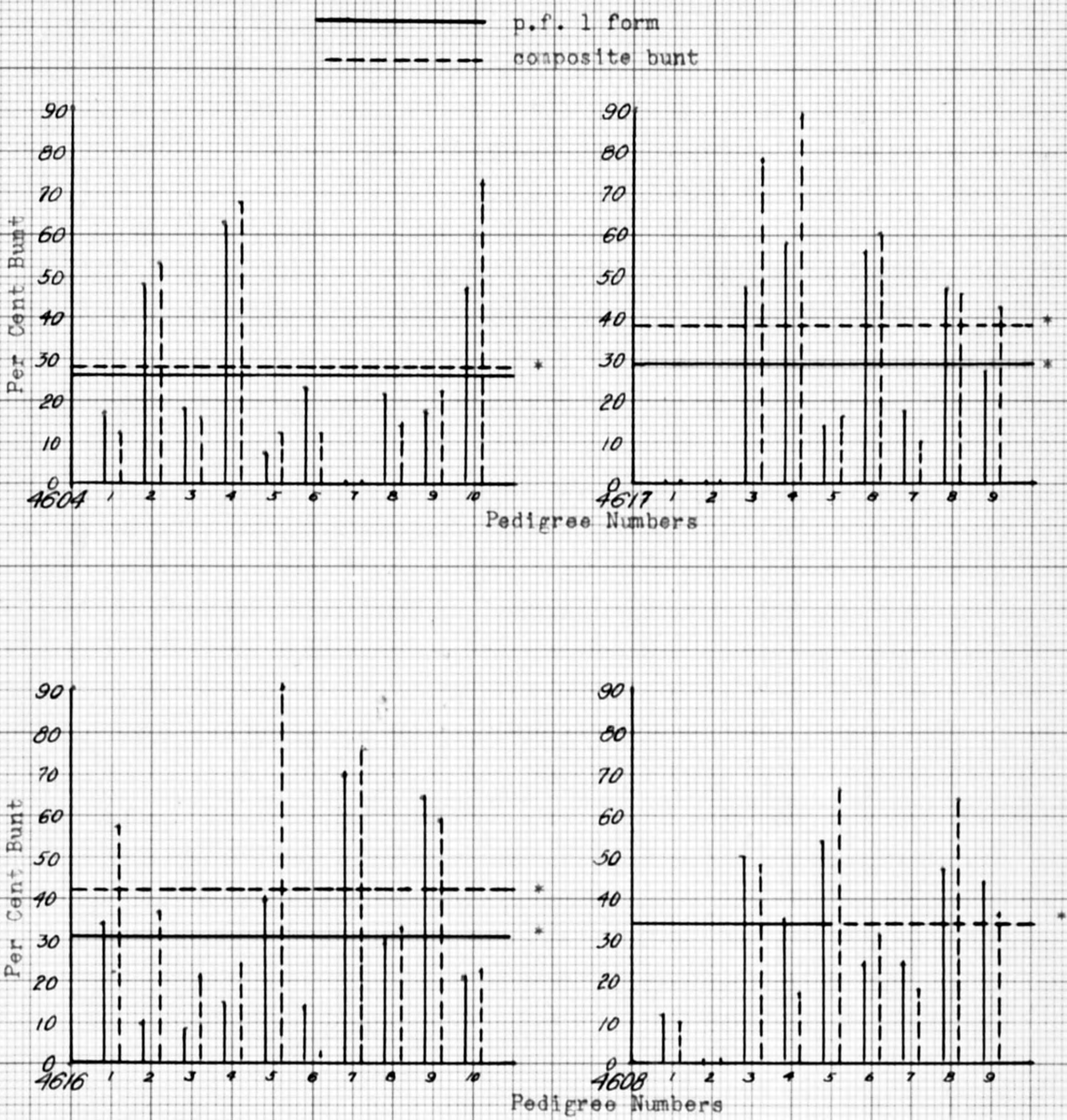

Fig. 14. Comparison of bunt infection percentages of F_4 lines from heterozygous F_3 lines of Oro X Tenmarq, inoculated with p.f. 1 and a composite of Kansas bunt forms.

* Average infection for each form of inoculum.

