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# Transference of Hessian Fly Resistance and Other Characteristics of Marquillo Spring Wheat to Winter Wheat

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# Transference of Hessian Fly Resistance and Other Characteristics of Marquillo Spring Wheat To Winter Wheat[1]

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The development of plant resistance to insect attack is one of the most promising methods of combating insect outbreaks in field crops where the margin of profit between production costs and market value does not justify the expense of chemical treatments. In the control of the Hessian fly, *Phytophaga destructor* (Say), important advances are being made toward the production of commercial varieties of wheat which carry resistance to this pest.

## REVIEW OF LITERATURE

The earlier literature has been reviewed in a publication by Painter, Salmon and Parker *(12)*[3] which also records the results of detailed counts on the fly infestation of about 400 varieties, selections and hybrids of winter wheat. The authors show that certain varieties, notably Illini Chief, Kawvale, Dawson and other varieties and hybrid selections involving some of these varieties are resistant to fly of the hard winter wheat belt of the western two-thirds of Kansas. In Kawvale there is an approach toward the objective of plant breeders and entomologists in the production of a winter wheat variety equal or superior in agronomic characters to those grown and in addition to be resistant to Hessian fly. Kawvale was distributed to farmers in 1931 and has met with favorable reception because of its high yield and other valuable characters. By 1938 it occupied about 30 percent of the total wheat acreage in the eastern one-third of Kansas *(4)*. So far there has not been any widespread fly infestation to make possible the test of resistance of Kawvale under farm conditions, but. it is known to be fairly susceptible in some experimental tests in the soft, wheat belt where it is best adapted *(12)*.

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3. Italic figures in parentheses refer to literature cited, p. 53.

Data gathered on varieties at the Nebraska Agricultural Experiment Station by Kiesselbach, Anderson and Suneson *(10)*, and by Suneson and Kiesselbach *(21)* agree in general with the fly infestation records for the same varieties at Manhattan. For instance, Kawvale at Lincoln, Neb., had seven percent of the plants infested in both fall and spring counts, while eight hard red winter wheat varieties in one test ranged from 76 percent to 95 percent of the plants infested in the fall and 82 percent to 91 percent in the spring.

Foster and Jeffery *(6)* report on a fly infestation at Saanichton, B. C., in which 29 varieties ranged from zero to 100 percent of the plants infested. The resistant varieties are in part the same ones found resistant at Manhattan, and in central California. The authors indicate that stage of growth may account for the differential resistance of the winter wheat varieties in their tests, but a study of their data and a knowledge of fly life history would suggest that the high positive correlation ($r = +0.84$) between maturity and infestation is the result, rather than a causal relationship, of the particular varieties in the test.

Cartwright and Wiebe *(3)*, working on the inheritance of resistance to Hessian fly of the spring generation in California in crosses between Dawson (resistant) and Big Club and Poso (susceptible), were among the first to place a case of insect resistance on a definite genetic factorial basis. They found that in Dawson there were two dominant factors for fly resistance which are perhaps cumulative.

Throughout the years of study of Hessian fly resistance in Kansas, there has been abundant evidence of the fact that fly resistance was inherited [Farrell *(5)* p. 78; Painter, Salmon, and Parker *(12)*; Hollingsworth *(8)*], but little evidence regarding its exact genetic basis. Several groups of facts have pointed toward a complex genetic situation in the inheritance of fly resistance when all the different resistant varieties are taken into consideration.

Evidence of resistance to Hessian fly in winter wheat has come mostly from the hard winter wheat belt or from the Pacific Coast region. In some localities in the Eastern soft wheat belt no winter wheat has shown similar resistance under comparable infestation intensities. The best explanation so far proposed for most of the differences in varietal behavior in different regions lies in the presence of biological strains of fly which differ in their ability to infest different varieties of wheat. On the Pacific coast the fly population appears fairly homogeneous, while in the hard winter wheat belt of Kansas samples of fly appear to have varying mixtures of two or more biotypes, with those unable to infest Illini Chief and certain other winter wheats in the majority. [Painter *(11)*; Painter, Salmon and Parker *(12)*; Strong *(20)*.]

Most of the earlier studies on fly resistance have been concerned with winter wheats *(Triticum vulgare)*. As occasion permitted spring wheats and species of *Triticum* other than *T. vulgare* have

been exposed to infestation by Hessian fly near Manhattan, Hays, Leavenworth and Oskaloosa, Kan. The results of these tests have been given briefly in the Sixth and Seventh Biennial Reports of the Director of the Kansas Agricultural Experiment Station *(13), (15)*, and at the North Central States Entomologists' Conference in 1933 *(14)*. In general, in each species of *Triticum* studied except *T. monococcum,* wherever a fairly large number of varieties was available, a wide range of difference in Hessian fly infestation could be found. Of particular interest has been the reaction to Hessian fly of the interspecific hybrids produced by plant breeders in a successful effort to transfer the high stem rust resistance of the wheat species with lower chromosome numbers to *Triticum vulgare.* Hope and H44, derived from a cross between Yaroslav emmer and Marquis common spring wheat, are both completely susceptible, although Yaroslav emmer is resistant. Marquillo, which is the result of an interspecific cross between Iumillo durum and Marquis spring wheat produced at the Minnesota station and discussed by Hays *(7)*, Wilson and Arny *(22)*, Powers *(16)*, has retained at least a part of the resistance to fly found in the Iumillo parent. More recent results [Eighth Biennial Report of the Director of the Kansas Agricultural Experiment Station; Strong *(20)*; Skinner *(18)*; Caldwell and Compton *(1)*] have also shown that a few common spring wheats have high resistance to the Hessian fly wherever, so far, tested.

## MATERIAL AND METHODS

So far as resistance to the Hessian fly is concerned, the importance of Marquillo is partly due to the fact that it was the first common wheat found that proved resistant to fly in the soft wheat belt. Its resistance in the soft wheat belt was first noted in counts made on varieties and hybrids of wheat grown in a Flag Smut Nursery at Leavenworth in 1931, that became infested with Hessian fly. In this nursery four percent of the Marquillo plants were infested, while the average infestation for the Harvest Queen checks was 54 percent. Fulhard, with 20 percent of the plants infested, had the lowest infestation among the varieties of winter wheat.

The first crosses between Marquillo and winter wheats were made in the greenhouse at Manhattan in 1932. Many Marquillo plants first were grown and exposed to Hessian fly infestation. Some of the plants became infested and were discarded. Crosses then were made between the remaining fly-free plants and the winter wheats Tenmarq, Minturki, Oro, Kawvale, and a selection of Kanred X Hard Federation. Since that time additional crosses have been made with Illini Chief sel. 223415, Michigan Wonder and Nebred as the winter wheat parents. Crosses have also been made in 1932 with Fulhard, and later with Clarkan, Chiefkan, Fultz, Honor, and Shepherd, but the $F_1$, plants died after reaching the three- or four-leaf stage, indicating the presence of one or more

lethal factors. The combination of fly resistant Marquillo hybrids with these varieties or their hybrids in 1937 and 1938 have sometimes given $F_1$ plants that died in the same stage, indicating that the cause of this condition is inherited. This lethal has also been studied at Purdue [Caldwell and Compton, *(1)*]. Besides the simple two-variety crosses mentioned, many back-crosses and compound crosses between fly resistant Marquillo hybrids and winter wheats have also been made, principally for the purpose of increasing the winter hardiness of desirable resistant lines.

The first generation hybrids were grown in the greenhouse. All the seed for the $F_2$ generation was sown in the Hessian fly nursery out-of-doors at Manhattan in 1932, where there was elimination of some plants by winter killing. The $F_3$ and $F_4$ selections were grown in the fly nursery at Manhattan and in special nurseries near heavily infested fields in the vicinity of Parsons, Kan., and Springfield, Mo. The $F_5$ and following generations were grown in nurseries near Springfield, Mo., and Manhattan.

