THE INHERITANCE OF RESISTANCE TO HESSIAN FLY IN A CROSS BETWEEN TENMARQ AND KAWVALE WHEAT

by

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INTRODUCTION

The resistance of plants to insect injury has been noted by entomologists for many years, but until comparatively recent years very few attempts have been made to use this quality to any extent in combating insect pests.

The purposes of this paper are: (1) to give a summary of the more important literature on insect resistance, with special reference to Hessian fly on wheat; (2) to give the results of a study which was made in order to learn more of the ways in which varieties of wheat that are resistant to Hessian fly may be developed, and the resistance quality transferred to other varieties.

The Hessian fly does not cause a heavy loss every year, but occurs in "outbreak numbers" at more or less irregular intervals. The average annual loss caused by this insect is estimated at ten per cent of the total winter wheat crop. Gossard and Houser (1906), Dean (1909), Howard (1931).

The damage in small areas often amounts to total destruction of the crop. This irregularity in the damaging results from the fly, and the fact that all control measures do not always conform to ordinary farm practices, causes the farmer to become lax in the use of any control method.

It can readily be seen that the production of wheat varieties immune or highly resistant to the fly, and at the same time desirable from an agronomic standpoint, would fill a distinct need in the wheat production industry. After purchasing seed of fly resisting wheat it would furnish protection without additional expense, thus eliminating or reducing the risk resulting from Hessian fly every year.

The specific object of this work is to develop, or add to the development of, a variety of wheat adapted to Kansas which will be equal or superior in agronomic characters to any now grown, and in addition will have a high degree of resistance to Hessian fly.

It is also hoped that the knowledge of the mode of inheritance gained will be of value, both from a scientific viewpoint and for use in economic plant breeding.

HISTORICAL REVIEW

General Discussion of Resistance

Some of the early writers noted that many insects show an apparent preference for certain strains of their host plants. Lindley (1831) mentions that the variety of apples "Winter Majestic" was almost free from the attack of woolly apple aphis.

Since the time of Lindley many entomologists have mentioned this phenomena in their writings and some have taken advantage of it in controlling insect pests. It would take too much space to review or even list all the papers that contain notes on the quality of resistance which certain members of a host group have toward insects. A bibliography of about five hundred entries on this subject has been compiled and no doubt many others could be added. In this thesis only the more important papers and a few of interest because of some special phase of the subject to which they pertain are cited.

Several papers should be mentioned here because they have added much to our knowledge of the principles involved in insect resistance. Walsh (1864) (1865) and Hopkins (1916) published papers calling attention to the fact some species of insects include groups of individuals having different food preferences. They thought such groups were incipient species, having acquired a hereditary preference for certain food plants--and that such groups are destined to diverge more widely in the course of time. Brues (1920) writes as follows: "It is very difficult to accept such evidence, as given by Walsh and Hopkins, at least as having any general application without very clear and incontrovertible proof... We can more easily believe that such species may have arisen through mutations in maternal instinct not incompatible with larval taste and then only in extremely rare cases and confined to certain groups."

Craighead (1922) reports on an extensive experiment with Cerambycid beetles and interprets his results to support the contentions of Walsh and Hopkins. However, his data can be, and possibly should be, interpreted to support conclusions reached by Brues. Larson (1927) asserts that "The Host Selection Principle as outlined by Hopkins (1916) does not appear to hold with the bean weevil."

Some of the recent text books on applied entomology discuss the occurrence and application of host resistance. The text books by Wardle and Buckle (1923), Wardle (1929), Imms (1931), and Graham (1929) have chapters on host resistance. Graham (1929) gives a good summary of the principles involved.

The books mentioned above give good reviews of the literature on resistance and have bibliographies of the more important writings. Others who have written good reviews and discussions are McColloch (1924), Lee (1926), and Parker and Painter (1932).

Wardle (1929) asserts that: "In the complex of environmental factors which oppose the unrestricted multiplication of an insect species, one of the most influential, and one of the least understood, is the resistance offered by potential animal and plant hosts to insect attack." This resistance may be of a general nature or it may be directed against only one insect species.

Forbes (1905) (1909) states that "through our cropping and plant breeding methods we have prevented all spontaneous adaptations of the plant to the condition of its own maintenance." He suggests that we should improve our method of selection by considering the ability of plants to resist insect attack.

McColloch (1924) states that the resistance of plants to insect enemies is a natural phenomenon, while susceptibility results from some change in the plant. Plants have been modified to no small extent in relation to insects, as is evident from their protective devices against unwelcome insects, and in the brilliant flowers which attract insects for aid in pollination.

Causes of Resistance

Very little conclusive evidence has been found on the causes why certain individuals of the insect host-group are resistant and others of the same taxonomic group are susceptible. More than 100 papers consulted contain some reference to the cause or possible cause for this difference in infestation. It is apparent that each plant has a different way of fighting its insect enemies and also a different way for each insect.

Habit of Growth. Roberts, Slingerland, and Stone (1901) stated that vigorous growing varieties of wheat are more resistant than slow growing varieties. Forbes (1905) in discussing the host of insect pests of the corn plant states that there is little in the structure or life history of this plant to suggest any special adaptation to its insect visitors, or any special apparatus of defense against those especially liable to injure it. With the exception of the ear the whole plant lies open and free to insect depredation, and it is able to maintain itself in the midst of its entomological dependents only by virture of its unusual power of vigorous, rapid, and superabundant growth.

Cook (1906) found that the cotton varieties possessing the greatest resistance to boll weevils are small, rapid growing, early maturing types.

Schneider-Orelli (1917) in referring to _Xyleborous dispar_ on apple and plumb, states that, "It has been erroneously assumed that very vigorous trees are chiefly attacked, but examination of the few borers in such trees shows that the work has been stopped by the flow of sap and that in cases where the oviposition has been affected the eggs rot."

Becker (1918) correlated susceptibility to the attack of woolly aphis with backwardness of growth in certain species of elm and apple.

Meyer (1924) found that the varieties of oats that develop rapidly are most resistant to frit fly.

Massie (1924) in listing the possible causes of resistance in some apples to the green apple aphis, states that vigorous individuals of a particular variety did show more susceptibility than the weaker neighbors.

Kleine (1925) asserts that the varying susceptibility of oat varieties to frit fly may arise from varying ability to obtain soil nutriment; a susceptible variety in heavy soil is not greatly affected by the fly, but in light soil it is severly affected merely because the insufficient nutriment in the latter environment delays the growth of the plant and allows time for the attack to occur.

The relation between internal condition of the plant and its endurance of insect damages has been ably discussed by Lee (1926). He states that any external condition which affects the growth of the plant indirectly affects its susceptibility to insects.

Felt and Bromley (1931) in discussing resistance or tolerance to insect attack assert that "feeding to promote a vigorous growth may be valuable preventive measures in the case of certain insects at least."

Physiological Characters of the Plant. A study of the physiological factors which influence resistance involves complex chemical substances found in the plant, such as oils, acids, resins, sugars, enzymes, and many others. In many cases these studies present problems which will have to be solved by the chemists and entomologists working together. Up to the present the field is practically untouched. Many entomologists have found evidence which causes them to believe certain physiological characters cause resistance, or at least, they are closely associated with resistance.

Petri (1911) asserts that "acidity of cell sap plays an important role with regard to infestation of vines by Phylloxera."

Comes (1917) writing of prophylaxis in vegetable pathology, states that resistance increases with the organic acids and that as the quantity of sugar, so much sought by insects, increases in vegetable tissues there is a corresponding decrease in the organic acids. Of the acids, he considers maltic acid as the most toxic.

Andrews (1921) found that an increase in the ratio of potash to phosphoric acid in the leaves of the tea plant increases the resistance to attack by <u>Helopeltis</u>.

Collins and Kempton (1917) found that plants avoided by corn ear worm moths are the ones that are distasteful to the larvae. They believe that this is possibly due to a chemical difference in the corn plant.

Davidson (1922) studied the biology of the bean aphis on different varieties of broad beans. His observations show that the insect exhibits a wide range of fecundity on different hosts. These differences are probably due to differences in the constitution and nutritive values of the cell-sap in the respective varieties. He suggests that the hydrogen-ion concentration of the sap of plants may be of importance in the relative resistance of plants to aphid attack.

McColloch and Salmon (1923) state that resistance of wheat to Hessian fly is possibly due to physiological causes and silica is in some way connected with it.

Monzen (1925) found resistance of apple trees to woolly aphis due to a specific repellent ingredient or a greater hydrogen-ion concentration. Trees with a pH value of 4.5 to 5 are susceptible and trees with pH value of 4.4 or less are resistant.

Whithcomb (1926) asserts that acidity of sugar cane has little to do with resistance to froghopper; extreme drouth or dampness decreases resistance; carbohydrates in wilting leaves are less abundant, more water soluble, and easily available to insects, than are those of normal leaves. He believes that the tannin content of leaves may have some effect upon the preference of the froghopper.

Fullaway (1926) writing of termites in Hawaii states that there seems to be little doubt but that the hardwoods were attacked as freely as the softwoods, and the examination suggests that it was chemical rather than physical factors which made certain woods resistant.

Carter (1927) found that beet leafhoppers avoid extremely high sap concentration in beets.

Maze (1927) emphasizes physiological vigor as a factor in insect resistance.

In his paper on curly-top disease of the sugar beet Mumford (1930) concludes that beets become less infected as they grow older. Physico-chemical measurements of the sap show the refracture index was greater in the resistant strains, it tended to increase with the development of the disease. The freezing point depression was greater in the susceptible strain than in the resistant strain and tended to increase with the disease. In general the results suggest that the sap from the resistant beets is less concentrated in total solids and non-electrolytes, and more concentrated in electrolytes than that from the susceptible. The figures point to a slight but general tendency towards greater acidity in leaves of the resistant as compared with the susceptible. The nitrogen content of the sap from the susceptible is greater than that from the resistant.

Painter (1930) after making observations on the biology of the Hessian fly found a decrease in the survival of eggs on leaves from the inner to the outer; this is paralleled by an increase in deposition of cellulose.

Person (1931) in his theory in explanation of the selection of certain trees by the western pine beetle expresses his belief that the initial attraction of beetles to a tree is due to the formation and escape of volatile aldehydes or esters which are a by-product of a respiratory fermentation resulting from abnormal enzyme activity in subnormal trees. The causes of this structural condition include drought and injuries of various kinds. In only slightly subnormal trees this attraction is probably only detected by beetles in the immediate vicinity, but after a few attacks are made, a second stronger attraction is started.

Cleare (1932) in a study of moth-borer damage in relation to sugar can varieties in British Guiana found that the degree of resistance varies markedly. It appears that the extent of damage is closely related to the percentage of sucrose in the canes. Canes having a high percentage of sucrose are damaged most.

Packard (1928) observed that fully as many Hessian fly larvae reached their normal feeding position in the resistant wheat as in the susceptible varieties. A very small proportion of the larvae in the resistant wheats made any appreciable growth; substantiating the evidence that resistant varieties possess some histological or biological peculiarity detrimental to the development of the larvae.

Morphological Characters of the Plant. The relation of morphological characters of the plant to resistance is emphasized in the writings of many entomologists. The following reports specify thickness of integument as important factors: Gernert (1917), Sharples (1918), Mason (1922), Davidson (1923), Mumford (1931), Shull and Wakeland (1931).

The prolongation of the shuck, its tightness and thickness, and the absence of husk leaves are considered by Collins and Kempton (1917), Kyle (1918), Phillips and Barber (1931), as protective factors against the ear worm and grain weevils. Freeborn and Wymore (1929) assert that length of shuck is not a factor in resisting these insects.

Hewitt (1913) reports on a variety of apples "Newton Pippin." The fruit of these apples was infested with woolly apple aphis which had entered through a small channel connecting the eye with the core. This opening does not occur in all apples.

Picard (1913) asserts that the potato moth deposits only on rough surfaces, therefore, the Flax variety is immune. Parnell (1925) reports that hairiness makes cotton resist Jassids.