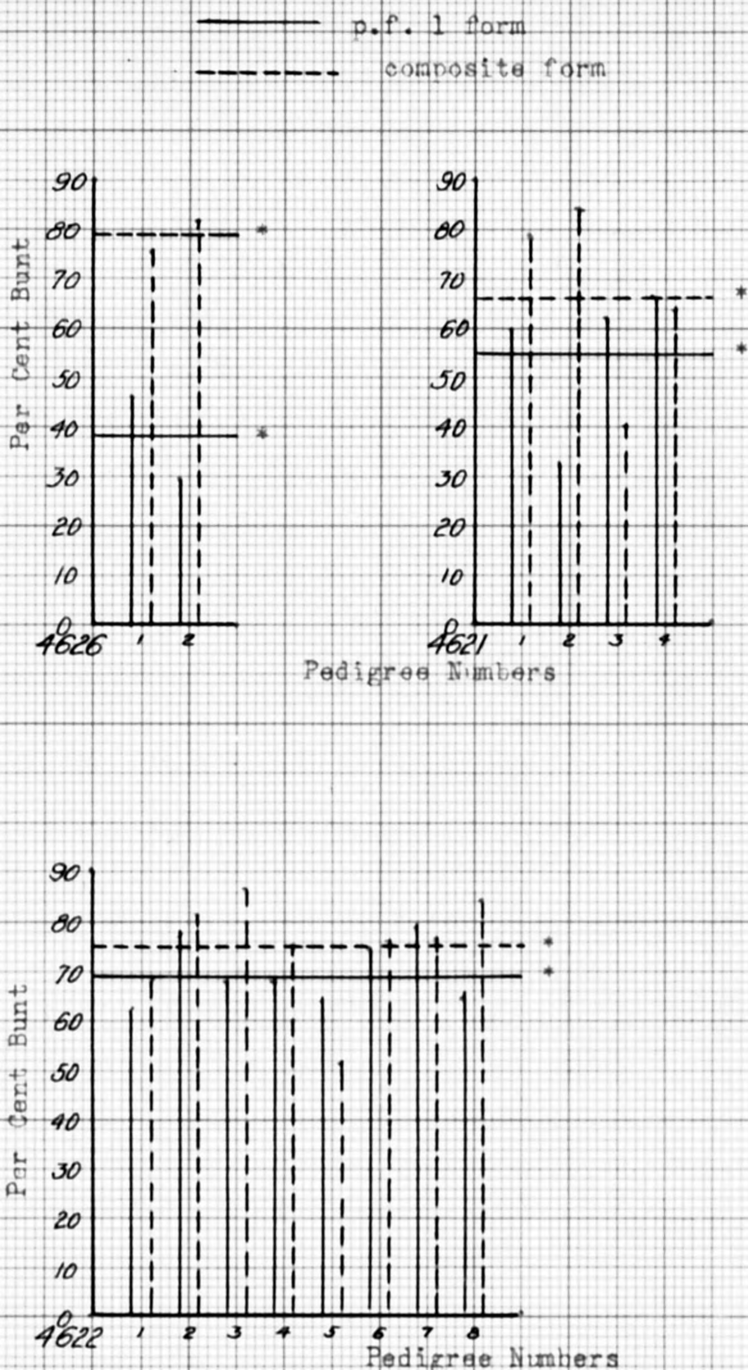

Fig. 15. Comparison of bunt percentages of susceptible F_4 lines from susceptible F_3 lines of Oro X Tenmarq, inoculated with p.f. 1 and a Kansas composite of bunt forms.

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* Average infection for each form of inoculum.

The relation of bunt infection of resistant F_4 lines from resistant F_3 lines, inoculated with p. f. 1 and with the composite is shown in Figures 10 and 11. The first group, representing F_3 row No. 4602, shows the lowest per cent bunt with p.f. 1 (0 per cent) while the per cent of infection is slightly higher when the composite is used (0.72 per cent). The composite bunt often produced slightly higher percentages of infection than p.f. 1.

Bunt percentages of F_4 lines from heterozygous F_3 lines inoculated with p.f. 1 and with the composite of Kansas bunt collections are shown in Figures 12, 13, and 14. The average per cent infection for p.f. 1 is represented in each family with a solid line and the average for the composite bunt with a dotted line. In most of these lines there is a high correlation between the infection percentage of p.f. 1 and the composite.