The infestations obtained at Manhattan were the result of the introduction of infested stubble or volunteer plants which were placed in trenches and partially covered with soil in the alleys and about the nursery. The infestations at Parsons and Springfield were those which occurred naturally as the result of nearby infested fields and early planting of the material to be tested. On all field sowings in fly nurseries from $F_2$ through $F_5$ kernels were spaced 2 inches apart in rows eight feet long and one foot apart. In $F_3$, and succeeding generations each row was the progeny of a single plant from the preceding year, the plants having been pulled and evaluated individually.

Following infestation, in the fall, each individual plant was examined, and if infested was marked by a small stake. While mostly noninfested plants were saved, occasional exceptionally good plants which had light, infestation and which might segregate for resistance in later generations, also were harvested. Wherever possible, records were made on individuals in the spring for agronomic characters as well as disease infection and fly [Jones *(9)*] and joint worm infestation. The detailed method of handling the Marquillo plants is indicated in figure 1. Natural stem rust infection occurred in the fly nursery in 1934 and 1936 and most strains were tested in disease nurseries for rust and bunt resistance in 1937 and following years. Notes on leaf rust infection were obtained each year.

The immediate purpose of the investigation has been the production of the best possible Hessian fly resistant winter wheats from each cross. Some information has been obtained in regard to mechanisms of resistance and the manner of inheritance of resistance, but because of limitations of space and funds, as well as destruction of individual plants by winter-killing and infestation by fly in early generations, it has been impossible to obtain exact genetic ratios or to make any detailed factorial analysis.

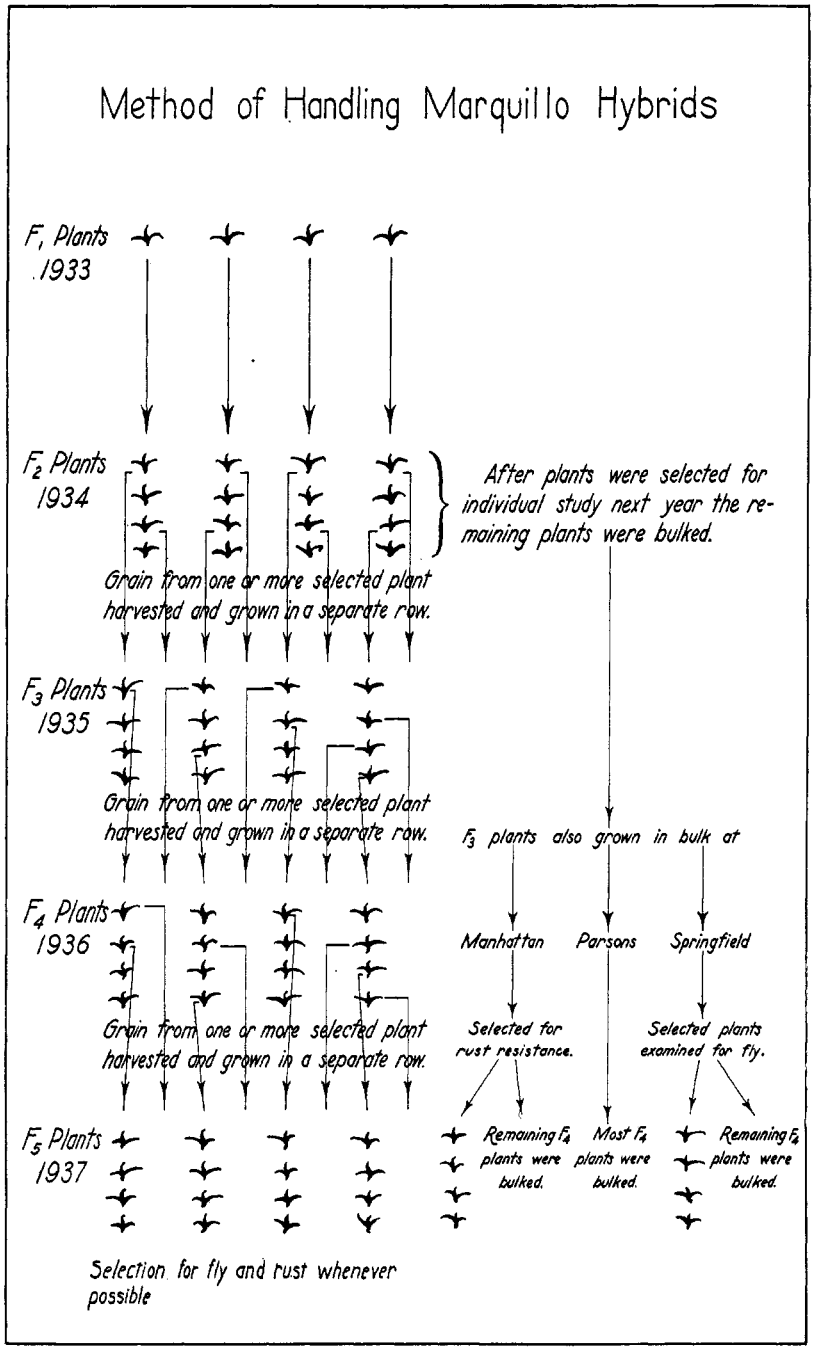



FIG. 1.—Method of handling Marquillo hybrids.

## EXPERIMENTAL RESULTS

### REACTION OF PARENTS TO HESSIAN FLY

There has been little difference in the susceptibility to Hessian fly of the four winter parents, Tenmarq, Minturki, Oro, and Kanred X Hard Federation wherever they have been grown. The other winter variety, Kawvale, carries some resistance to Hessian fly at Manhattan and in certain other localities. The spring wheat variety, Marquillo, has shown approximately the same low intensity of infestation at each of the three places where these experiments have been carried on. Information regarding the relative infestation of the several parental varieties in different years and localities is given in table 1. In this table it will be noticed that in

TABLE 1.—*Infestation of parental varieties in different localities and tests, 1933-1937*

| YEAR, SEASON, AND STATION. | Winter parents. | | Marquillo spring parent. |
|---|---|---|---|
| | Average of susceptible varieties. | Kawvale. | |
| 1933 Fall: | | | |
| Manhattan— | | | |
| Percentage plants infested | 33 | 2 | 2 |
| 1934 Fall: | | | |
| Manhattan— | | | |
| Percentage plants infested | 84 | 8 | 9 |
| Parsons— | | | |
| Percentage plants infested | 69 | 75 | 2 |
| Springfield— | | | |
| Percentage plants infested | 75 | 66 | 6 |
| 1935 Fall: | | | |
| Springfield— | | | |
| Percentage plants infested | 100 | 100 | 44 |
| Percentage spring survival | 0 | 21 | 0 |
| 1936 Fall: | | | |
| Manhattan— | | | |
| Percentage plants infested | 48 | 2 | 0.6 |
| Springfield— | | | |
| Percentage plants infested | 87 | 77 | 0.8 |
| 1937 Spring: | | | |
| Springfield— | | | |
| Percentage culms infested | 36 | 34 | 5 |

the fall of 1934 the infestation at Manhattan was slightly higher than in the other two localities, while in other years the infestation has been lacking or considerably less at Manhattan than elsewhere because of drouth conditions which have prevailed through these years. In the fall of 1935 the infestation at Springfield was so heavy that the majority of susceptible plants were killed by the fly before the advent of winter. The highest winter survival in any variety following this infestation occurred in Kawvale, with 21 per-