<u>Ability of the Plant to Recover from Injury</u>. Some plants are able to maintain an apparent resistance to insects by their ability to withstand the insects or recover from their injury.

Flint (1921) and Flint and Hackleman (1923) assert that chinch bugs attack all varieties of corn the same, but varieties differ in their ability to withstand the damage.

Harper-Gray (1923) tested twenty-seven varieties of oats for resistance to frit fly. Emphasis was placed on the ability of varieties to recover from initial attack of the fly. Cunliffe (1929), in studies on the same insect, divides resistance into "direct resistance," in that the shoot can resist larval entry directly or bring about death before damage is done, and "indirect resistance" where biological factors, stooling, rapid growth and recovery power make the plant able to produce a good yield in spite of the fly.

Painter, Salmon, and Parker (1931) describe Blackhull wheat as a tolerant variety which is also semi-resistant to Hessian fly.

Different Degrees of Resistance in Different Localities

Different degrees of resistance for the same variety of host plant have been noted by several writers.

Borner (1927) found that the same variety of vine was attacked to varying degrees in different localities of Europe. Others who have noted a variance in infestation by particular insects on a particular host variety grown in different localities are: Lee (1926), Misra (1920), Monzen (1925) (1926), Muller (1927), Painter, Salmon, and Parker (1931), Roberts, Slingerland, and Stone (1901), Pictet

(1905), Roubaud (1920) (1921), Staniland (1924), Thiele (1902).

The fact that a host variety may be infested to a varying degree in different localities, considering that a uniform infestation is possible in each locality, may be explained in two ways:

1. Ecological conditions are different in different localities. As has been stated under the heading "Causes of Resistance," the rate of plant growth and the chemical concentration of cell sap are important factors of insect resistance. It is well known that temperature, humidity, and soil-composition affect both of these factors and are likely to differ for each locality. 2. Different biological strains of the insect may occur in each locality. A thorough discussion of biological races in insects and allied groups was presented by Thorpe (1930). He discussed most of the important papers that have been published on this subject and gave a bibliography of 142 references. It has been shown by Painter (1930) and by Painter, Salmon, and Parker (1931) that the populations of Hessian fly in any locality are mixed genetically and differ in their ability to infest wheat. They suggest, with respect to the use of resistant varieties, two courses are open, one to develop resistant varieties which may be used alternately for periods of years in a given region. The other to synthesize

the resistant quality of several wheat varieties through hybridization and selection.

Series of Varieties Tested for Insect Resistance

It is evident, that many entomologists are aware of the necessity to have a better knowledge of the degree of resistance in the various varieties of crops, by the number who have made comparative varietal tests.

Some of the ones who have tested wheat in relation to Hessian fly are: Harmon (1844) tested several varieties. Woodworth (1891) tested 125 varieties. Keller (1892) made infestation notes on a large number of varieties as "none", "badly", etc. Roberts, Slingerland, and Stone (1901) gave results on six varieties. Gossard and Houser (1906) studied 76 varieties. McColloch and Salmon (1918) tested about 87 varieties. Stahl (1921) tested several varieties. McColloch (1923) reported a test of 200 varieties of small grain, mostly wheat. Painter, Salmon, and Parker (1931) gave an extensive report on 400 varieties, selections and hybrids of wheat. Packard (1928) tested all varieties of wheat thought to be suitable for commercial production in the fly infested districts of California.

Plants Bred for Insect Resistance

Advantage has been taken of the fact that insect resistance is a heritable quality and plants have been bred and selected for resistance. One of the earliest records where use was made of crossing of resistant and non-resistant varieties was made by Harland (1916). He found that resistant cotton could be propagated by budding and that resistant cotton remained resistant when budded on a susceptible scion. In the case of hybrids the F_1 of the cross "immune" by "susceptible" is almost immune when Sea Island cotton is the susceptible parent, but when Upland cotton is used as the susceptible parent, the F_1 is also susceptible. The F_1 of the cross, "susceptible" by "susceptible" is susceptible, as is also the case when "susceptible" is crossed with "fairly resistant."

Harland (1919) from experiments with leaf blister mites in cotton reported on the F_1, F_2, and F_3 generations of a cross between the immune type, St. Vincent Native, and the susceptible type, Southern Cross Upland. The F_1 was intermediate, though inclinging toward the susceptible parent. In F_2 segregation occurred into immune and non-immune. In F_3 the immune bred true, while the non-immune segregated into immune and non-immune.

Gernert (1917) observed that when Teosinti, which is resistant to corn-root aphis and corn leaf aphis is crossed with yellow dent corn, which is susceptible, the F_1 hybrids are resistant.

McColloch (1924) states that 50 strains of a resistant variety of Illini Chief were studied for six years, two of them were always susceptible under varying conditions, the other 48 remained resistant. This illustrates that selection can be used within an agronomic variety. Forbes (1909) suggests this line of work, when he states that selection can be improved by giving preference, in saving seed, to those plants which have best withstood unfavorable conditions, instead of making our choice, as we now invariably do when we choose at all, from among the plants which have succeeded best where all conditions have been favorable. He suggested that the selection of seed corn from the few best stalks of a field which has been over-run with insects might gradually develop varieties capable of withstanding insect attack.

Webster (1924) asserts that resistance to microbes in white mice can be increased by selective breeding.

Marston (1929), (1930), (1931), (1933) in a series of papers on breeding corn to resist the European corn borer reports the results of crossing Maize Amargo, a borer resisting variety with common Michigan field corn. He was able to select F_2 hybrids carrying the resistant quality of Maize Amargo coupled with the grain producing qualities of the common varieties of dent corn. He concluded that the evident resistance of Maize Amargo to corn borer attack is a recessive character to the characteristics of standard Michigan varieties which make them susceptible. Barnes (1931) suggested the use of hybridization in producing desirable basket willows resistant to button gall insects.

Painter, Salmon, and Parker (1931) present evidence which shows that factors for resistance are inherited and that Hessian fly resistance may be combined with other desirable characters. They also presented evidence which indicates that varieties may be pure or homozygous so far as agronomic characters are concerned and impure or heterozygous for fly resistance factors. Their papers indicate the feasibility of developing through modern plant breeding methods, strains which combine desirable agronomic qualities with resistance.

Packard (1928) published results from selecting Baart wheat for Hessian fly resistance and concluded that fly injury can be reduced materially by the process of selection.

Resistance is Inherited

That resistance to insects is a heritable character has been well established in the literature by many writers.

Schroder (1903) (1907) asserts that plants acquire resistance and this resistance is transmitted to the next generation. Becker (1918) in studying the elm woolly-aphis found resistance apparently inherited in some cases and not in others. Butler (1918) asserts that resistance is the outcome of heriditary composition. It was believed by Davidson (1922) that resistance was present in the wild state of the plants and was largely determined by genetic factors. Parnell (1925) asserts that resistance can be combined with other good plant qualities and may be increased by selection. Le Pelley (1927) made crosses of apple varieties and found the factors for immunity inherited according to the Mendelian laws. The variety Northern Spy was heterozygous for immunity. Lambert and Knox (1928) assert that resistance to foul typhoid in chickens depends upon multiple genetic factors. Parker (1931) states that resistance to Hessian fly in wheat and to chinch bugs in sorghum are heritable characters. Roubaud (1930) reported that ordinary corn plants develop three times as many corn borer larvae as those from infested parents. Painter, Salmon, and Parker (1931) in their report on resistance of varieties of winter wheat to Hessian fly assert that resistance is inherited independantly of most varietal characters.

Resistance to Hessian Fly

Written accounts of Hessian fly according to Fitch (1856) date back as early as 1732, but very little was written on this insect until after its introduction into America about 1776. Since 1776 numerous papers have been written, Osborn (1898) gives a bibliography of 141 references including most of the important papers written up to that time. More recent literature has been cited by McColloch (1923) and Painter, Salmon, and Parker (1931).

Wheat is the principal food plant of the Hessian fly, although it is able to develop on a number of other plants of the grass family. McColloch and Salmon (1918), McColloch (1923), and Noble (1931) have conducted experiments showing that the fly may develop on other cereals and grasses.

There are many varieties or strains of wheat, and it has been known for a long time that certain varieties are less susceptible to Hessian fly injury than others. Packard (1883) states that for nearly a century the "fly-proof" variety Underhill has been highly recommended. Gaylord (1843) reports that varieties like Mediterranean with thick, hard stems suffer the least damage. Harmon (1844) mentions Mediterranean and White Flint as resistant varieties and Old Red Chaff, Indiana Wheat, Yorkshire and others as susceptible. The Spelter, China, and White Flint are mentioned by Fitch (1856) as fly-proof varieties. Devereaux (1878) noted that Clawson, Soule and similar wheats were susceptible to fly, while Lancaster and most of the red wheats were resistant to fly. Woodworth (1891) observed 125 varieties of wheat in California over a period of three years. The varieties Volo and Washington Glass remained free, and several others had only slight infestations. Kellner (1892) reported on the fly infestation of a large number of wheats under remarks such as "badly infested", "none", and "few." Roberts, Slingerland and Stone (1901) found that varieties vary in resistance. Those with large, coarse, strong straw are less injured than weak-strawed varieties. The six most resistant varieties for this season in New York were Dawson Golden Chaff, Prosperity, No. 8, Democrat, Red Russian, and White Chaff Mediterranean. In the same paper they quote two cases where Dawson Golden Chaff was seriously injured in Canada.

Gossard and Houser (1906) made observations on 76 varieties of wheat in Ohio for three seasons. They found some difference in the ability of different varieties to withstand any fly attack, but gave little support for the idea of resistant varieties.

Bruner and Swenk (1907) report Underhill, Clawson, Red Cap, and Turkish Amber as resistant varieties.

Headlee and Parker (1913), Haseman (1916), Haseman, Sullivan, and McLane (1921) report that varieties show some difference in their resistant quality but not enough to be of value.

Davis (1918) states that Illini Chief and Dawson Golden Chaff are resistant.

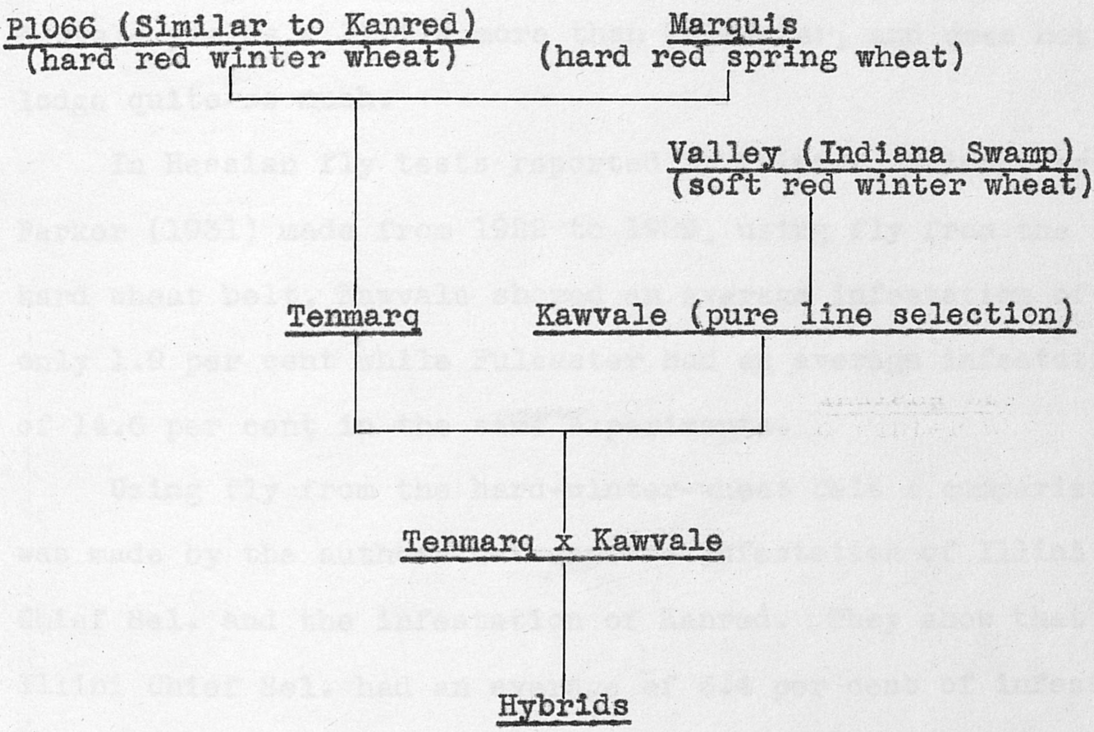
McColloch and Salmon (1918), (1923) concluded from tests on 87 varieties of wheat, oats, and rye, that Hessian fly is able to distinguish between different kinds and varieties of grain. McColloch (1923) has shown that while there is considerable variation in the number of eggs laid by Hessian fly on different varieties, this difference is not sufficient to explain this variation in amounts of damage suffered by the different varieties. He found Illini Chief and Dawson Golden Chaff to be the more resistant varieties of wheat.