The relation of bunt infection, using p.f. 1 and the composite, in susceptible F_4 lines from susceptible F_3 lines is shown in Figure 15. One F_3 line, Row No. 4626, which is represented by only two rows, shows a rather wide difference in the average per cent infection, that for p.f. 1 being much lower than the average infection for a composite of bunt forms.

These figures indicate a very high correlation between percentages of bunt secured as a result of inoculating the F_4 lines of Oro X Tenmarq with the two types of inoculum, p.f. 1 and the Kansas composite. The correlation surface and coefficient for the two sets of data are shown in Table 4. In the greater number of lines infection percentages are low for both p.f. 1 and the composite bunt. Deviations are usually in the direction of lower percentages of infection for p.f. 1 and higher for the composite of Kansas bunt.

It is of interest to note that 30 F_4 lines show zero bunt infection to both p.f. 1 and the composite. An additional 49 rows come within the interval 0 to 5 per cent bunt for both sources of inoculum.

Table 4.--Correlation of percentages of bunt infection in F_4 lines of Oro X Tenmarq, inoculated with physiologic form 1 and with a composite of Kansas bunt forms.

	Per cent bunt																
	Physiologic form 1																
Composite forms	0-4.9	5-9.9	10-14.9	15-19.9	20-24.9	25-29.9	30-34.9	35-39.9	40-44.9	45-49.9	50-54.9	55-59.9	60-64.9	65-69.9	70-74.9	75-79.9	
Per cent bunt																	
95-100																	
90-94.9									1								1
85-89.9												1		1			2
80-84.9						1	1		1				1			1	5
75-79.9										2		1		2		1	6
70-74.9									1	2		1		1	1		6
65-69.9					1			1			1		2				5
60-64.9					1					1		1		1			4
55-59.9							1		1			1		1			4
50-54.9						1				1		1	1				4
45-49.9										1	1						2
40-44.9						1							2				3
35-39.9		1							1								2
30-34.9				1	2	1	1										5
25-29.9	1			2	2	1											6
20-24.9		1	2	2	3			1									9
15-19.9		2	2	3	5		1	1									14
10-14.9	2	4	1	3	4		1	1									16
5-9.9	2		2	2													6
0-4.9	79	3	1														83
	84	11	8	13	18	5	5	4	5	7	2	6	6	6	1	2	183

Correlation coefficient r = 0.8875 ± 0.0106.

Natural Infection of Leaf Rust

A natural infection of leaf rust occurred on the F_4 hybrids of Oro X Tenmarq grown in 1932. Leaf rust notes were taken on plants in a foot length of each row in the composite bunt series left standing in the field for this purpose.

The Oro parent is highly susceptible to leaf rust infection, while Tenmarq is only moderately susceptible. The F_4 lines of Oro X Tenmarq show a wide range of infection with evidence of transgressive segregation. A number of the F_4 lines show very high resistance to leaf rust. The data on leaf rust infection are summarized in Table 5.

A study was made of the relation of percentage of leaf rust and bunt infection among the F_4 lines of Oro X Tenmarq. These data are shown graphically in Figure 16. It is evident that in this material there is no correlation between reaction to leaf rust and bunt. The F_4 lines in Figure 16 are arranged in order from the highest bunt infection to the lowest, while the leaf rust percentages are simply recorded and allowed to fall where they will in the graph.

Table 5.--Leaf rust infection of parents and F_4 lines of Oro X Tenmarq, into 5 per cent classes.

Per cent rust	Oro	Tenmarq *	F_4 hybrid
5-9.9			16
10-14.9			47
15-19.9			6
20-24.9			20
25-29.9		1	6
30-34.9			
35-39.9			
40-44.9		3	2
45-49.9		3	2
50-54.9			
55-59.9			
60-64.9			
65-69.9	1		9
70-74.9			
75-79.9			
80-84.9	6	2	13
85-89.9	3		28
Ave. per cent rust	80	48.9	37.2
Total No. rows	10	9	139 **

* 1 row showed segregation for leaf rust.