TABLE 2.—*Infestation of Marquillo under various intensities of infestations as measured by the infestation of a susceptible check.*

| NUMBER PLANTS COUNTED. | Percentage tillers or culms infested, Marquillo. | Number fly forms on Marquillo. | Percentage plants infested. | | Remarks. |
|---|---|---|---|---|---|
| | | | Variety Marquillo. | Susceptible variety and percentage plants infested in the same test. | |
| 100 | 0 | 0 | 0 | Ceres.....25 | Fall 1933 F. N. (a) Manhattan. |
| 14 | 0 | 0 | 0 | Ceres.....69 | Fall 1930 F. N. Manhattan. |
| 21 | 0 | 0 | 0 | Tenmarq.....52 | Spring 1939 F. N. Springfield, Mo. |
| 120 | 0 | 0 | 0 | Ceres.....92 | Greenhouse 1939 Junction City flies. |
| 310 | | | 0.6 | Tenmarq.....35 | Fall 1936 F. N. Manhattan. Space planted. |
| 486 | | | 0.8 | Tenmarq.....80 | Fall 1936 F. N. Springfield, Mo. Space planted. |
| 100 | 1 | 2 | 1.0 | Tenmarq.....45 | Fall 1936 F. N. Manhattan. Drilled. |
| 75 | | | 1.3 | Tenmarq.....92 | Fall 1938 F. N. Springfield, Mo. Space planted. |
| 281 | | | 1.5 | Ceres.....99 | Fall 1938 F. N. Springfield, Mo. Spring wheats. |
| 50 | 0.6 | 2 | 2.0 | Tenmarq.....66 | Fall 1936 F. N. Springfield, Mo. Drilled. |
| 42 | | | 2.0 | Tenmarq.....72 | Fall 1934 Parsons, Kan. |
| 47 | 0.3 | 1 | 2.1 | Ceres..... 7 | Spring 1936 Wichita, Kan. |
| 73 | 0.4 | 2 | 2.7 | Tenmarq.....38 | Fall 1936 U. S. D. A. U. F. N. (b) Space planted. |
| 100 | 0.9 | 1 | 3.0 | Ceres.....70 | Fall 1936 Springfield, Mo. Spring wheats. |
| 50 | 0.1 | 5 | 4.0 | Ceres.....47 | Fall 1931 Leavenworth, Kan. |
| 22 | | 1 | 4.5 | Tenmarq.....96 | Fall 1938 F. N. Springfield, Mo. Drilled. |
| 300 | 2.8 | 39 | 5.3 | Ceres.....53 | Spring 1939 F. N. Springfield, Mo. Spring wheats. |
| 34 | | | 6.0 | Tenmarq.....77 | Fall 1934 Springfield, Mo. |
| 100 | 1.3 | 6 | 7.4 | Tenmarq.....74 | Fall 1936 Junction City, Kan. |
| 101 | 6 | 9 | 8.0 | Tenmarq.....76 | Spring 1936 Springfield, Mo. |
| 400 | 2.4 | 9.4 | 8.7 | Ceres.....58 | Fall 1937 F. N. Springfield, Mo. Spring wheats. |
| 46 | | | 9.0 | Tenmarq.....97 | Fall 1934, Manhattan. |
| 106 | 5.3 | 24 | 11.7 | Tenmarq.....82 | Spring 1937 F. N. Springfield, Mo. Space planted. |
| 86 | 3.3 | 17 | 12.0 | Ceres.....67 | Spring 1936 Springfield, Mo. |
| 50 | 8.8 | 9 | 14.0 | Ceres.....57 | Spring 1932 Oskaloosa, Kan. |

(a) Fly Nursery.
(b) Uniform Fly Nursery.

*Continued on page 10*

TABLE 2—*Concluded*

| NUMBER PLANTS COUNTED. | Percentage tillers or culms infested, Marquillo. | Number fly forms on Marquillo. | Percentage plants infested. | | Remarks. |
|---|---|---|---|---|---|
| | | | Variety Marquillo. | Susceptible variety and percentage plants infested in the same test. | |
| 113 | ..... | ..... | 16.0 | Tenmarq.....96 | Fall 1937 F. N. Springfield, Mo. Space planted. |
| 37 | 12.5 | 22 | 16.0 | Tenmarq.....62 | Spring 1938 F. N. Springfield, Mo. Space planted. |
| 25 | 6.7 | 28 | 20.0 | Ceres.....96 | Spring 1932 Manhattan, 2d generation fly. |
| 50 | 14.9 | 14 | 22.0 | Tenmarq.....55 | Spring 1934 Parsons, Kan. |
| 84 | 18.0 | ..... | 23.0 | Tenmarq.....95 | Greenhouse 1936 Wichita flies. |
| 150 | 17.5 | 112 | 25.2 | Ceres.....68 | Spring 1935 Parsons, Kan. |
| 52 | 27.0 | 196 | 37.0 | Tenmarq.....94 | Fall 1935 Springfield, Mo. |
| 61 | 35.0 | 111 | 43.0 | Tenmarq.....97 | Fall 1935 Parsons, Kan. |
| 111 | ..... | ..... | 44.0 | Tenmarq.....100 | Fall 1935 Springfield, Mo. |
| 85 | 34.0 | ..... | 46.0 | Tenmarq.....96 | Greenhouse 1936 Springfield flies. |
| 350 | 25.2 | 1192 (c) | 52.0 | Ceres.....84 | Spring 1937 Springfield, Mo. Spring wheats. |

(c) Includes many small larvae; 4,831 forms on Ceres in same test.

cent of surviving plants. Marquillo, being a spring wheat, also failed to survive the winter.

The infestation of Marquillo under varying intensities is given in table 2 and figure 2. In these records the infestation of Marquillo is compared with the susceptible varieties Ceres or Tenmarq in the same test. It will be seen that in most of the tests in which the susceptible varieties had less than 90 percent of the plants infested, the infestation of Marquillo was usually below 10 percent.

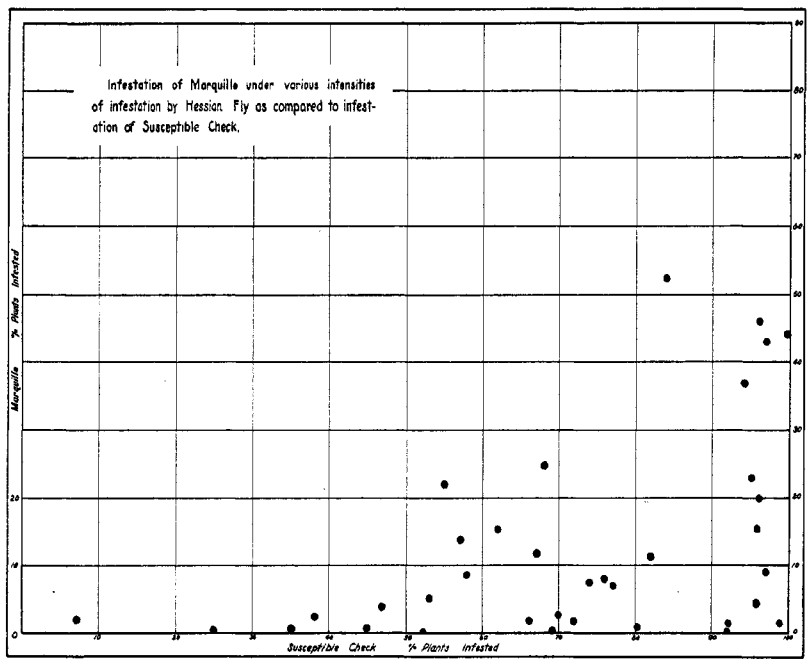



FIG. 2.—Infestation of Marquillo under various intensities of infestation by Hessian fly as compared with infestation of susceptible check.

Thus, while the infestation of Marquillo is relative with respect to the general level of infestation, it is low enough to be of economic importance, since infestations occuring in farmers' fields are generally below 90 percent infested plants.

Most of the resistance to fly found in Marquillo probably comes from its durum parent, Iumillo, as indicated in the data in table 3. Several different selections of Iumillo have been tested and all have given infestations approximately similar to that of Marquillo in the same test.

The resistance of Marquillo appears to consist of several different mechanisms herein designated as low larval survival, low oviposition, and tolerance or ability of plants to survive an infestation.