Painter, Salmon, and Parker (1931) give data on the susceptibility of about 400 strains of what to fly from the hard-wheat belt. The varieties and several pedigree selections of varieties were divided into three groups: (1). Those which are highly resistant to fly, including such varieties as Kawvale, Illini Chief Sel., and Dawson Golden Chaff. (2). Those with medium infestation, including Blackhull, Superhard and Harvest Queen. (3). Very susceptible strains, for example, Tenmarq, Kanred, and Turkey. Fulhard, a hard wheat, and Kawvale, a semi-hard variety, as well as a number of soft wheats were found to be resistant to fly of the hard wheat area. They noted considerable progress in the production by selection and crossing of wheat varieties adapted to Kansas, which combine desirable agronomic characters and the quality of resistance to Hessian fly.

MATERIAL

Parent Varieties

The following pedigree chart shows the varieties from which the material for this study evolved.



Kawvale. The variety Kawvale was developed at the Kansas Agricultural Experiment Station from a selection made from Indiana Swamp by Dr. John H. Parker at Manhattan in 1918. The variety Indiana Swamp is usually known as Valley. Kawvale is a semi-hard, rather than a true hard wheat. Milling and baking tests made by Dr. C. O. Swanson in the Department of Milling Industry at Kansas State

College show that Kawvale wheat mills like a hard wheat, has good breadmaking qualities, and is not a typical soft red winter wheat. It is more winter hardy than Fulcaster and Currell, the varieties which it is now replacing in southeastern Kansas. Grain of Kawvale has a tendency to shatter from the heads if allowed to stand after it is ripe. Kawvale yields a little more than Fulcaster, and does not lodge quite so much.

In Hessian fly tests reported by Painter, Salmon, and Parker (1931) made from 1922 to 1929, using fly from the hard wheat belt, Kawvale showed an average infestation of only 1.9 per cent while Fulcaster had an average infestation of 14.6 per cent in the same experiments.

Using fly from the hard-winter-wheat belt a comparison was made by the authors between the infestation of Illini Chief Sel. and the infestation of Kanred. They show that Illini Chief Sel. had an average of 6.4 per cent of infested tillers, while Kanred had 40.5 per cent of infested tillers. By using fly from the soft-winter-wheat belt Illini Chief Sel. had an average of 53.4 per cent of infested tillers and Kanred had an average of 45.3 per cent of infested tillers. It is evident from these data that the Hessian fly from different wheat belts differ in its ability to infest the same wheat variety. They explain that these differences in degrees of infestation is due to the presence of at least two biological strains of Hessian fly, each of which vary in distribution and their ability to infest different wheats. A variety of wheat may be resistant to fly from one area and not to fly from another. Tests made with fly from both the hard and soft-winter-wheat belts of Kansas, indicate that Kawvale has a marked power to resist fly from each of these areas.

Mr. C. O. Johnston of U. S. D. A. cooperating with the Botany department of Kansas Agricultural Experiment Station, has made an extensive study of the resistance of Kawvale wheat to red leaf rust at stations in Texas, Kansas, Oklahoma, and Nebraska. He has found that over a period of years it is highly resistant to leaf rust under most conditions in the southwest.

Kawvale has high yielding capacity, resistance to red leaf rust, greater winterhardiness than some of the common soft wheats, resistance to Hessian fly, and good bread-making qualities. Its tendency to shatter badly in the field under dry, windy conditions is a serious defect in Central and Western Kansas, but is not an important limiting factor in Eastern Kansas.

Tenmarq. This variety is a selection from a cross between Marquis and P1066. The latter is a selection similar to Kanred, both Tenmarq and P1066 are from Crimean,

C. I. No. 1435. The cross was made by M. N. Levine under the direction of Dr. John H. Parker in 1917 at Manhattan. The selection named Tenmarq was made in 1921.

Tenmarq is bearded and has white glabrous glumes, long beaks on the outer glumes and short hard red kernels. It is a winter wheat, but the grain is sometimes graded as hard red spring or mixed because of the short kernels resembling the Marquis parent. It is characterized by a moderately stiff straw, moderate resistance to leaf rust, and high susceptibility to Hessian fly as shown by Painter, Salmon, and Parker (1931). Tenmarq is slightly more winterhardy than Blackhull, as shown in the uniform winterhardiness nurseries, but is less winterhardy than Turkey and Kanred. Tenmarq heads and ripens from one to three days earlier than Kanred. Rather extensive yield tests of Tenmarq was reported by Salmon and Laude (1932). At Manhattan Tenmarq was the highest yielding variety in plots for the period in which it was grown, producing an average of 5.2 bushels more than Kanred for a seven year period. It has produced the highest yields or almost the highest in many tests where it has been grown.

In Hessian fly tests made by Painter, Parker, and Salmon (1931), Tenmarq has ranked high in infestation in comparison with other varieties, averaging slightly higher than Kanred.

Milling and baking tests made by Dr. C. O. Swanson in the Department of Milling Industry, show that flour milled from Tenmarq wheat ranks about the same or slightly better in "strength" as flour of Turkey and Kanred and is much superior to Blackhull in certain respects.

Tenmarq has a high yielding capacity, is fairly resistant to leaf rust, is not as winterhardy as Turkey, Kharkov and Kanred but is equal to Blackhull in cold resistance. It is susceptible to Hessian fly, has excellent milling and baking qualities, has much stiffer straw, and is slightly earlier than Kanred.

Hessian Fly Resistance of Tenmarq and Kawvale

Comparitive data of a representative nature on Hessian fly infestation of Tenmarq and Kawvale, with six other varieties as given by Painter, Salmon, and Parker (1931) are given in Table 1.

Table 1. Summary of infestations of check rows in the 1929 fly nursery at Manhattan as determined by different methods of recording infestations. (Based on 50 plants in each of five series).

Variety	Per cent of tillers infested	Per cent of plants infested	Av. number of fly on 50 plants	Av. number of fly on each infested plant
Kanred	32.0±3.06	57.2±2.78	61.6±5.87	2.12±0.16
Tenmarq	29.0±1.32	61.6±4.12	78.0±9.79	2.64±0.30
Blackhull	12.8±1.98	19.2±2.07	20.6±2.68	2.16±0.13
Early Blackhull	8.2±0.90	17.2±2.11	19.4±2.87	2.24±0.15
Superhard Blackhull	7.4±1.34	14.0±2.17	14.6±2.98	1.92±0.25
Fulhard	2.8±0.33	4.8±0.54	4.0±0.85	1.66±0.21
Illini Chief Sel. No. 223415	2.6±0.27	5.2±0.54	3.2±0.65	1.30±1.30
Kawvale	2.2±0.74	4.4±1.31	3.6±1.44	1.14±0.09
Av. P. E.	1.24	1.96	3.39	0.20

In all the methods of recording infestation used, except one, Tenmarq has the highest infestation. In the column "Per cent of plants infested", which is the method used in this thesis, Tenmarq has 61.6±4.12 per cent infestation. In the same test Kawvale had the lowest infestation, with 4.4±1.31 per cent of plants infested. Other tests reported by the same authors indicate that these percentage differences in fly infestation are typical of the two varieties.

Why Kawvale is not Immune to Hessian Fly

In all tests in the hard wheat belt, Kawvale has proven to be highly resistant to fly, but is not immune. There are several possible explanations of this lack of immunity.

1. Kawvale may be pure in so far as agronomic characters are concerned but not pure for the factors determining fly resistance in wheat varieties or populations. Selections have been made which vary in resistance to leaf rust, to Hessian fly, and in some other characters.

2. A few plants of other varieties may be mixed with Kawvale. These mixtures may be of varieties very similar in appearance to Kawvale, making a separation of the varieties very difficult.

3. As has been shown by Painter (1930), there are two or more strains of Hessian fly. It may be that Kawvale is resistant to some of these strains and not to others, thus giving Kawvale a low percentage of infestation. Other varieties not resistant to as many strains of fly would have a higher percentage of infestation, as was discussed on pages 27 and 28 of this thesis. Painter, Salmon, and Parker (1931) have shown that Kawvale is less resistant to fly from the soft wheat area than from the hard wheat area.

4. There is a small percentage of natural crossing among wheats grown in the field. Field hybrids between Kawvale and some susceptible variety may occur. Some of these natural crosses would be susceptible to fly.

5. Kawvale may have some resistance to all strains of fly but the intensity of the resistance may not be strong enough under certain unfavorable environmental conditions to prevent the development of a small number of flies.

Source of Seed

The results reported in this paper were obtained from an experiment begun in 1928, when a cross was made by Dr. John H. Parker between Tenmarq and Kawvale wheats. The experiment was designed in part to study the resistance to Hessian fly, but mainly to develop a wheat similar to Tenmarq that is resistant to Hessian fly, and adapted to at least a part of the hard wheat areas of Kansas.

Previous testing had shown the varieties crossed to be particularly suited for a study of this problem. Notes on rows of Tenmarq and Kawvale wheats from which seeds were selected to grow plants used in making the cross are given in Table 2.

Table 2. Comparative notes on rows of Tenmarq and Kawvale wheats from which parental seed was selected. (Winter Wheat Nursery 1926-1927).

Kan. No.	C. I. No.	Lodging %	Fully Headed May	Ripe June	Head Length mm.	Kernel Texture	Kernel Plumpness %	Yellow berry %	Bu. wt. in lbs.	Protein %
					Tenmarq Row 175					
439	6936	50	23	25	60	SC.	75	10	54.6	16.05
					Kawvale Row 574*					
2593	8180	60	26	27	75	SC-	75	20	55.5	15.54

*Kawvale was marked very resistant to leaf rust.

The cross was made and the F_1 plants were grown in the greenhouse. There were four crosses made of Kawvale x Tenmarq and three of the reciprocal, Tenmarq x Kawvale. In one cross and its reciprocal the Kawvale used had purple straw. Plants with purple straw are not uncommon in Kawvale and it was thought that this character might be associated with resistance to Hessian fly.

The F_2 generation was grown in 49 rows of the Agronomy Nursery in 1929-1930. Notes were not taken on the fly infestation of these rows, since the fly was not abundant in the nursery that season.

METHODS

Tests giving data for this paper were conducted at Manhattan, Kansas, during the seasons of 1930-31, and 1931-32. Data are presented from plants grown in both field and greenhouse. The greenhouse data were obtained from plants which were of the same pedigree as the field grown plants, and the data obtained in the greenhouse are combined with the data obtained in the field.

In September, 1930, the seeds from some of the better F_2 plants in each row of the crop harvested in June, 1930, were planted in the Hessian fly nursery. Seed from all the plants of one row number 5617, were planted. In every case only the seeds from one plant were used in planting a row.