** Rows which were segregating for resistance to leaf rust infection are not included.

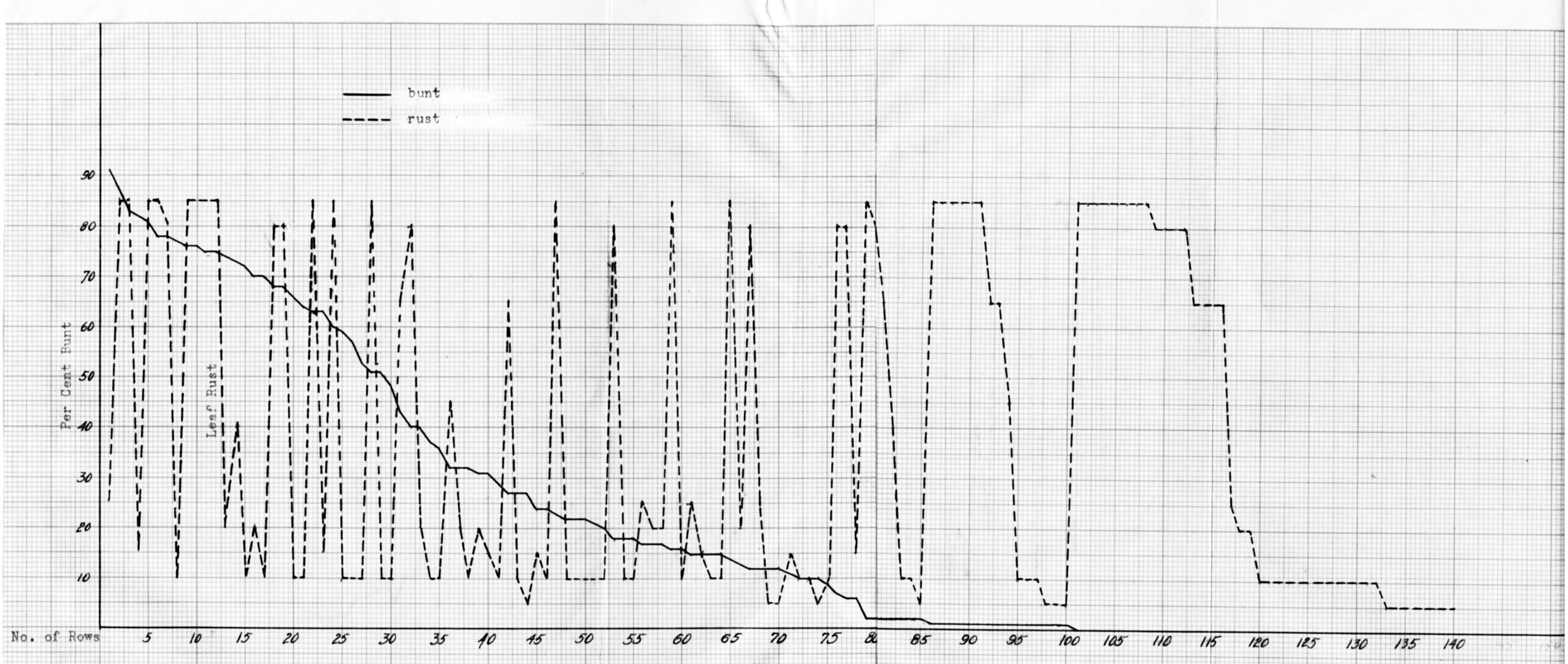

Fig. 16. Relation of bunt and leaf rust percentages in F_4 lines of Oro X Tenmarq, 1932

In some F_4 lines the percentages of both leaf rust and bunt are high, while other lines are resistant to both diseases. Some lines are resistant to leaf rust and susceptible to bunt, others show a reciprocal reaction. Selections from F_4 rows resistant to leaf rust and bunt are of particular interest and value.

The correlation coefficient of rust and bunt percentages in these F_4 lines has no significance, $r = 0.0151 \pm 0.5760$.

Winter Hardiness

The winter of 1931-1932 was so mild that there was no observable winter injury to either parents or hybrids.