TABLE 3.—*The origin of Marquillo fly resistance from Iumillo durum is indicated by data secured at Springfield, Mo., fall, 1936.*

| VARIETY. | Percent plants infested. | Percent tillers infested. |
|---|---|---|
| Iumillo Sel 86 | 0 | 0 |
| Marquillo Sel 32LRN31 | 3 | 0.9 |
| Marquis | 62 | 23 |
| Ceres | 70 | 35 |

The first and principal mechanism involved is that on Marquillo and its hybrids; much smaller numbers of larvae survive and grow, after migration to the normal feeding position. The exact reason for this low larval survival is as yet unknown. The second mechanism entering into Marquillo resistance is that under some conditions fewer eggs are laid on Marquillo than on most other wheat varieties. Table 4 gives an example of this type of difference be-

TABLE 4.—*Part of the resistance of Marquillo is at times the result of a lower oviposition rate as indicated by data secured at Manhattan fly nursery, April, 1935.*

| VARIETY. | Number plants. | Actual number of eggs. | Calculated number eggs on 60 plants. |
|---|---|---|---|
| Marquillo | 60 | 5 | 5 |
| Kawvale | 20 | 5 | 15 |
| Turkey | 20 | 13 | 39 |
| Ceres | 60 | 41 | 41 |

tween varieties. It should be indicated, however, that for some reason yet unknown, Marquillo does not always call forth this low oviposition reaction in greenhouse tests. In addition to these two resistance mechanisms, Marquillo plants and their hybrids have sometimes shown a third mechanism consisting of greater ability to survive under heavy infestations than do other spring or winter wheats. This type of tolerance, and the two resistance mechanisms mentioned previously, appear to be independently inherited. There has been some evidence that strains of Marquillo differ in their degree of resistance. This is not surprising, since Marquillo is known to be somewhat unstable cytologically, according to Powers *(16)*.

## INFESTATION OF $F_1$ MARQUILLO HYBRIDS

No information was obtained on the Hessian fly susceptibility of $F_1$ plants of the original Marquillo crosses, but subsequently the three sets of data recorded in table 5 have been obtained in green-

TABLE 5.—*The Hessian fly infestation of $F_1$ plants involving fly resistance from Marquillo compared to susceptible winter wheat parents, Marquillo, and to winter habit fly-resistant Marquillo hybrids used as parents at greenhouse, Manhattan, Kan.*

| WHEAT STRAINS AND CONDITIONS OF EXPERIMENT. | Total plants. | Percent plants infested. | Percent tillers infested. | Total fly. | Fly per infested tiller. |
|---|---|---|---|---|---|
| **1935 Fly from Parsons, Kan.** | | | | | |
| Marquillo | 27 | 4 | 4 | 1 | 1 |
| Resistant $F_3$ Marquillo Hybrid Parents | 56 | 14 | 7 | 11 | 1.4 |
| $F_1$ Susceptible winter wheat ♂ / Resistant $F_3$ Marquillo Hybrid ♀ | 46 | 78 | 39 | 338 | 4.8 |
| Susceptible winter wheat Parents | 46 | 91 | 54 | 247 | 4.4 |
| **1938 Fly from Springfield, Mo.** | | | | | |
| Resistant $F_5$ Marquillo Hybrid Parents | 13 | 46 | 9 | 53 | 5 |
| $F_1$ Susceptible winter wheat ♂ / Resistant $F_5$ Marquillo Hybrid ♀ | 34 | 100 | 33 | 997 | 88 |
| $F_1$ Susceptible Nebred CI10094 ♂ / Marquillo ♀ | 4 | 100 | 61 | 119 | 60 |
| Susceptible winter wheat Parents | 31 | 100 | 60 | 1,091 | 56 |
| **1939 Fly from Manhattan, Kan.** | | | | | |
| Marquillo × Oro $F_6$ Parent | 6 | 0 | 0 | 0 | 0 |
| $F_1$ Susceptible Nebred CI10094 ♂ / Resistant Marquillo × Oro ♀ | 8 | 50 | 46 | 48 | 4 |
| Susceptible Nebred Parents | 6 | 67 | 42 | 20 | 2 |

house tests. These data concern mostly compound crosses and back crosses between resistant Marquillo hybrids and susceptible winter wheats. In 1935 ten different crosses were studied, in 1938 four crosses, and 1939 one cross, totaling 92 individual $F_1$ plants. There was considerable difference in the intensities of infestation of the three different tests. In one test, fly from the hard wheat belt was used; in others, fly from the soft wheat belt was used. Despite these differences in conditions of the experiments, as well as certain differences in handling, all tests agree in indicating that susceptibility tends to be a dominant character in Marquillo crosses (fig. 3). This susceptibility probably concerns the resistance mechanism for low oviposition as well as for low larval survival. Although no actual egg counts were made, the data in table 5 indicate that, on the average, more larvae survive on the $F_1$ plants than on

the susceptible winter parents in the same test. Thus, it would appear that at least as many eggs were deposited on these $F_1$ plants as on their susceptible parents, although the increased number of larvae is probably not significant.

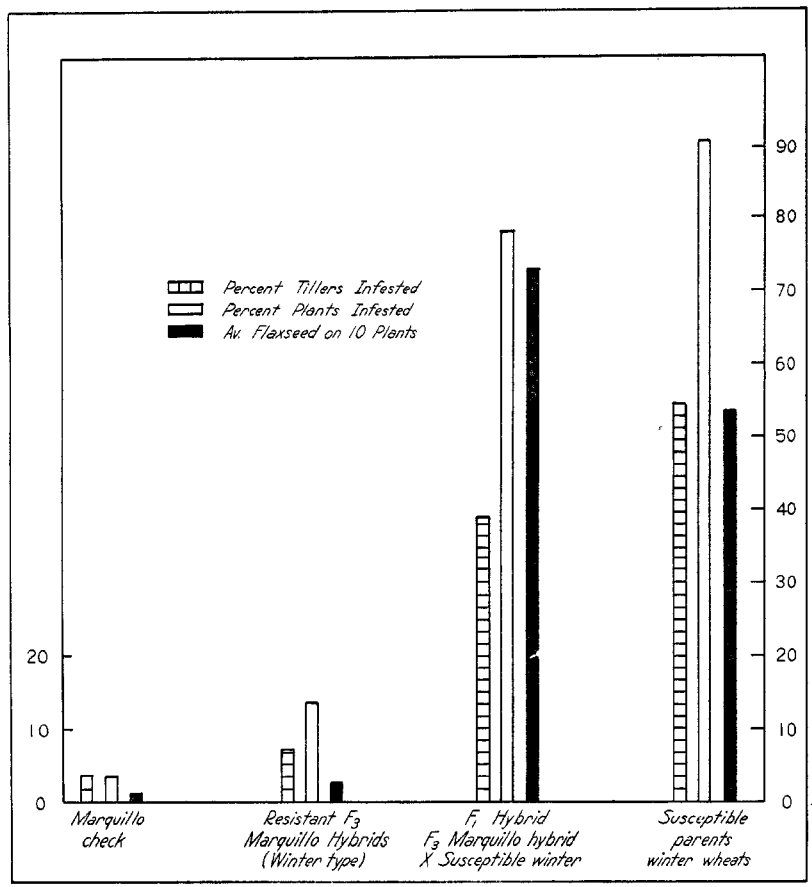



FIG. 3.—The susceptibility of $F_1$ hybrids involving Hessian fly resistance from Marquillo, compared with the resistant and susceptible parents; fly from Parsons, Kan., 1935.

## INFESTATION OF $F_2$ MARQUILLO HYBRIDS

In five field tests data were obtained on the infestation by Hessian fly of $F_2$, hybrid plants involving resistance inherited from Marquillo. These data are presented in table 6 and figure 4. In the fall of 1933 at Manhattan information was obtained on the infestation of the original Marquillo crosses. In the fall of 1937 and 1938 information was obtained at both Manhattan and Springfield on the infestation of $F_2$, back-crosses and compound hybrids between resistant Marquillo hybrids in $F_3$, and $F_5$, susceptible winter wheats. The infestations at Springfield were approximately twice as heavy as any of the Manhattan infestations. Notwithstanding

TABLE 6.—*The field infestation of $F_2$ hybrid plants, which carry resistance to fly from Marquillo, compared with susceptible and resistant parents.*

| VARIETY. | Percent of plants infested. | | Total plants in $F_2$. | |
|---|---|---|---|---|
| | Manhattan. | Springfield. | Manhattan. | Springfield. |
| **Fall 1933** | | | | |
| Marquillo | 2.4 | ..... | ..... | ..... |
| $F_2$ Marquillo × Susceptible Parents | 11.6 | ..... | 1,185 | ..... |
| Susceptible Parents | 32.7 | ..... | ..... | ..... |
| **Fall 1937** | | | | |
| Resistant $F_2$ Marquillo Hybrids | 4 | 8 | ..... | ..... |
| $F_2$ Resistant $F_3$ Marquillo Hybrids × Susceptible Parents | 10 | 30 | 512 | 1,254 |
| Susceptible Parents | 38 | 87 | ..... | ..... |
| **Fall 1938** | | | | |
| Resistant $F_3$ Marquillo × Tenmarq | 18 | 7 | ..... | ..... |
| $F_2$ (Marquillo × Tenmarq $F_5$) × Oro | 21 | 38 | 209 | 208 |
| Susceptible parent Oro | 50 | 80 | ..... | ..... |

the difference in locality and in intensity of infestation, all of the data obtained are in general agreement. The $F_2$ population in all cases was less than one-half as susceptible as the susceptible parent, although usually more than twice as susceptible as the resistant parent. This apparent reversal of dominance as compared to the results in the $F_1$ generation would appear to indicate either that results In greenhouse and field were not comparable or that resistance was due to two or more genes. Probably both genetic and environmental factors entered into these results.