Although the seeds were selected from plants having desirable agronomic characters, they were necessarily chosen at random from the standpoint of Hessian fly resistance. Therefore, the behavior of any plant-row of 1930-31 can be taken as an index to the genetic composition, in relation to Hessian fly resistance, of the F_2 plant which produced the seed for planting the F_3 row.

If notes on infestation of F_2 plants had been taken, they would not give data from which the mode of inheritance of resistance could be worked out, because 100 per cent of the plants in a row rarely are infested in the most susceptible varieties.

There were 95 F_3 rows of this cross, each from an individual F_2 plant, grown in the nursery in 1930-31. For every row grown in the nursery, five pots of wheat of the same pedigree were grown in the greenhouse. The seed used to plant a row in the nursery and a corresponding five pot group in the greenhouse were taken from the same F_2 plant.

Infestation of Plants Grown in the Hessian Fly Nursery

The Hessian Fly Nursery is laid out in eight foot rows, spaced one foot apart. A three foot alley was left between each plot.

The rows were planted September 13 to 18, 1930, one seed to a place and about three inches apart. This spacing allowed for a more uniform condition of growth and fly exposure. It also gave an opportunity for taking notes, keeping records, and making selections on an individual plant basis.

Rows of Tenmarq and Kawvale, the parental varieties, were planted at intervals throughout the plots as check rows.

In addition to the natural infestation due to local fly, stubble of wheat known to contain Hessian fly puparia was used. This stubble was gathered at Hays, Kansas, and kept dry until September and was then scattered along alleyways of the plots. Emerging adult flies from this stubble laid eggs on the plants. Several burlap bags of volunteer wheat containing puparia were gathered from near Ashland, Kansas, and scattered around the plots.

In spite of these efforts to build up a large infestation of fly only a small percentage of the plants were infested.

Examination of plants in the nursery was made in the fall of 1930. With practice and careful observation infested plants can be distinguished from non-infested plants without pulling the plants up. The infested plants show a distinctly blue-green color, the central leaf becomes dwarfed but does not die, and the plants take on a rosette appearance. In cases where there appeared any doubt of the infestation, the soil around the plant was dug away and the plant examined carefully. This examination can be made without killing the plant. Results obtained from this examination showed that there was a very small percentage of the plants infested, therefore, the data are not presented.

The infestation of nursery plants in the fall of 1931 was also determined by this method. Results from this examination are given later in this paper under the data and discussion of the F_4 generation.

Infestation of Plants Grown in the Greenhouse

A planting of all the hybrid lines planted in the nursery was made during October, 1930, in the Agronomy Greenhouse. These plants were grown in four-inch clay pots. Each pot had an average of seven plants, making a total of 35 plants of each pedigree line as grown in a corresponding nursery row.

The greenhouse was kept at a temperature and humidity as near as possible as that ordinarily experienced by fall planted wheat. When the plants were up to a height of about four inches the pots were transferred to the Entomological Greenhouse. Here the pots were put in a long screen cage which was large enough to hold all the 500 pots.

Between the dates of December 16, 1930, and June 1, 1931, 124 female and 90 male Hessian flies were released in the cage with the wheat plants. These flies were well distributed along the cage so that no pots had a better chance for infestation than others. The Entomological Greenhouse was being used for other purposes so that the temperature often ran above 80° F., which is higher than the plants would normally experience at this stage of their growth. Therefore, the pots were moved back to the Agronomy Greenhouse, as soon as the flies were through laying eggs.

As soon as the eggs laid on these plants hatched and developed to the flaxseed stage, the plants were dug up and examined for percentage of infestation. When all the plants of a pot were not infested one uninfested plant was left in each pot to produce seed.

EXPERIMENTAL RESULTS

Fly Resistance of F_3 Hybrids

As was explained on pages 37 and 38 of this paper the 1930 infestation in the Hessian fly nursery was not heavy enough to be of any significance. However, the infestations of the greenhouse plants were heavy enough to give valuable data.

Notes were taken on the number of plants grown, the number infested with fly, and the intensity of the infestation of hybrid cultures grown in the greenhouse and in the nursery.

A summary of the data on fly infestation taken on the F_3 hybrids and their parental checks is listed in Table 3.

The column headed "plants % infested" gives the percentage of plants in each group that were infested. It will be noted that the arrangement of the table is based upon this column. The first hybrid row, number 511, had no infestation, and the range extends to the last row in the column, number 605, with 55 per cent infestation. It will be noticed that a close correlation exists between the three columns, "plants number infested", "total number of fly", and "plants % infested." Any one of the three columns might be taken as a basis for arranging the table without changing the rank of the strains very much.

The total range of the percentage infestation of F_3 hybrids and their parental checks were divided into classes, having their range centers five units apart. The number of hybrids and parental checks belonging in each group are given in Table 4. This table will be discussed later in this report.

Table 3. Infestation of F_3 plants grown in greenhouse 1930-31. (Hessian fly from hard wheat belt Jan.-Feb. 1931).

Name	Pot No.	Plants Total No.	No. Inf.	% Inf.	Total No. of Fly
Kv. x Ten.	511	44	0	0	0
"	518	36	0	0	0
"	568	36	0	0	0
"	575	34	0	0	0
"	549	33	0	0	0
Ten. x Kv.	584	31	0	0	0
Kv. x Ten.	510	48	1	2.08	1
"	501	43	1	2.33	1
"	508	43	1	2.33	1
Ten. x Kv.	588	40	1	2.50	1
Kv. x Ten.	523	39	1	2.53	1
"	530	39	1	2.53	1
"	544	35	1	2.86	1
"	526	36	2	4.32	3
"	506	44	2	4.54	2
"	507	43	2	4.65	2
"	504	43	2	4.65	5
KAWVALE	(Check)	37	2	5.40	3
Ten. x Kv.	597	35	2	5.72	2
Kv. x Ten.	552	34	2	5.90	2
"	550	34	2	5.90	3
"	572	34	2	5.90	3
KAWVALE	(Av. Checks)	67	4	5.97	6
Ten. x Kv.	604	31	2	6.46	6
"	590	46	3	6.53	6
KAWVALE	(Check)	30	2	6.70	3
Kv. x Ten.	502	39	3	7.70	3
"	520	38	3	7.90	5
"	524	36	3	8.33	4
"	532	36	3	8.33	9
"	566	34	3	8.40	3
"	577	35	3	8.58	4
"	573	33	3	9.10	5
"	505	43	4	9.32	4
Ten. x Kv.	587	43	4	9.32	6
Kv. x Ten.	509	43	4	9.32	5
"	522	40	4	10.00	5
"	519	40	4	10.00	12

Table 3--Continued

Name	Pot No.	Plants Total No.	No. Inf.	% Inf.	Total No. of Fly
"	542	39	3	10.33	5
"	539	38	4	10.53	11
Ten. x Kv.	591	47	5	10.64	6
Kv. x Ten.	563	37	4	10.80	7
"	529	35	4	11.40	8
"	567	35	4	11.40	8
"	547	25	3	12.00	5
TENMARQ	(Check)	34	4	12.10	14
Ten. x Kv.	595	33	4	12.20	9
Kv. x Ten.	515	39	5	12.80	9
"	521	39	5	12.80	6
"	516	38	5	13.15	9
"	536	38	5	13.15	23
"	527	36	5	13.88	5
"	528	36	5	13.88	13
"	512	36	5	13.88	14
Ten. x Kv.	582	35	5	14.28	6
Kv. x Ten.	569	35	5	14.28	7
"	571	35	5	14.28	10
Ten. x Kv.	598	34	5	14.70	7
"	600	33	5	15.15	11
Kv. x Ten.	531	36	6	16.2	18
"	564	36	6	16.65	6
"	576	36	6	16.65	10
Ten. x Kv.	583	35	6	17.10	13
Kv. x Ten.	513	40	7	17.50	15
Ten. x Kv.	581	34	6	17.65	7
Kv. x Ten.	553	34	6	17.65	8
"	578	34	6	17.65	10
Ten. x Kv.	599	34	6	17.65	12
Kv. x Ten.	548	28	5	17.85	5
"	565	38	7	18.40	21
"	517	38	7	18.40	23
Ten. x Kv.	586	44	8	19.5	15
Kv. x Ten.	545	25	5	20.0	8
Ten. x Kv.	580	35	7	20.0	15
Kv. x Ten.	570	34	7	20.30	8
Ten. x Kv.	589	44	9	20.40	18
"	592	39	8	20.50	13
Kv. x Ten.	574	33	7	21.20	9
Ten. x Kv.	594	33	7	21.20	9

Table 3--Concluded

Name	Pot No.	Plants Total No.	No. Inf.	% Inf.	Total No. of Fly
Ten. x Kv.	596	33	7	21.20	16
Kv. x Ten.	503	42	9	21.40	11
"	540	41	9	21.90	26
Ten. x Kv.	603	32	7	21.90	13
Kv. x Ten.	535	39	8	22.50	28
"	537	39	9	23.05	13
"	534	39	9	23.10	27
Ten. x Kv.	593	39	9	23.10	22
Kv. x Ten.	538	41	10	24.40	19
"	514	40	10	25.0	21
"	551	36	9	25.0	12
Ten. x Kv.	602	35	9	25.70	20
Kv. x Ten.	541	34	9	26.40	30
"	525	39	11	28.20	17
TENMARQ	(Av. Checks)	70	21	30.0	81
Ten. x Kv.	579	32	10	31.3	22
Kv. x Ten.	543	34	12	35.3	25
Ten. x Kv.	601	33	12	36.4	35
"	585	34	14	41.3	20
TENMARQ	(Check)	36	17	47.2	67
Kv. x Ten.	546	25	12	48.0	21
Ten. x Kv.	605	40	22	55.0	118

Table 4. Infestation of parents and 95 F_3 lines of Tenmarq x Kawvale grown in greenhouse, 1930-1931.

Variety or Cross	Number of lines with per cent infestation indicated. 0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	Total No. Lines
TENMARQ (check)			1							1		2
KAWVALE (check)		2										2
Tenmarq x Kawvale	2	4	4	5	7	1	1	1	1		1	27
Kawvale x Tenmarq	15	12	17	9	9	4		1		1		68
Total Hybrids	17	16	21	14	16	5	1	2	1	1	1	95

A summary of the infestation notes, taken on the ten rows which were the most resistant to the fly and the ten rows which were the least resistant to the fly, along with similar notes of the parental check rows, is given in Table 5. For convenience throughout this discussion, the ten rows of hybrids having the smallest percentage of plants infested, the first ten rows listed in Table 5, will be called resistant. The ten rows of hybrids having the largest percentage of plants infested, the last ten rows listed, will be called susceptible.

The resistant rows in the table do not go above 2.5 per cent of infestation, which is below the infestation of the resistant Kawvale parent used as a check in this test.

Several possible reasons why Kawvale is not immune to fly have been given on pages 32 and 33 of this paper. Both rows of the Kawvale check, as shown in Table 5, had infested plants. The fly infesting these plants developed into very small and weak puparia. There is little probability that they would have developed into adults strong enough to perpetuate the family. The weakened condition of these puparia would lead one to think that the plants were not of another variety, resulting from a mixture, but that the resistance of Kawvale is not quite strong enough to prevent a partial development of some flies.

The highest infestation of any series of pots of

Tenmarq, the susceptible parent used as a check in this experiment, was 47.2 per cent. This is somewhat lower than the highest infestation of the hybrids. This difference is possibly due to chance variation, or a recombination of factors which make these hybrids more susceptible.

Resistance of F_4 Hybrids

Eighty F_4 families were grown in the fly nursery from seed selected from individual F_3 plants. For the most part, seeds were selected from rows combining low fly infestations and other desired characters. A few lines of high fly infestation were continued to compare with the low fly lines.

The infestation in the field plots was great enough to show some rather significant results. A summary of the data on some lines that were continued is given in Table 5.

The column headed "total number of plants" gives the number of plants that were grown from the rows listed on the same line of the table in the column headed "row and pot number." The column headed "total number of plants infested" gives the number of plants that were infested with fly in the fall of 1931.