Earliness

The average heading date for the Oro parent grown as check rows in 1932 is May 22+, while the average heading date for the Tenmarq parents is May 18. These results are shown in Table 6, together with the heading dates for the hybrids.

Table 6.--Distribution of heading dates for Oro and Tenmarq and their hybrids grown at Manhattan, Kansas, 1932.

	May											Ave. heading date	Total number of rows
	15	16	17	18	19	20	21	22	23	24	25		
Parents													
Oro								9	2	2		22+	13
Tenmarq		1		6	4	3						18	14
Hybrids F_2		1			1							17+	2
F_3				1		1	4	4	7			22	17
F_4	1	4	7	13	6	42	48	23	31	5	1	20.7	181 (a)

(a) Heading dates were not taken on 2 rows which were very late.

The F_2 populations were recorded as fully headed, May 16-19, in about the same period as Tenmarq, and earlier than Oro.

Most of the F_3 lines headed in about the same period as Oro and later than Tenmarq. Six F_3 rows are earlier than Oro.

The heading dates for the F_4 lines range from a day earlier than Tenmarq to a day later than Oro. The average heading date for the F_4 population (May 20.7) is about a day earlier than the average heading date for Oro (May 22+) but nearly three days later than the average for Tenmarq (May 18). A large number of F_4 lines are earlier than Oro and provide the possibility of producing a bunt resistant variety as early as Tenmarq.

Relations of Several Characters

Notes were taken on individual rows if they showed any special promise or were distinctly inferior to the average of the rows. The relations of these field notes to weight of grain per head, kernel plumpness, earliness, bunt, and rust reaction are shown in Table 7.

Naturally more plant selections were made from desirable than from undesirable rows. Thus the means for various characters listed in Table 7 are not strictly comparable. Probable errors of the means and probable errors of the differences give some idea of the statistical reliability of the results.

Weight of grain per head in the desirable types is higher than in the late or weak types, but the difference is small and is not statistically significant. Kernels of plants in desirable type rows are plumper than kernels of plants in undesirable type rows and the difference is statistically significant. Experience has shown that under the conditions at Manhattan kernel plumpness is a very useful index of adaptation in winter wheat. Desirable types headed about 2 days earlier than undesirable types. The mean difference is not statistically significant but a difference of 2-3 days in heading dates of two selections is believed to be of some

Table 7.--Relation of the field appearance of rows in an F_4 population of Oro X Tenmarq to grain yield, kernel plumpness and disease reaction.

Characters of F_4 hybrids	Desirable types: Number of rows	Desirable types	Late or weak types: Number of rows	Late or weak types	Difference of means and P.E.d	Dev. / P.E.
Grain yield (gm. per head)	26	0.90 ± 0.0015	4	0.86 ± 0.0684	0.10 ± 0.0684	1.46
Kernel plumpness (per cent)	26	83.5 ± 0.508	4	78.8 ± 1.07	4.7 ± 1.18	3.88
Earliness (May)	40	19.97 ± 1.78	9	21.88 ± 1.51	1.91 ± 2.33	0.82
Bunt Reaction (p.f. 1	39	7.3 ± 1.16	10	6.4 ± 2.99	0.9 ± 3.20	0.03
(per cent) (composite	39	8.3 ± 1.20	10	11.5 ± 4.95	3.2 ± 5.09	0.63
Leaf Rust Reaction (per cent)	29	33.1 ± 3.99	8	64.4 ± 6.62	31.3 ± 8.33	3.75

practical importance. The earlier types are usually superior to the later ones. Differences in bunt percentages of desirable and undesirable types are not significant. The average leaf rust infection of desirable lines is only about half that of the late or weak types. The means are 33 and 64 per cent and the difference is statistically significant and important.

The relations of the percentage of plumpness to grain yield, bunt infection to earliness, and leaf rust infection to earliness, grain yield, and kernel plumpness are shown in Tables 8 to 12, inclusive. A study of these tables shows that there are no cases of high correlation between any pair of these characters. For example, in the case of bunt reaction in relation to date of heading shown in Table 9, rows which headed early had both high and low bunt infection, as did also rows which headed at a later date. When two variables are highly correlated, they tend to lie on a diagonal straight line on the scatter diagram, which is not the case in any of these tables.