The estimated amount of winter injury on the original $F_2$ Marquillo hybrids was approximately parallel with the known winter hardiness of the winter parents. The actual estimated percentages of winter injury were as follows: Marquillo X Minturki, 20; Marquillo X Oro, 23; Marquillo X Tenmarq, 37; Kawvale X Marquillo, 45; and (Kanred X Hard Federation) X Marquillo, 81.

A varying number of $F_2$ hybrid plants were killed by the winter, but in this test there was no evidence of relationship between winter killing and fly infestation or between winter habit of growth and infestation by fly.

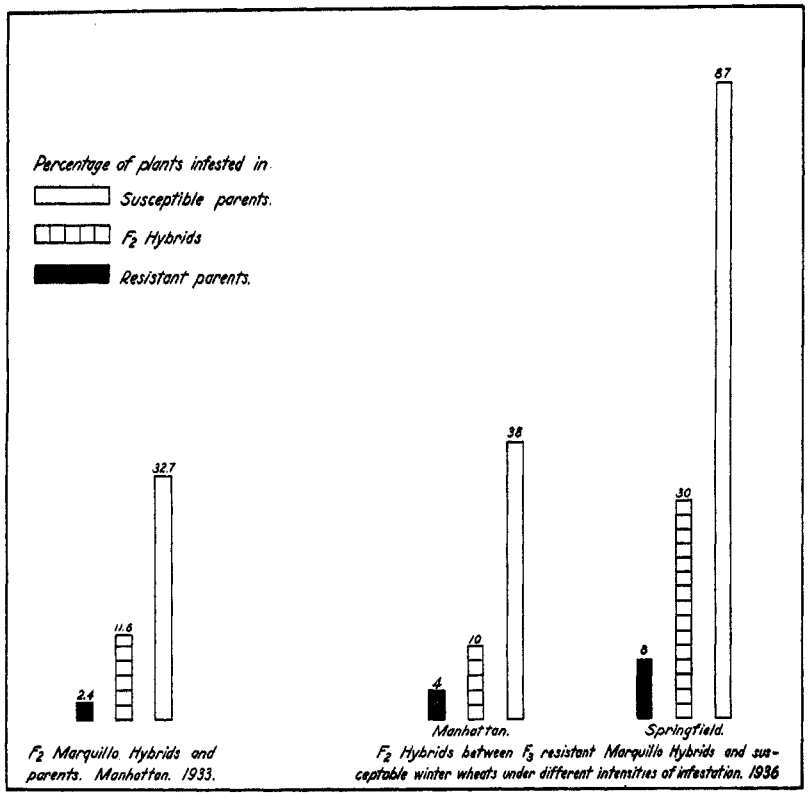



FIG. 4.—Comparison of infestation by Hessian fly in $F_2$ Marquillo hybrid populations with that in resistant and susceptible parents.

## OBSERVATIONS ON $F_3$ MARQUILLO HYBRIDS

In the spring of 1934 the $F_2$ plants infested by Hessian fly were discarded and 135 selections on the basis of plant and grain characters were made from the plants which survived the winter. In this and the succeeding generations an attempt was made to select mostly segregates with soft kernels from the Minturki cross and segregates with hard kernels from the other crosses. Segregates with white kernels appeared in the Minturki cross and in the cross with Kanred X Hard Federation; some of these were fly resistant. Seventy-three of the selections were planted at Manhattan only; 23 were planted at Parsons and Springfield; and the grain from

39 plants was divided into three parts and planted in all three nurseries.

A satisfactory fly infestation was secured in all the nurseries in the fall. As measured by the susceptible winter wheat varieties the infestation was nearly equal at the three places, but slightly greater at Manhattan (table 1). In the three nurseries the Marquillo parent ranged in infestation from two to nine percent and the susceptible winter wheat parents from 67 to 97 percent of the plants infested. The hybrid $F_3$ populations, each derived from a single $F_2$ plant, ranged in infestation from zero to 93 percent on

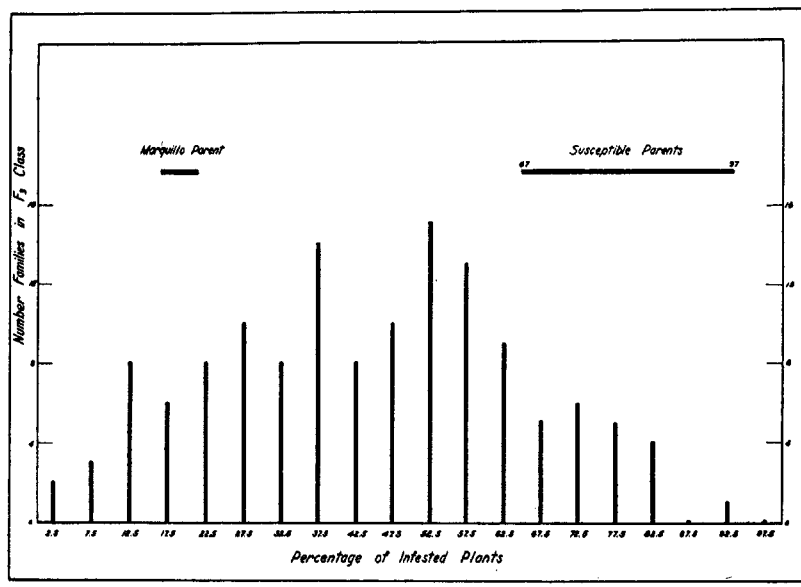



FIG. 5.—Frequency distribution of Hessian fly infestation of 135 rows of $F_3$ hybrids between Marquillo and winter wheats, fall of 1934

plants infested. In comparing the results obtained at the three stations the highest correlation was found between the percentage of plants infested among the 62 hybrid lines representing five crosses grown both at Parsons and Springfield ($r = +0.72$; p. less than 1 percent). Highly significant correlations also were secured in a comparison of 40 hybrids other than Kawvale X Marquillo grown at both Manhattan and Parsons ($r = +0.66$) and the same 40 hybrids grown at both Manhattan and Springfield ($r = +0.70$).[4] The Kawvale X Marquillo hybrids were omitted from the latter two comparisons, since at Manhattan these hybrids represent a cross be-

4. In testing the significance of the correlation coefficients, use has been made of Table 7.2 by Snedecor (18).

tween two resistant parents while the other crosses are between resistant and susceptible parents.

A study of the frequency distribution of the percentage of plants infested among $F_3$ hybrids and based on records from all the nurseries (fig. 5) indicates no clear cut divisions between susceptible and resistant segregates. Considering especially the discarding of susceptible $F_2$ plants the distribution confirms the probability of a complex genetic basis for resistance.