One column gives the percentage of plants infested. It will be noted that in general the percentages increase from top to bottom of the column, very much as they did on greenhouse infestations of F_3 plants. This relationship shows that by selection of seed from segregates of low infestation it is possible to decrease the infestation of the following generations below the average infestation of plants grown from seed not selected for fly resistance. It also shows that the infestation in the greenhouse is a reasonably good index of the fly infestation of plants of the following or of the same generation grown in the field.

The number of rows grown from the various F_3 plants is shown in the column headed "number rows represented." Not as many rows were continued from the susceptible lines as from the resistant ones, but the numbers are large enough to make the two groups comparable. The columns under "number rows infested", and "per cent of rows infested" compared with the column under "per cent of plants infested" show that either of the columns might be used as a basis for arranging the table without changing the present arrangement very much.

The relation between the fly infestation of these two generations, that is, the F_3 and F_4 is shown by a graph, Figure 1.

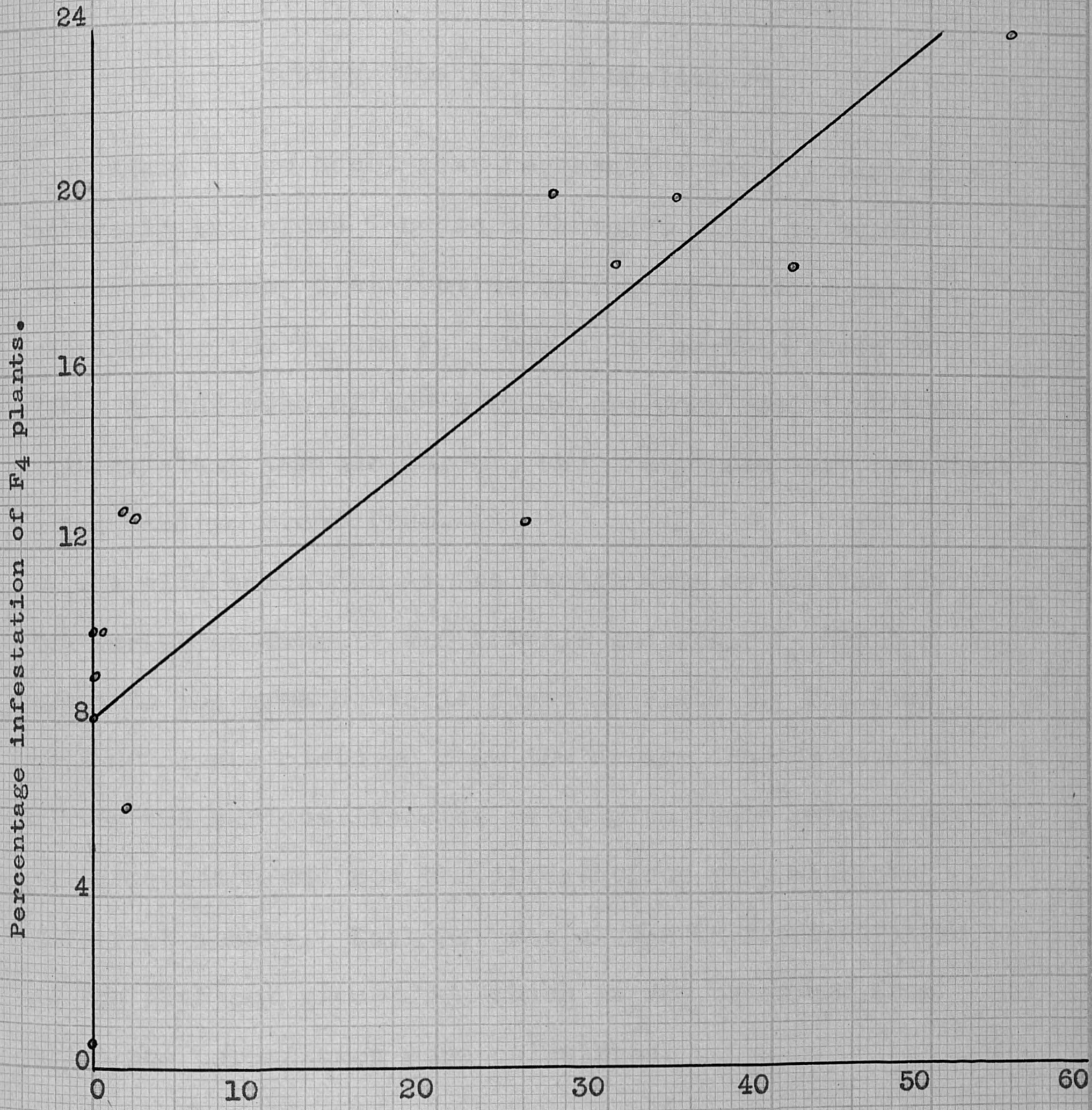


Figure 1. Correlation between percentage of fly infestation of F_3 plants and their F_4 progenies.

Segregation for Fly Resistance

There is no doubt that segregation for fly resistance occurs in the cross Tenmarq x Kawvale. This is evident in the frequency distribution of fly infestation percentages in the F_3 and F_4 lines. It has been shown in Table 5 that some of the hybrids are more resistant than the resistant Kawvale parent, and that these very resistant lines tend to breed true.

A wide variation in the damage done by Hessian fly to the varieties Tenmarq and Kawvale and their F_3 hybrids grown in the greenhouse is shown in Plate 1. The four pots of plants pictured show the damage done by Hessian fly on the various lines of wheat with their percentages of infestation and how the infestations vary with the different wheats. Each pot was chosen as representative of the five-pot group from which it was taken and from which the percentages were calculated.

Cross and Reciprocal

There were four crosses made by plants of Kawvale being pollinated with pollen from Tenmarq, and three crosses made by pollinating plants of Tenmarq with pollen from Kawvale. A study made of the percentages of infestation

Pot No. 533-5 was chosen from the pots containing the parental check Kawvale and having 6.0 per cent of their plants infested.

Pot No. 605-5 was chosen from the pots containing the F_3 hybrids of Tenmarq x Kawvale and having 55 per cent of their plants infested.

Pot No. 575-1 was chosen from the pots containing the F_3 hybrids of Tenmarq x Kawvale and having no plants infested.

Pot No. 500-3 was chosen from the pots containing the parental check Tenmarq and having 30 per cent of their plants infested.

Plate 1. Photograph showing two representative pots of wheat from the five-pot groups growing parental checks and two from their F_3 hybrids having high and low percentages of infestation.

Pot No. 533-5 Pot No. 605-5 Pot No. 575-1 Pot No. 500-3

Table 5. Fly Infestation of Ten Resistant and Ten Susceptible Hybrid Rows and Parental Check Rows.

	F_3 Greenhouse plants of 1930-1931					F_4 Nursery plants of 1931-1932					
Row and pot Nos.	Number of plants in row	Number plants in pots	Number plants infested	Total number of fly	Percent of plants infested	Total number of plants	Total No. plants infested	Per cent of plants infested	Number rows represented	No. rows infested	Percent of rows infested
Resistant Checks (KAWVALE)											
533	18	37	2	3	5.4	37[1]	1	2.7	4	1	33.3
554	13	30	2	6	6.7			3.78[2]			
Susceptible Checks (TENMARQ)											
500		36	17	67	47.2	53[1]	26	51.00	3	3	100
606	23				30.0			73.5[2]			
Resistant Hybrids											
511	14	44	0	0	0	109	10	9	12	5	41.6
518	18	36	0	0	0	77	7	9	11	5	45.4
568	20	36	0	0	0	83	1	1.2	9	1	11.1
575	18	34	0	0	0	67	5	7.4	13	3	23
549	7	33	0	0	0	61	3	4.9	6	2	33
584	17	31	0	0	0	77	7	9.0	9	3	33
510	12	48	1	1	2.1	14	1	7.1	2	1	50
501	16	43	1	1	2.3	37	4	10.8	6	2	33
508	3	43	1	1	2.3						
588	13	40	1	1	2.5	8	1	12.5	2	1	50
Susceptible Hybrids											
551	16	36	9	12	25.0	16	2	12.5	2	2	100
602		35	9	20	25.7	10	2	20.0	1	1	100
541	17	34	9	30	26.4						
525	12	39	11	17	28.2						
579	14	32	10	22	31.3	11	2	18.0	1	1	100
543	19	34	12	25	35.3						
601	17	33	12	35	34.4	5	1	20.0	1	1	100
585	23	34	14	20	41.3						
546	15	25	12	21	48.0	5	1	20.0	2	1	50
605	32	40	22	118	55.0	25	6	24.0	3	3	100

[1] Parental checks in F_4 tests were not grown from seed of checks used in F_3 tests.

[2] Average percentage infestation of all the rows in nursery growing parental varieties.

of the F_3 hybrids shows very little difference between the cross and its reciprocal. There were 74 lines of F_3 plants from the crosses of Kawvale x Tenmarq and 24 rows of Tenmarq x Kawvale. The Kawvale x Tenmarq group had an average of 13.2 per cent of the plants infested, and 24.6 per cent of the rows had a lower infestation than the resistant checks of Kawvale. The Tenmarq x Kawvale group had an average of 18.2 per cent of the plants infested and 12.5 per cent of the rows had a lower infestation than the resistant checks of Kawvale.

The data on the percentage of fly infestation, grouped in classes with a range of 5, has been given in Table 4. It will be noted that the proportion of rows falling in each group is about the same from both the cross and reciprocal.

The percentage difference in the cross and the reciprocal is not considered great enough to justify separate treatment of the two. The data on the F_4 plants grown in the nursery show a similar difference in the cross and reciprocal. The F_4 plants of Kawvale x Tenmarq have an average infestation of 6.8 per cent, while those of Tenmarq x Kawvale have an average infestation of 16.1 per cent. The range in percentage infestation is somewhat greater in the Tenmarq x Kawvale hybrids than in Kawvale x Tenmarq. Both groups contain segregates that have a lower infestation than Kawvale, the resistant parent. Because of the small differences in the percentages of infestations, and the large amount of variation, the data from the cross and its reciprocal are combined for discussion.

Manner in Which Fly Resistance is Inherited

Because of the lack of data on the infestation of the F_2 plants it is necessary to classify the F_2 plants on the basis of percentage infestation in the F_3 plants. The F_2 would not give data from which the mode of inheritance of resistance could be worked out, because 100 per cent of the plants in a row rarely are infested even in the most susceptible varieties.

The data on F_3 rows are used for genetic analysis of the F_2 generation. These F_3 data can be used because each F_3 row was grown from the seed of an individual F_2 plant. The fly reaction of the F_3 row then indicates what the fly reaction of the F_2 plant would have been had they been able to express their exact genetic composition. The number of fly-free rows is small, but, as has been explained, the resistant parent Kawvale is not immune. Therefore, all hybrid lines that have an infestation as low as Kawvale may be classed as resistant.

This division point between resistance and susceptibility is possibly a justified one because the infestation of Kawvale is fairly stable, usually remaining in the same relative position when grown in comparable tests with other varieties. It may be assumed that the factors for resistance in Kawvale are in a homozygous condition, or nearly so. Therefore, any increase in infestation in the hybrids above the infestation of Kawvale is probably due to the influence of the Tenmarq parent.

The average percentage of infestation of Kawvale in the greenhouse tests was 6.05. As shown in Table 3 there are 21 hybrid lines which have a smaller infestation than 6.05 per cent and 74 lines which have a higher percentage of infestation. By accepting the average of the resistant parental check, Kawvale, as the dividing line between resistance and susceptibility these data indicate that in the cross Tenmarq x Kawvale, susceptibility is dominant and resistant is recessive.