The lack of correlation between grain yield and kernel plumpness shown in Table 8 is probably due to the fact that plant selection for desirable types has been practiced and these data do not represent a random population.

Pages 66–70 were reserved for plates and they were inserted elsewhere

Scatter diagrams were not made for bunt in relation to grain yield or kernel plumpness as such notes were taken only on individual plants selected from lines resistant to bunt. Fifteen of the 27 very susceptible lines with 85 per cent leaf rust headed May 23-24, while a majority of the rust resistant lines headed May 20-21. All of the lines with the lowest grain yield were very susceptible to leaf rust.

Table 8.--Relation of kernel plumpness to yield in F_4 lines of Oro X Tenmarq.

Grain yield (gm. per head)	Kernel plumpness, %														
	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
1.10-1.15											2				
1.05-1.099											2	1			1
1.0-1.049	1						1		1	2	1	2		1	1
0.95-0.999											1	2		1	
0.90-0.949				1				1	1	3	5	4	5	1	
0.85-0.899							1				5	3	2		
0.80-0.849					1	1				1		2		2	
0.75-0.799							1			3		2	1	1	
0.70-0.749											1	2	1		
0.65-0.699								1			1	1			
0.60-0.649															
0.55-0.599										1				1	
0.50-0.549										1					
0.45-0.499	1														

Table 9.--Relation of percentages of bunt infection to earliness in F_4 lines of Oro X Tenmarq.

Date of heading	Per cent bunt																		
May	0-4.9	5-9.9	10-14.9	15-19.9	20-24.9	25-29.9	30-34.9	35-39.9	40-44.9	45-49.9	50-54.9	55-59.9	60-64.9	65-69.9	70-74.9	75-79.9	80-84.9	85-89.9	90-95
25			1																
24	5																		
23	15		2	2	2	1					2			1	1	2	2	1	
22	7		4	3	2				1		1	1	1		2	1	1		
21	23		3	3	3		2	1	1			2	2	3		2	2	1	
20	23	3	1	3	1	2		1	1	2		1	1		1	1			1
19	4	1	1																
18	3	1	2	1		3	2								1				
17			2	1			1				1			1	1				
16	1	1		1	1														
15	1																		

Table 10.--Relation of percentages of leaf rust infection to earliness in F_4 lines of Oro X Tenmarq.

Date of heading	Per cent leaf rust																
May	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85
25			1														
24	1	2														1	1
23	4	6	2						1							1	14
22	1	8		2	1												4
21	5	17	2	3	2			1					1			1	5
20	3	12		1	3								4			6	1
19				1												1	2
18	3			1				1	1				2			1	
17				2												2	
16		1	1										1				
15													1				

Table 11.--Relation of leaf rust infection to yield in F_4 lines of Oro X Tenmarq.

Grain yield (Gm. per head)	Per cent leaf rust																
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85
1.10-1.15		2			1												
1.05-1.099	1	2															
1.0-1.049	4	2		1													
0.95-0.999	1	1											1			1	
0.90-0.949	4	7		1									3				2
0.85-0.899		3														1	
0.80-0.849	2	1											2			1	1
0.75-0.799		1			1				1								1
0.70-0.749		1															
0.65-0.699																	1
0.60-0.649																	
0.55-0.599																	2
0.50-0.549																	1
0.45-0.499																	

Table 12.--Relation of percentages of leaf rust infection to kernel plumpness in F_4 lines of Oro X Tenmarq.

Kernel plump-ness, %	Per cent leaf rust 5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85
86	1												4				1
85		3			1								2				1
84	5	5														2	1
83	1	9			1												1
82	4	2							1								3
81																	
80	1																
79				1													
78																	1
77																1	
76				1													
75																	
74																	
73		1															1

DISCUSSION

These studies suggest the presence of several factors in the inheritance of resistance to bunt in the cross, Oro X Tenmarq. The number of zero and near zero bunt lines observed in F_3 and F_4 progenies indicates that high susceptibility to bunt is recessive in this cross. Although Tenmarq is susceptible to bunt, it may carry one or several factors for resistance which differ from the factors for resistance in Oro, the resistant parent. The breeding behavior of apparently immune, highly resistant, and susceptible lines in 1933 will throw some further light on the question.