Where sufficient lines were continued to make it possible, a rough classification can be made of these $F_3$ families based on the behavior of their progeny in $F_4$ and $F_5$ generations. Such a classification is given in table 7. The average of the resistant families

TABLE 7.—*Classification of $F_3$ families based on the behavior of their progeny in later generations where sufficient lines were continued to make this classification possible.*

| $F_4$, $F_5$ BASIS FOR CLASSIFICATION. | Percent plants infested in $F_3$ row. | Average percent plants infested for class named. | Average for segregating rows. |
|---|---|---|---|
| Resistant | 3, 8, 11, 16 | 9.5 | |
| Segregating, mostly resistant | 14, 19, 21, 21, 27, 28, 30, 37, 38 | 26.2 | 32.1 |
| Segregating | 16, 43, 45, 54, 56 | 42.8 | |
| Segregating, mostly susceptible | 22, 22, 29, 32, 39, 55 | 33.1 (a) | |
| Susceptible | Insufficient lines continued for classification. | | |

(a) Insufficient lines continued to give reliable classification.

in $F_3$ is approximately the same as the average for Marquillo in the same tests. Based on this classification, with rows from zero to 15 percent considered resistant, there are only 13 segregates out of the 135 families from $F_2$ plants which approach the resistance of the Marquillo parent. This is again evidence that resistance tends to be inherited as a recessive character and apparently more than one genetic factor is involved.

The first information on stem and leaf rust resistance in these hybrids was obtained in the $F_3$ generation at Manhattan, where leaf rust infection ranged from a trace to 80 percent in various hybrid lines. Many lines were segregating at various levels of infection. The stem rust infection was lower and somewhat less uniform, but a rough classification was made of the various lines as being susceptible, intermediate, resistant, or segregating. No relationship was evident between resistance to either leaf or stem rust or fly, and any other character recorded. This lack of relationship was confirmed in later generations.

Many of the $F_3$ lines of all crosses were evidently segregating for fly resistance, for winter hardiness, and for spring or winter habit of growth. If infestation by fly had made the wheat more easily killed by cold weather this weakness should be apparent in a comparison between infested and uninfested plants of rows with varying degrees of winter survival. The percentage of spring survival of all plants in each $F_3$ row at Manhattan with the percentage

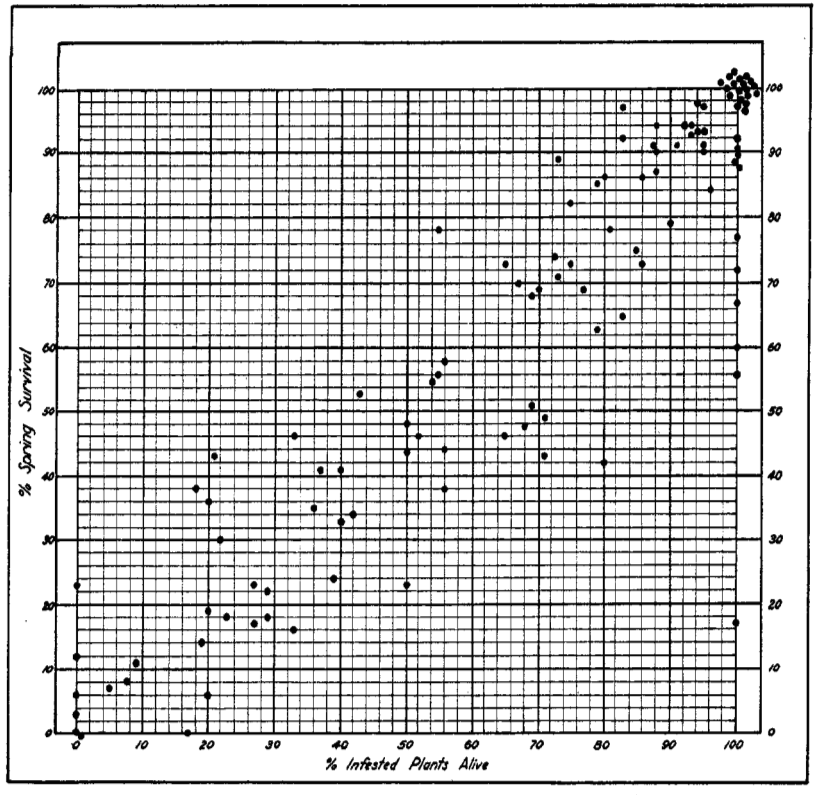



FIG. 6.—Comparison of percentage of spring survival of all plants in $F_3$ rows of Marquillo hybrids with the percentage of survival of infested plants in the same row.

of infested plants in the same row which were alive in the spring is diagramed in figure 6. It is quite evident that in almost all cases infested and uninfested plants had about the same percentage of winter survival. This appears to indicate that fly resistance is inherited independently of susceptibility to winter killing and that under the conditions in this particular season infested plants showed very little more susceptibility to winter injury than did the uninfested sibs in the same row.

Only seven $F_3$ Kawvale X Marquillo hybrid lines were grown at Manhattan (fig. 7). The infestation in these rows ranged from four to 78 percent of the plants infested; most of the rows having a low infestation as did both Kawvale and Marquillo in the nursery. The presence of the susceptible hybrid from a cross between two resistant lines is good evidence that the resistance of Kawvale and of Marquillo at Manhattan is the result of distinct genetic factors. Another Kawvale X Marquillo line had zero percent plants infested

FIG. 7.—Infested plants in the 1934-'35 fly nursery, Manhattan, Kan., each marked by a small stake. Left, row 758, Oro, 87 percent plants infested; right, row 766 Kawvale, 1 infested plant (8 percent); seven rows between are Kawvale × Marquillo $F_3$, 4 percent to 78 percent infested plants.

at Manhattan and an average of 45 percent at Parsons and Springfield in $F_3$. In later generations this $F_3$ was evidently segregating for resistance to the eastern type of fly, but all lines continued to have a low infestation at Manhattan.

## OBSERVATIONS ON $F_4$ MARQUILLO HYBRIDS

The only $F_3$ hybrids that were continued in $F_4$ were those which had good records in several of the observed characters. Of these there was a single selection from one family, two selections from three families and three to nineteen selections among the remaining 58 families represented. An interannual correlation between the fly infestation of these 62 families showed a highly significant relationship ($r = +0.54$; $p = <1\%$). The comparison was made between the $F_4$ infestation at Springfield and the percentage of plants infested in $F_3$ at Manhattan, or an average of the percent of plants infested at the eastern nurseries in those cases where the selection was not grown at Manhattan. This relationship between the infestation in $F_3$ in 1935 and $F_4$ in 1936 is indicated in figure 8.

The infestation at Springfield in the fall of 1935 was the heaviest natural infestation seen by the writers. All the susceptible winter

wheat plants, which were space-planted as checks among the hybrids, were infested by fly and many of them were dying at the time infestation records were being taken, November 8 to 12. A number of winter wheat varieties and non-Marquillo hybrids were also destroyed by the infestation.

As high as 270 larvae (fig. 10) were removed from a plant consisting of a single tiller. Some concept of this infestation may be obtained by examination of figures 9 to 12, which show plants and

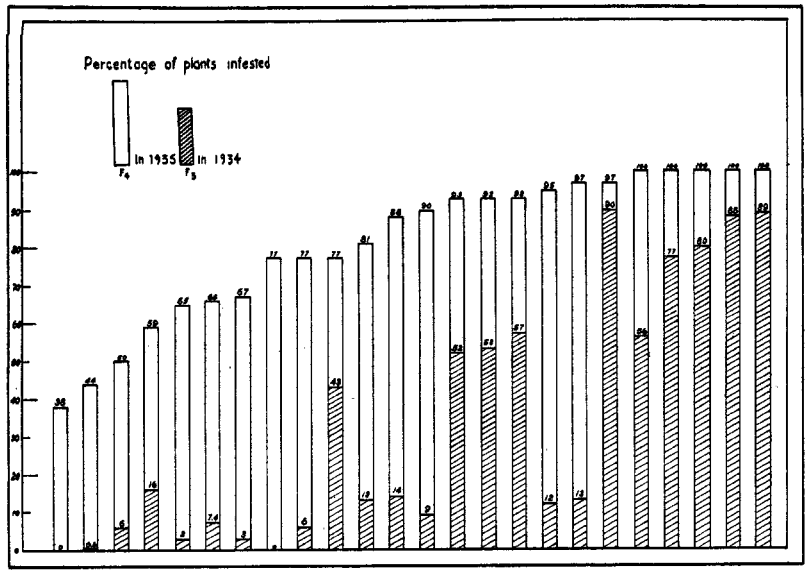



FIG. 8.—Comparison between infestation of $F_3$ hybrid families in the fall of 1934 with the infestation of progeny of the same families in the fall of 1935.

larvae taken from adjacent rows in this nursery. The plants shown carried more than the usual number of larvae, but all susceptible plants in the nursery had an average of more than 20 larvae each. These counts were made after shipping the plants to Manhattan. By that time many leaf sheaths were being broken open by the growing larvae, and undoubtedly many larvae were lost from the more heavily infested plants.