While the observed numbers in the susceptible and resistant groups, 74:21, is a close fit to a 3:1 ratio, one is not entirely justified in concluding that the fly susceptibility or resistance in the cross of Kawvale x Tenmarq is dependent upon one factor pair. Thus, the percentage infestation of the 74 lines classed as susceptible range from 6 to 55, and the 21 lines classed as resistant range from 0 to 6. These wide ranges can hardly be explained on a monohybrid basis, since they exceed the limits of both parents.

Furthermore, the data on F_4 lines do not indicate that the 3:1 ratio calculated from the F_2 data can be accepted as a final or complete solution of number of factors influencing resistance in this cross. There were 40 lines grown from fly-free F_3 rows. Among these 40 lines, 19, or 47.5 per cent were infested. In no case did all the rows grown from a single fly-free F_3 row remain fly-free in the F_4 generation; although at least one approached this condition as closely as did the Kawvale check.

The parent varieties do not stand at the extreme limits of infestation obtained in the F_2 lines. If we assume that fly resistance is the result of multiple factors, it is likely that some of the F_2 combinations would contain more factors, or perhaps a more effective combination of factors, for resistance than either of the parents possessed. Knowing that neither of the parents have all their plants infested by fly, this may be considered as evidence that they both may contain factors for resistance, but different factors in the two cases. The same is true when we consider that neither parent is entirely immune to fly and both may lack factors which would give immunity. In this case Tenmarq would be considered to contain fewer, or different factors for this character.

It would commonly be the result, through natural selection, that factors favoring resistance have been preserved in each parent, and the varieties from which they were derived, during the many generations that they have been grown in the presence of Hessian fly. It is likely that in the two separate lines, different sets of factors for producing resistance have accumulated. Therefore, we would expect segregation and recombination to take place when Kawvale and Tenmarq varieties are crossed and as a result either parental limit would be likely to transgress in the F_2 hybrids.

In the case of the cross Tenmarq x Kawvale the two characteristic signs of multiple cumulative factors for fly resistance are conspiciously present. (1). The great variability of the F_2 lines as compared with that of the parent indicates that resistance to fly in this cross is dependent upon more than one pair of factors. The variability between the infestation of parents and the F_2 lines is shown in Figure 2. Tenmarq has a wide range of percentage infestation, but does not approach the F_2 limits. The infestation range of Kawvale is very small, and well within the limit of the low range of infestation. (2). The greater smoothness of the curve, resulting from the number of F_2 lines and their infestation as compared to a curve made by combining the data on the two parents, is also an indication that more than one pair of factors are involved. If the difference in fly resistance between Kawvale and Tenmarq depended upon a single pair of factors, a curve of the F_2 data should show one or more distinct breaks as a result of a 1:2:1 or a 3:1 ratio. An infestation curve is given in Figure 3, which shows the smoothness of the F_2 curve. There are no sharp breaks in the curve that could be taken as a point separating the hybrids into two or more classes.

Within each parental variety there is a variation in the percentage of plants infested. Some highly resistant plants may be infested and some susceptible plants may be missed by the fly; this variation would have a tendency to make the infestation curve smoother.

The data on the hybrids of this cross indicate that several crosses and back crosses would have to be studied before the exact number of factors influencing fly resistance could be definitely determined.

Agronomic Characters

Notes were taken on the characters of plants, grown in the fly nursery, that the plant breeder generally uses as a basis for making his selections. A summary of the

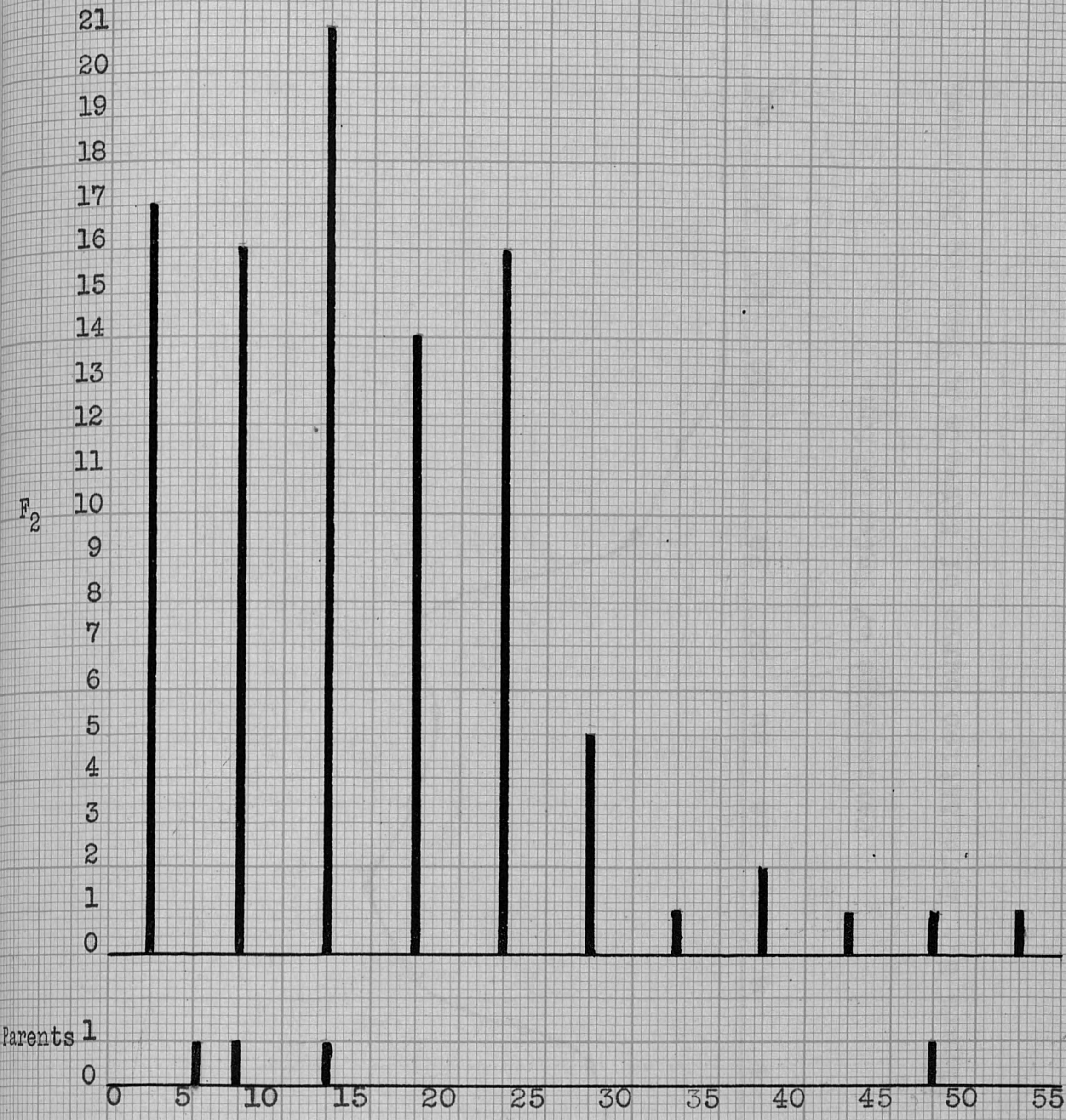


Figure 2. Diagram to show variation in infestation of parental varieties and their F_2 hybrid offspring.

Figure 3. Infestation curve of Kawvale x Tenmarq hybrids.

agronomic notes taken on the ten rows which were the most resistant to the fly and the ten rows which were the least resistant to the fly is given in Table 6.

Due to the fact that each five-pot group of greenhouse plants has the same pedigree as a corresponding nursery row, the data on plant characters, obtained from plants grown in the fly nursery, can be combined with the data on the infestation of plants grown in the greenhouse.

Similar agronomic notes were taken on the remaining 75 rows, but are not presented in this thesis. Among these there was no disagreement with the data of those given below.

Color of straw. There are two columns of notes on straw color recorded in Table 6, the first of these columns gives the color of straw produced by plants grown in the nursery. In the second column are notes on the color of straw produced by the greenhouse plants that were transplanted to the field. With a few exceptions the straw color developed on plants of a given line is the same in the greenhouse and nursery. Straw color did not develop plainly on a good many of the plants grown in the greenhouse.

Notes on the straw color were taken for two reasons: (1). Because it was thought that possibly the substance or character giving the purple appearance to the straw might also have some effect on the Hessian fly larvae. (2). If an easily detected character could be found that is closely linked with fly resistance it would be a great help to the plant breeder or entomologist in breeding for fly resistance. It might also simplify the problems of working out the inheritance of fly resistance.

Kawvale has purple straw under certain environmental conditions, while Tenmarq always has yellow straw.

The data indicate that there is no relation between the occurrence of purple straw and fly resistance. The resistant group has the same number of rows with purple straw as the susceptible group. Purple and yellow straw types occur at random or at irregular intervals in the list of hybrids arranged according to fly infestation.

Length of Beak. The beak length of the hybrid lines of Tenmarq x Kawvale is a variable character. In no individual row examined were the beaks of all the plants in the row the same length. The length of the beaks was determined by measuring several beaks of each head of a plant and taking an average of these measurements.

Kawvale has a beak that is typically less than two mm. long, while Tenmarq has a beak that varies from 3 to 12 mm. long. The average beak length of the fly-resistant and fly-susceptible groups is given in Table 6. It can

Table 6. Agronomic Data on Ten Resistant and Ten Susceptible Rows of Hybrids and Parental Check Row.

Row No.	Heading date May	Color of straw	Color of straw in trans-plants	Number plants in row	Number of plants selected	Average number of heads per plant	Average length of beak in mm.	Average weight of grain per plant, gms.	Average kernel plumpness per cent	Average yellow berry per cent	Grain type
Resistant Checks (KAWVALE)											
533	26	Y[1]		18	4	24	1 to 2	22	82.5	Tr	
554		P[2]						190 (Bulk)	80.0	10	
562								145 (Bulk)	75.0	5	
Susceptible Checks (TENMARQ)											
500					2	21		21.7	80.0	5	
606	27	Y		22			3 to 12	80 (Bulk)	80.0	90	
Fly Resistant Hybrids											
511	27	Y		14	14	18	4	14.5	80.7	1.0	K[3]
518	27	Y	2Y	18	15	18	5	13.8	79.6	1.0	K
568	27	P		20	16	15	2	11.2	75.6	22.8	Seg[4]
575	29	Y	2P 1Y	18	16	13	5	10.8	80.0	34.0	Seg
549	27	Y	3P	7	6	30	2	27.3	84.1	9.1	Seg
584	27	Y	Y	17	16	14	4	10.6	76.8	10.6	Seg
510	27	Y	Y	12	12	17	4	11.1	70.4	0.0	
501	26	Y		16	16	28	4	27.3	80.0	9.0	Seg
508	29	Y		3	3	22	4	21.0	73.0	0.0	T[5]
588	29	P	3P 2Y	13	10	10	1	9.0	80.5	19.5	Seg
Average						19	3	15.7	77.8	10.7	
Fly Susceptible Hybrids											
551	27	P	2P 1Y	16	16	26	4	20.5	83.7	28.4	T
602	29	M			12	13	3	10.2	84.1	75.8	T
541	27	Y		17	14	23	8	13.5	71.4	0	Seg
525	27	M	3P	12	12	21	5	20.6	78.3	0	K
579	29	Y	2Y	14	13	13	6	9.7	75.3	25.7	Seg
543	27	Y	Y	19	18	19	3	12.4	71.9	0	Seg
601	29	Y	Y	17	18	17	2	12.8	81.1	0	T
585	29	P	P	23	19	10	1	9.5	74.7	33.1	Seg
546	27	Y		15	13	25	4	18.2	73.4	0	
605	27	Y	Y	32	29	11	2	8.0	81.1	71.1	
Average						18	4	13.3	77.5	23.4	

[1] Y - yellow

[2] P - purple

[3] K - Kawvale

[4] Seg - segregating

[5] T - Tenmarq

be seen from inspection of the data that there is no relation between the degree of fly infestation and length of beak. The average of the column in both the resistant and susceptible groups is nearly the same. There is more variation in beak length within the susceptible group.