The number of F_3 lines was far too small to permit a genetic analysis of resistance to bunt in this cross. The behavior of the F_4 lines has therefore been used to determine as nearly as possible the mode of inheritance of bunt resistance. The results suggest that in this cross a number of factors are operative in governing reaction to bunt. There is evidence of transgressive segregation. The large number of zero lines suggests that Tenmarq carries a factor or factors for resistance, which when combined with factors for resistance from Oro, produce greater resistance in some of the hybrids than expressed by the resistant Oro parent.

The larger number of F_3 and F_4 lines are grouped near the average bunt percentage of the resistant Oro parent, which suggests that in this cross resistance to bunt is partially dominant and that high susceptibility is recessive.

On the basis of F_4 tests, the F_3 lines may be grouped into an 8:12:3 ratio, representing homozygous resistant, heterozygous, and homozygous susceptible families, respectively. This grouping roughly approximates a 1:2:1 ratio. However, the number of F_3 lines represented is too small to show definitely that such a ratio should be used in interpreting the results.

Previous selection on the basis of plant and kernel characters has been practiced. This may have affected the bunt reaction observed in F_4, although as far as known, the selection was random for bunt resistance. Any association between reaction to bunt and other characters would tend to cause considerable deviation. No association between the resistance to bunt and other characters has been observed.

The high correlation between reaction to physiologic form 1 and a Kansas composite of bunt forms suggests that possibly there is only one form of bunt in Kansas so far as indicated in the cross, Oro X Tenmarq. However, several rows show considerably greater susceptibility to the composite bunt, and any deviation is usually in the direction of higher bunt infection in the composite series. Physiologic form 1 was represented to a much greater extent than any other form in this composite inoculum, and this form probably caused a large part of the infection. It is possible that only occasionally a row was infected with another form, present in smaller quantity, but more virulent than p.f. 1.

Oro is very susceptible to leaf rust; Tenmarq is only moderately susceptible. Transgressive segregation for resistance to leaf rust indicates that both parents carry factors for resistance to this disease. The plants of both parents were rather uniformly and characteristically infected. Hence it seems evident that the rows with low leaf rust infection are really resistant and did not merely escape infection. Certain groups of F_4 lines from particular F_3 lines were uniformly resistant to leaf rust, others were susceptible. The inheritance of leaf rust resistance in the cross, Oro X Tenmarq, can probably best be explained on a multiple factor basis.

Since no association between agronomic characters and bunt resistance has been observed in this cross, it should be possible to select a strain in which several if not all important desirable characters are present. Thus F_5 lines of Oro X Tenmarq are now on hand which are resistant to leaf rust, that are as early as Tenmarq and which have the desirable plant characters of this high yielding variety, combined with the bunt resistance of Oro.

Because of the mild winter of 1931-1932, no information is available on the winter hardiness of the hybrids, but it should be possible to select segregates as hardy as Oro.

SUMMARY

A study of resistance to bunt, Tilletia levis, was made in F_2, F_3, and F_4 generations of Oro X Tenmarq hybrids. Other characters such as resistance to leaf rust, earliness, grain yield, and kernel plumpness were also studied.

The results indicate that high susceptibility to bunt is recessive in this cross.

F_4 lines were grown which showed greater resistance to bunt than the resistant Oro parent, indicating that the susceptible Tenmarq parent may carry a factor or factors for resistance to bunt.

There is evidence of multiple factors governing the inheritance of resistance to bunt in this cross.

There is a high correlation between the reaction of the hybrid selections to physiologic form 1 and the reaction of the same selections to a composite of Kansas bunt collections, $r = 0.8875 \pm 0.0106$.

Transgressive segregation was noted in a study of leaf rust reaction, indicating that factors for resistance to leaf rust are probably present in both parents.

No correlation was found between bunt and leaf rust infection, r = 0.0151 $\pm$ 0.5760. The independence of these 2 characters in this cross is shown clearly in Figure 16.

A large number of F_4 lines appear to be as early as Tenmarq.

No close association of bunt and leaf rust reaction to agronomic characters such as earliness, grain yield, or kernel plumpness was observed in this cross.

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