The Marquillo X Oro plant, shown in figures 10 and 12, was from selection 35 FN 742 a family which later gave rise to selections resistant to fly, leaf and stem rust, and bunt. This plant was from a drilled row of bulk $F_4$ seed which had been planted in the dissection series. In examining a number of plants from this row and in counting under the microscope the small first instar larvae which were present, it was noted that there was a wider variation in the number of larvae present on the different plants than in the

case of the Tenmarq plants examined. It is possible that this line was segregating for the character of low oviposition rate expressed under some conditions by the Marquillo parent. It has not been possible to get further information on this point.

FIG. 9.—Plant of Tenmarq infested with 217 larvae, Springfield, Mo., fly nursery, fall of 1935, natural infestation.

FIG. 10.—Plant of Marquillo × Oro hybrid infested with 270 larvae, Springfield, Mo., fly nursery, fall of 1935, natural infestation.

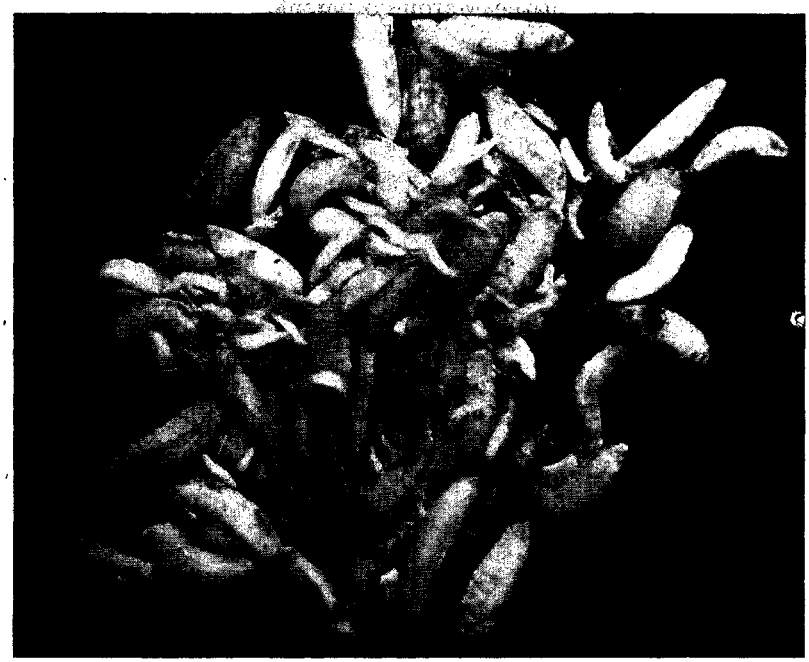


FIG. 11.—Larvae removed from Tenmarq plant of single tiller shown in figure 9. Seventy-four percent of the larvae showed evidence of feeding and growth.

FIG. 12.—Larvae removed from Marquillo × Oro hybrid plant of single tiller shown in figure 10. Only 11 percent of the larvae showed some evidence of feeding and growth.

The various rows of the Marquillo parent ranged from 20 to 85 percent of the plants infested with an average of 44 percent. Under these same conditions the infestation of the 266 hybrid lines ranged from 32 to 100 percent. Only five hybrids had less than the average of the resistant Marquillo parent, but 64 percent of them had an infestation below that of the highest, Marquillo check row,

Whereas the winter wheats, except Marquillo hybrids, were severely injured by fly, most of the hybrid rows, even those with high infestation, were materially better in vigor and in general appear-

TABLE 8.—*Comparison of percentage of plants infested by Hessian fly and spring survival in $F_4$ lines with lowest infestation and in all lines with more than 90 percent spring survival. Springfield, Mo., and Manhattan, Kan., 1935-'36.*

| RANK. | 1936 Row number. | Springfield. | | Manhattan. | Winter parent. |
|---|---|---|---|---|---|
| | | Percent of plants infested. | Percent survival after killing by fly and winter. | Percent survival from winter killing only. | |
| ROWS WITH LOWEST FLY INFESTATION AT SPRINGFIELD | | | | | |
| 1 | 623 | 32 | 57 | 45 | Tenmarq |
| 2 | 606 | 38 | 100 | 91 | Tenmarq |
| 3 | 653 | 41 | 69 | 100 | Tenmarq |
| 4 | 787 | 41 | 59 | 89 | Oro |
| 5 | 677 | 42 | 74 | 95 | Minturki |
| 6 | Marquillo | 44 | 0 | 0 | ..... |
| 7 | 818 | 47 | 95 | 94 | Kawvale |
| 8 | 605 | 50 | 67 | 95 | Tenmarq |
| 9 | 843 | 52 | 76 | 90 | Kawvale |
| 10 | 790 | 54 | 79 | 84 | Oro |
| 11 | 607 | 54 | 92 | 100 | Tenmarq |
| 12 | 740 | 54 | 23 | 75 | Minturki |
| ROWS WITH HIGHEST SURVIVAL AT SPRINGFIELD | | | | | |
| 1 | 606 | 38 | 100 | 91 | Tenmarq |
| 2 | 824 | 63 | 100 | 96 | Kawvale |
| 3 | 833 | 97 | 100 | 83 | Kawvale |
| 4 | 818 | 47 | 95 | 94 | Kawvale |
| 5 | 813 | 95 | 95 | 95 | Oro |
| 6 | 607 | 54 | 92 | 100 | Tenmarq |
| 7 | 848 | 82 | 91 | 100 | Kawvale |

ance. While the winter parental plants, each consisting of only one tiller, were dying as a result of the infestation, the better hybrid plants each had four or five uninjured tillers. Frequently it was impossible to determine the presence of larvae on these hybrids without digging the plants. Thus, under an extremely heavy infestation many of the Marquillo hybrids, even though infested, represent a marked advance over their winter parents.

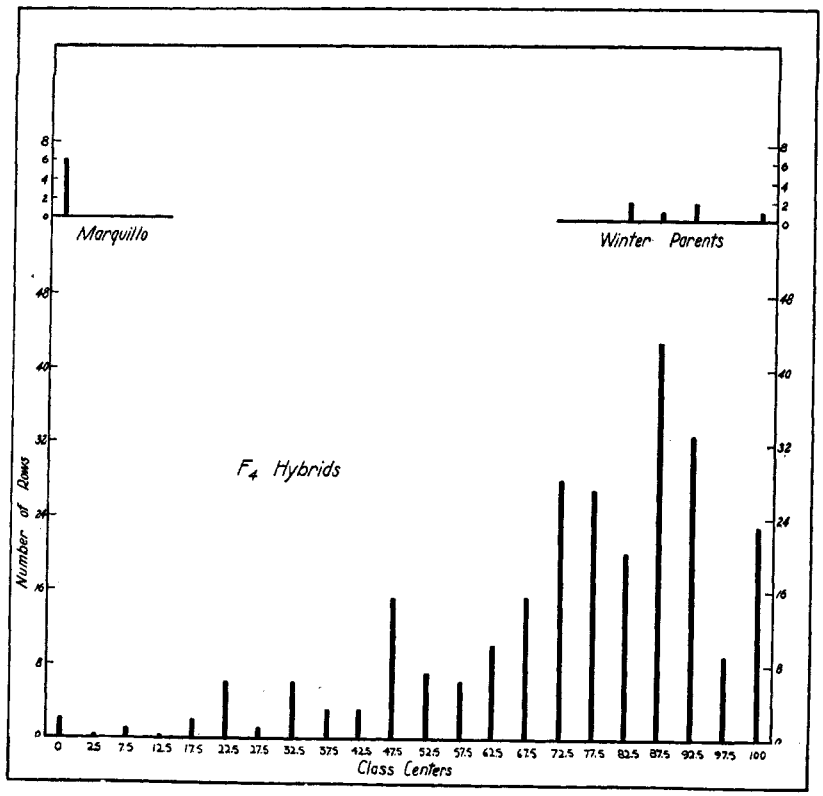



FIG. 13.—Comparison between the winter hardiness of parents and $F_4$ Marquillo hybrids in the absence of Hessian fly infestation, Manhattan, Kan., 1935-'36.