Factors Used as Yield Indicators

(Average number of heads to the plant, Kernel plumpness, Weight of grain to plant).

It may be seen from Table 5 that there is very little difference between the average number of heads produced by plants of the resistant group and the number of heads produced by plants of the susceptible group. The same is true of the kernel plumpness. Hayes, Aamodt and Stevenson (1927) found that plumpness of grain was rather highly correlated with yield, giving a value of $r = +0.6228$.

The column on the "average weight of grain to the plant" is the best of the three available methods for estimating the yielding capacity of the line. The resistant lines yielded an average of two grams of grain to the plant more than the susceptible lines.

A study of the number of heads to the plant, kernel plumpness, and yield do not indicate that there is any association between these characters and resistance or susceptibility of a strain. A high yield is the summation of the action of a large number of desirable plant characters, and the absence of undesirable characters which act to prevent the production of high yield. Resistance to Hessian fly under conditions of possible heavy infestation, would be a factor influencing yield when other factors do not change.

Kernel plumpness and average number of heads to the plant are factors which are often correlated with yield. They are not known to be correlated with fly resistance. Plants that are resistant to fly may also be high yielding. Thus, from the genetic data it should be possible to produce a new wheat variety from the cross Tenmarq x Kawvale that will yield well, and that is also resistant to fly.

Type of Kernel. There is a great amount of variation in the type of grain produced by the F_3 plants. This variation ranges from the typical short hard kernel type produced by Tenmarq through all the gradations possible to the type of long, slender, semi-hard kernel produced by Kawvale. Notes on kernel type were made by comparing the grain of each plant in each row with typical samples of Tenmarq and Kawvale grown under the same conditions. In several rows, as will be noted from Table 6, more than one type of grain was produced by individual plants in the same row. Where all the plants produced grain that was like either of the parents it was described as of that type. Rows having plants producing grain of both parent types were marked as segregating. Grain of an intermediate type, that is, not having the typical characters of either parent was described as intermediate. When the bulk sample of grain from a row was mixed, showing part of the kernels to be in the intermediate class and others of either or both parental types, such samples were marked as segregating.

In the group of resistant rows it will be noted that the kernel type of the resistant parent, Kawvale is present in more cases than types of the susceptible parent. This indicates that the hybrids are segregating for kernel characters and that types showing the most fly resistance tend to have the Kawvale kernel characters. This may indicate that the resistant quality of Kawvale is linked with the grain type of that variety, but that the linkage is not close.

These data can not be taken as positive proof that the Kawvale type of grain is linked with the resistance quality, although they suggest there may be some association between these two characters. Another possible explanation of this association between Kawvale type of kernel and fly resistance is that the fly resistance of Kawvale is due to several factors. Thus, rows 511 and 518 may have obtained many of their factors from the Kawvale parent. These several Kawvale characters acting together produced resistance and one more may include or be linked with factors producing the Kawvale grain type.

Yellow Berry. There are several factors associated with grain quality in wheat. The well-known "yellow berry", or the appearance of yellow, mealy or half mealy, or spotted kernels in hard wheats is usually associated with low protein. Thus, the protein and gluten content, and the breadmaking quality of wheat is affected by the "yellow berry" condition.

Different varieties of wheat grown under the same conditions and producing different amounts of "yellow berry" show that some heritable varietial piculiarity is associated with these differences. The varietial differences are only relative in nature. The amount of "yellow berry" occurring in any season depends upon moisture conditions and the available supply of plant food, particularly nitrogen. More "yellow berry" is produced under humid, than under dry conditions.

It will be noted from Table 6 that the Kawvale checks have less than 10 per cent "yellow berry" while one of the Tenmarq checks has as high as 90 per cent of the grain showing "yellow berry". They hybrids show varying amounts of "yellow berry" but the susceptible group averages more than twice the amount of "yellow berry" that the resistant group does. Therefore, there is some evidence of correlation between the high "yellow berry" percentages in the hybrids and susceptibility to Hessian fly.

Correlation of Agronomic Characters and Fly Resistance

Summarizing what has been mentioned under the various headings of this thesis on agronomic characters, we may state that no definite linkage relation between the factors for resistance and factors for any of the characters studied has been found. The characters studied are: date of heading, color of straw in nursery plants and in plants transplanted to the nursery from the greenhouse, number of heads to the plant, length of beak, weight of grain to the plant, kernel plumpness, "yellow berry", and grain type. Although there was not a definite linkage between fly resistance and any of these characters, there was some evidence of an association, or loose linkage between fly resistance and the Kawvale kernel type.

The condition known as "yellow berry" is one often found in Tenmarq wheat. It was shown that lines having a high percentage of their plants infested also had a distinct tendency to have a high percentage of "yellow berry."

Further testing, by making more crosses, will have to be carried on before it can be definitely stated that the relationships shown between Kawvale kernel type and resistance, as well as between "yellow berry" and susceptibility, are due to linkage and not to chance association.

A Very Promising Line

The ultimate aim of this work is to develop a fly resistant variety of wheat that also has as many desirable agronomic characters as possible. Rows having these qualities were selected for further testing. Row number 568 is apparently one of the best lines. Plants in this row produced a comparatively small number of tillers. A large amount of grain to the plant, in proportion to the number of tillers, was produced. The "yellow berry" percentage is above the average of its group but not the highest. The row is still segregating for kernel type and further selection is needed and is possible. The predominating grain type of plants in this row is that of the Tenmarq parent. The Tenmarq grain type is preferable to that of Kawvale. As shown in the column under "heading date" of Table 6, all the heads of this row matured about the same time.

Row 501 was the only row that started heading before row 568. The parent line represented by row 568 was not infested with fly in the F_3 greenhouse plants as shown in Table 6. From this promising row 83 plants were grown in the nursery during 1931-32 and only one was infested.

CONCLUSIONS

1. This paper included a brief review of some of the more important literature on insect resistance in crop plants, and methods used in breeding plants for resistance to insects.

2. Descriptions are given of the varieties Tenmarq and Kawvale.

3. Differences in fly infestation of the two parents over a period of years have been shown to exist. Parent varieties grown as checks of the hybrids show that Tenmarq has an average fly infestation of 30 per cent, and Kawvale 5.97 per cent.

4. Infestation by Hessian fly in the F_3 and F_4 hybrids of Tenmarq x Kawvale varied from 0 to 55 per cent.

5. Resistance to Hessian fly was found to be a heritable character that can be secured in a relatively pure form by selection in F_3 and F_4 of this cross.

6. By selecting resistant hybrid strains, several fly resistant wheats have been developed, some of which are promising in agronomic respects.

7. By taking the infestation of the resistant parent as a division line between resistant and susceptible hybrids, a 3:1 ratio was calculated. This calcualted ratio

does not necessarily indicate that susceptibility and resistance to fly in this cross depend upon a single factor difference.

8. The infestations of F_4 plants grown from seed of fly free F_3 plants indicate that fly resistance is dependant upon more than a single pair of factors.

9. The data indicate that resistance to Hessian fly in the cross of Kawvale x Tenmarq is probably dependant upon multiple factors which may be combined in the hybrids to give a higher degree of resistance than the resistant parent has.

10. No definite linkage relations could be found between fly resistance and color of straw, average number of heads to plant, length of beak, yield, and plumpness of kernel. There was evidence of an association between fly resistance and Kawvale kernel type, and between fly susceptibility and high percentage of "yellow berry."

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LITERATURE CITED

Andrews, E. A.
Some notes on attempts to produce immunity from insect attack on tea. Rpt. Proc. Fourth Ent. Meeting, Pusa, Calcutta. p. 56-59. 1921. (Abstract Rev. Appl. Ent. Ser. A. 10 p. 153, 1922).

Barnes, H. F.
Further results of an investigation into the resistance of basket willows to button gall formation. Ann. Appl. Biol. 18: 75-82. 1931.

Becker, G. C.
Notes on the woolly aphis. Jour. Econ. Ent. 11: 245-255. 1918.

Borner, C.
Ueber den einfluss der nahrung auf die Entwickelungsdauer von pflanzen-parasiten. Ztschr. Angew. Ent. (Abstract by Wardle 1929). 1927.

Brues, C. T.
The selection of food plants by insects with special reference to lepidopterous larvae. Amer. Nat. 54: 313-332. 1920.

Bruner, L. and Swenk, M. H.
Some insects injurious to wheat during 1905-1906. Neb. Agr. Exp. Sta. Rpt. 1907. p. 23.

Butler, E. J.
Conditions influencing the severity of disease. In Fungi and disease in plants. Calcutta. Thacker, Spink. p. 106-130. 1918.

Carter, W. C.
Population of Eutettix tenella Bak. and the osmic concentration of its host plants. Ecology 8: 350-362. 1927.

Cleare, L. D.
Moth-borer damage in relation to sugar-cane varieties in British Guiana. Trop. Agr. 9: 264-271. 1932.

Collins, G. N. and Kempton, J. H.
Breeding sweet corn resistant to the corn earworm.

Jour. Agr. Res. 11: 549-572. 1917.

Comes, H.
Prophylaxis in vegetable pathology [in Spanish]. Bol. Agr. Tecnica Y Economica, Madrid, 9: 508-514. 1917. (Abstract in Rev. Appl. Ent., Ser. A. 6: 55-56, 1918).

Cook, O. F.
Weevil resisting adaptations of the cotton plant. U. S. Dept. Agr. Bur. Plant Ind. Bul. 88, 87 p. 1906.

Craighead, F. C.
Hopkins host selection principle as related to certain Cerambcid beetles. Jour. Agr. Res. 22: 189-220. 1922.

Cunliffe, N.
Studies on <u>Oscinella frit</u> Linn... Ann. Appl. Biol. 16: 135-169. 1929.

Davidson, J.
Biological studies of <u>Aphis rumicis</u> Linn: Reproduction on varieties of <u>Vicia faba</u>. Ann. Appl. Biol. 9: 135-145. 1922

Davidson, J.
Biological studies of <u>Aphis rumicis</u> Linn. The penetration of plant tissues and the source of the food supply of aphids. Ann. Appl. Biol. 10: 35-54. 1923.

Davis, J. J.
The control of three important wheat pests in Indiana. Purdue University Agr. Exp. Sta. Circ. 82: 1-11. 1918.

Dean, Geo. A.
Insects injurious to farm crops (Farmers Institute series) Agricultural Education. 1: 91 p. (Ref. p. 30-49). 1909.

Devereaux, W. L.
The Hessian fly's favorite wheat. Rural New Yorker, 37: 376-377. 1878.

Felt, E. P. and Bromley, S. W.
Developing resistance or tolerance to insect attack. Jour. Econ. Ent. 24: 437-443. 1931.

Fitch, A.
Noxious and other insects. Hessian fly, C. destructor. Seventh Report New York State Agr. Soc. 8: 133-144. 1856.

Flint, W. P.
Chinch-bug resistance shown by certain varieties of corn. Jour. Econ. Ent. 14: 83-85. 1921.

-----, and Hackleman, J. C.
Corn varieties for chinch-bug infested areas. Ill. Agr. Exp. Sta. Bul. 243: 540-550. 1923.

Forbes, S. A.
A monograph of insects injurious to Indian corn, Part 2. 23rd. Rept. State Ent. Ill. 273 p. 1905.

Aspects of progress in economic entomology. Jour. Econ. Ent. 2: 25-35. 1909.

Freeborn, S. B. and Wymore, F. H.
Attempt to protect sweet corn from infestation of H. obsoleta. Jour. Econ. Ent. 22: 666-677. 1929.

Fullaway, D. T.
Termites or white ants in Hawaii. Hawaii Forester and Agriculturalist. 23: 68-88. 1926.

Gaylord, Willis
A treatise on insects injurious to field crops. Trans. N. Y. State Agr. Soc. 3: 129-174. 1843.

Gernert, W. B.
Aphis immunity of teosinte corn hybrids. Science 44: 390-392. 1917.

Gossard, H. A. and Houser, J. S.
The Hessian fly. Ohio Agr. Exp. Sta. Bul. 177, 39 p. 1906.

Graham, S. A.
Environmental resistance. In Principles of forest entomology N. Y. McGraw-Hill, p. 32-37. 1929.

Harland, S. C.
Notes on resistance to cotton-leaf blister mite with special reference to budded cottons and cotton hybrids. West Indian Bul. 16: 78-82. 1916.

Harland, S. C.
The inheritance of immunity to leaf blister mite in cotton. West Indian Bul. 17: 162-166. 1919.

Harmon, R.
Report of experiments on the varieties of wheat cultivated in the state of New York, New York State Agr. Soc. Trans. 3: 217-231. 1844.

Harper-Gray, R. A.
Frit fly on oats in the four Northern counties. Jour. Ministry Agr. 29: 1109-1114. 1923.

Haseman, L.
An investigation of the supposed immunity of some varieties of wheat to the attack of Hessian fly. Jour. Econ. Ent. 9: 291-294. 1916.

--------, Sullivan, K. C. and McLane, S. R.
Entomological investigations, 1919-1920. Mo. Agr. Exp. Sta. Bul. 179, p. 26-30. 1921.

Hayes, H. K., Aamodt, O. S. and Stephenson, F. J.
Correlation between yielding ability, reaction to certain diseases, and other characters of spring and winter wheat in rod-row trials. Amer. Soc. Agron. Jour. 19: 896-910. 1927.

Headlee, T. J. and Parker, J. B.
The Hessian fly. Kans. Agr. Exp. Sta. Tech. Bul. 188, 138 p. 1913.

Hewitt, T. R.
Notes on the occurrence of the woolly aphis. Schizoneura lanigera, in the core of apples. Jour. Econ. Biol. 8: 95-98. 1913.

Hopkins, A. D.
U. S. Dept. Agr. program of work for (fiscal year 1917), Economic investigations of the scolytid bark and timber beetles of North America. p. 353. 1916.

Howard, L. O.
The Insect Menace. N. Y. Century. 347 p. 1931. (Ref. p. 189).

Imms, A. D.
Resistant varieties. In Recent advances in entomology. Philadelphia, Blakiston. p. 240-249. 1931.

Kellner, E.
Report of field work at the Central Experiment Station, Berkeley. Calif. Agr. Exp. Sta. Rpt. 1891-1892, p. 137-144. 1892.

Kline, R.
Beschadigung des Hafers durch Thysanopteren. [The injury to oats by Thysanoptera]. Zeitschr. Angew, Ent. 11: 113-131. 1925. (Abstract in Rev. Appl. Ent. Ser. A. 13: p. 203, 1925).

Kyle, C. H.
Shuck protection for ear corn. U. S. Dept. Agr. Bul. 708, p. 16. 1918.

Lambert, W. V. and Knox, C. W.
The inheritance of resistance to fowl typhoid in chickens. Iowa State Col. Jour. Sci. 2: 179-187. 1928.

Larson, A. O.
The host-selection principle as applied to Bruchus quadrimaculatus Fab. Ann. Ent. Soc. Amer. 20: 37-77. 1927.

Lee, A. H.
Insect attack and the internal condition of the plant. Ann. Appl. Biol. 13: 506-515. 1926.

Le Pelley, R. H.
Studies on the resistance of apple to the woolly aphis. Jour. Pomology and Hort. Sci. 6: 209-241. 1927.

Lindley, G.
Guide to the orchard and kitchen garden. London. Longman, p. 32. 1831. (Abstract in McColloch 1924).

Marston, A. R.
Progress in breeding corn to resist the European corn borer. 60th. Ann. Rpt. Ent. Soc. Ontario, p. 51-54.

Breeding corn for resistance to the European corn borer. Jour. Amer. Soc. Agron. 22: 986-992. 1930.

Breeding European corn borer resistant corn. Jour. Amer. Soc. Agron. 23: 960-964. 1931.

Recent progress in breeding borer resistant corn. The Quarterly Bul., Mich. Agr. Exp. Sta. 15: 264-268. 1933.

Massee, A. M.
The resistance of apple stock to attacks of the green apple aphis. Jour. Pomology and Hort. Sci. 3: 191-200. 1924.

Mason, A. C.
Biology of the papaya fruit-fly in Florida. U. S. Dept. Agr. Bul. 108, 10 p. 1922.

Maze, P.
Mineral nutrition in the living cell, vitamins, and natural resistance to infectous disease [in French]. Ann. Inst. Pasteur. 41: 948-981. 1927.

Meyer, R.
Neuere studien uber die frit fliege. [New studies on the frit fly]. Oscinella frit. Angewandte Botanik 5: 132-142. 1924. (Abstract in Rev. Appl. Ent. 14. p. 190, 1924).

Misra, R. K.
Woolly aphis attack on apples. Agr. Jour. India, 15: 627-642. 1920.

Monzen, K.
The woolly apple aphis, Eriosoma lanigera, in Japan, with special reference to its life history and susceptibility of the host plant. Verh. 3rd. Internat. Ent. Cong. Zurich. p. 249-275. 1925.

Muller, K.
Remarks on the infestation by phylloxera of Oberlin on 595 vines [in German]. Weinbau u. Kellerw. No. 2: p. 9-18. 1927.

Mumford, E. P.
On the curly-top disease of the sugar beet; a biochemical and histological study. Summary of results. Ann. Appl. Biol. 17: 28-35. 1930.

Studies in certain factors affecting the resistance of plants to insect pests. Sci. 73: 49-50. 1931.

McColloch, J. W.
The Hessian fly in Kansas. Kans. Agr. Exp. Sta.

Tech. Bul. 11 (Resistance of Varieties, p. 75-76). 1923.

The resistance of plants to insect injury. Bien. Rpt. Kans. State Hort. Soc. 37: 196-208. 1924.

----------, and Salmon, S. C.
Relation of kinds and varieties of grain to Hessian fly injury. Jour. Agr. Res. 12: 519-527. 1918.

Resistance of wheat to Hessian fly, a progress report. Jour. Econ. Ent. 16: 293-298. 1923.

Noble, W. B.
Two wild grasses as host of the Hessian fly, Phytophaga destructor. Jour. Agr. Res. 42: 589-592. 1931.

Osborn, Herbert
The Hessian fly in the United States; in U. S. Bur. Ent. Bul. 16: 57 p. 1898.

Packard, C. M.
The Hessian fly in California. U. S. Dept. Agr. Tech. Bul. 81: 20-24. 1928.

Packard, S. A.
The Hessian fly... In 3rd. Rpt. U. S. Ent. Com. p. 227-228. 1883.

Painter, R. H.
The biological strains of Hessian fly. Jour. Econ. Ent. 23: 322-326. 1930.

--------, Salmon, S. C. and Parker, John H.
Resistance of varieties of winter wheat to Hessian fly. Kans. Agr. Exp. Sta. Tech. Bul. 27: 58 p. 1931.

Parker, John H.
Insect resistance in wheats and sorghums a heritable character. U. S. Dept. Agr. Yearbook, 1931. p. 316-317.

Parker, John H. and Painter, R. H.
Insect resistance in crop plants. Sixth Internatl. Cong. of Genetics Proc. 2: 150-152. 1932.

Parnell, F. R.
Breeding of jassid-resistant cottons. Empire Cotton Growing Rev. 2: 330-336. 1925.

Person, H. L.
Theory in explanation of the selection of certain trees by the western pine beetle. Jour. Forestry 29: 696-699. 1931.

Petri, L.
Studi sulle Malattie dell Olivo, Rome, Riv Patol. Veg. 5: 37-39. 1911. (Abstract in Exp. Sta. Record 25: p. 849, 1912).

Phillips, W. J. and Barber, G. W.
The value of husk protection to corn ears in limiting corn earworm injury. Va. Agr. Exp. Sta. Tech. Bul. 43, p. 24. 1931.

Picard, F.
Parthenogenesis and oviposition in the potato moth in French . Comp. Rend. Acad. Sci. (Paris), 156: 1097-1101, Janvier.-Juin. 1913. (Abstract in Wardle and Buckle (1923) p. 7).

Pictet, A.
Influence de l'alimentation et de l'humidite sur la variation des papillons. Mem. Soc. Phys. Nat. Geneve, 35: 45-127. 1905. (Abstract in Brues 1920).

Roberts, I. P., Slingerland, M. V. and Stone, J. L.
The Hessian fly. Its ravages in New York in 1901. N. Y. Cornell, Agr. Exp. Sta. Bul. 194: 226-260. 1901.

Roubaud, E.
<u>A. maculipenis</u> of Northern Europe prefer domestic animals to man, [in French]. Ann. Inst. Past. 34: p. 181. 1920.

<u>A. maculipenis</u> of Northern Europe prefer domestic animals to man [in French]. Bul. do la Soc. Path. Exot. 14: p. 557. 1921. (Abstract in Larson 1927).

Biological research on <u>Pyrausta nubilalis</u>. Third Internat. Corn Borer Invest. Sci. Rpt. p. 1-27. 1930.

Salmon, S. C. and Laude, H. H.
Twenty years of testing varieties and strains of winter wheat. Kans. Agr. Exp. Sta. Tech. Bu. 30: 73 p. 1932.

Schneider-Orelli, O.
Ueber den ungleichen borkenkäfer an obstbäumen im sommer 1916. Schweiz. Zeitschr. f. Obst-u Weinbau, Frauenfeld, 26: 5-9 and 17-21. 1917. (Abstract in Rev. Appl. Ent. Ser. A. 5:).

Schroder, Chr.
Ueber experimentall erzirlte instinkt variationen. In Verhandl. Deut. Sch. Zool. Gesell., Jahresversamml. 13: 158-166. 1903. (Abstract in Craighead 1922).

Die literatur ueber die farbung. Der insekten des jahres. In Ztschr. Wiss. Insektenbiol. 3: 162-164. 1907. (Abstract by Craighead 1922).

Sharples, A.
The lactiferous system of <u>Hevea brasiliensis</u> and its protective function. Ann. of Bot., London. 32: 247-251. 1918.

Shull, W. E. and Wakeland, Claude
Tarnished plant bug injury to beans. Jour. Econ. Ent. 24: 326-327. 1931.

Stahl, M. G.
The relation of varieties of wheat to Hessian fly injury. Kans. State Agr. Col. thesis (unpublished). Kans. State Libr. p. 163-227. 1921.

Staniland, L. N.
Possible factor in making plants resistant to the sclerenchymatous ring. Bul. Ent. Res. 15: 157 p. 1924.

Thiele, R.
Die Blutlaus <u>Schizoneura lanigera</u> Stuttgart. Zeitschr. Naturw. 1902. p. 340-361. (Abstract in Imms (1931) p. 244).

Thorpe, W. H.
Biological races in insects and allied groups. Biol. Rev. 5: 177-212. 1930.

Walsh, B. D.
On phytophagic varieties of phytophagic species. Ent. Soc. Philadelphia. 3: 403-430. 1864.

On the phytophagic varieties of phytophagic species, with remarks on the unity of coloration in insects. Ent. Soc. Philadelphia. 5: 194-216. 1865.

Wardle, R. A.
Host resistance. In The problems of applied entomology. Manchester, University Press, p. 1-40. 1929.

------, and Buckle, P.
Host resistance. In The principles of insect control. Manchester, University Press, p. 1-16. 1923.

Webster, L. T.
Microbic virulence and host susceptibility. Jour. Exp. Med. 39: 874-886. 1924.

Withycombe, C. L.
Studies in the aeticology of the sugar-cane froghopper blight in Trinidad... Ann. Appl. Biol. 13: 64-108. 1926.

Woodworth, C. W.
Variation in Hessian fly injury. Calif. Agr. Exp. Sta. Rpt. (1890) p. 312-318. 1891.