There was no clear-cut parallel between infestation and the survival following infestation in the various families when one considers the entire group of Marquillo hybrids. This is best illustrated by table 8, in which a comparison is made between the rows with the highest survival at Springfield and those with the lowest percentage of plants infested. The loss of stand shown in the column giving the percentage of survival at Manhattan, where there was no fly infestation, is the result principally of winter kill-

ing, while the reduced stand shown in the column giving the percentage of survival at Springfield is the result of killing by both fly and winter. It will be noted that the survival of the 11 rows of hybrids with the lowest percentage of plants infested was no greater both at Springfield and Manhattan than for those rows with the highest infestation. Among these same 11 $F_4$ lines there were four in which the survival was at least 25 percent less at Springfield than at Manhattan. Among the group of seven rows with survival above 90 percent both at Springfield and Manhattan there was only one row with an infestation less than the average for the Marquillo check, while there were three rows with high survival with an infestation above 80 percent.

These facts would appear to indicate that in these hybrids there is little or no relationship between intensity of infestation and survival in the spring. The results obtained individually on approxi-

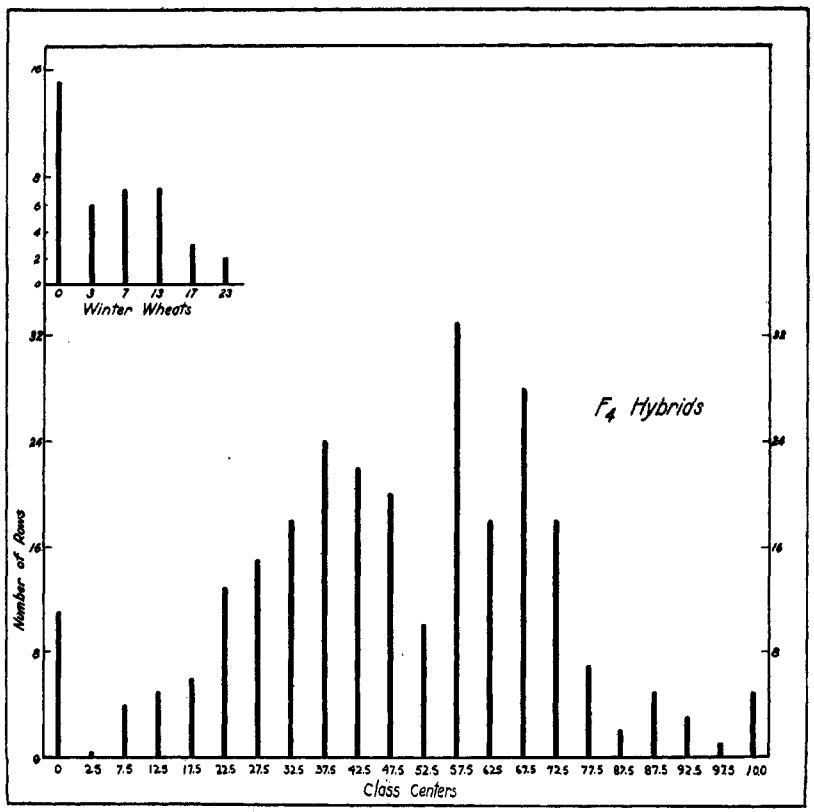



FIG. 14.—Comparison between survival of winter wheats and $F_4$ Marquillo hybrids after heavy infestation by Hessian fly, Springfield, Mo., 1935-'36. The same hybrid lines are involved in figures 13 and 14.

mately 266 $F_4$ hybrids confirm this lack of relationship between intensity of infestation and survival in the spring.

Among 48 $F_4$ Marquillo hybrids with 100 percent of the plants infested, more than one-half had a better spring survival than did any row of susceptible winter wheat variety in the nursery.

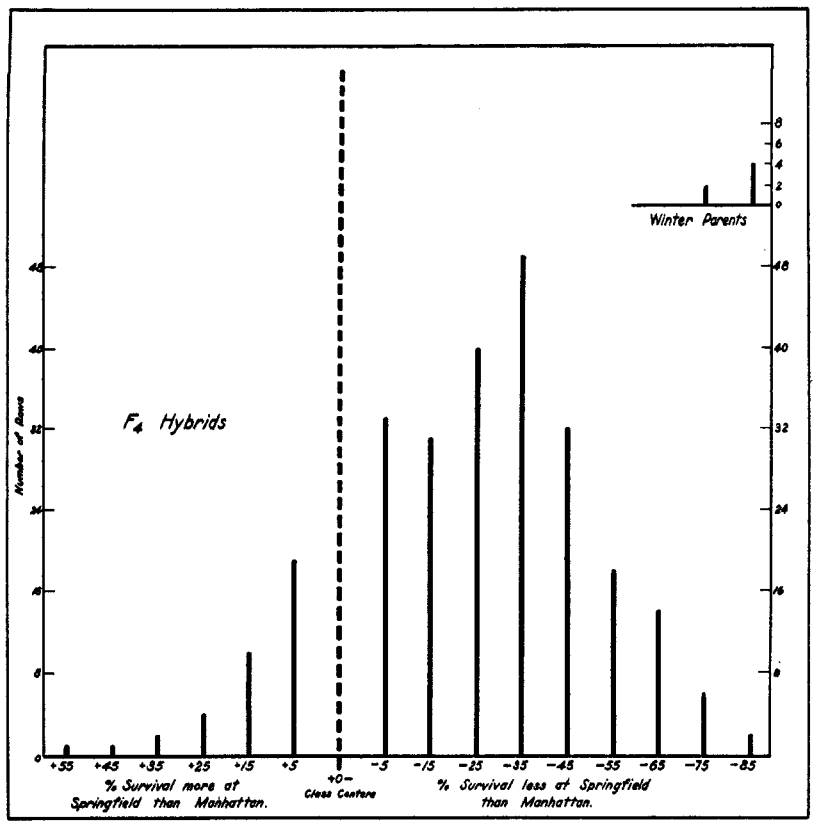



FIG. 15.—The difference in survival between the same lines of $F_4$ Marquillo hybrids after killing by winter and heavy fly infestation at Springfield, Mo., and after winter killing only at Manhattan, Kan., 1935-'36.

An examination of the frequency distribution for percentage of spring survival in the absence of fly at Manhattan among the $F_4$ Marquillo hybrids shows that selection in the direction of the winter-hardy parents has been fairly successful, since almost one-half of the hybrids had a survival figure as high as that of the winter parents (fig. 13). A comparable frequency distribution for the $F_4$ Marquillo hybrid rows and their parents at Springfield after infestation by Hessian fly shows an entirely different picture (fig. 14) as a result of the killing by fly that took place there. As re-

corded above, all the winter wheats other than Marquillo hybrids had less than 25 percent survival under the heavy Hessian fly infestation, while more than 80 percent of the $F_4$ Marquillo hybrids had a better survival than any individual row of a winter wheat variety. Thus these hybrids possess a resistance to killing by the fly that the winter wheat varieties do not show and which Marquillo cannot show, since it is a non-winterhardy spring wheat.

FIG. 16.—Two large bundles representing the total yield from duplicate rows of Marquillo × Oro $F_4$ plants of selection 35 FN 742 which was partially resistant to Hessian fly and winter killing compared with small bundles representing total yield of an ordinary hardy but fly-susceptible winter wheat in adjoining rows, Springfield, Mo., 1935-'36.

Some evidence was given above that genetic factors resulting in low infestations were not the same as those resulting in resistance to killing by fly. It is possible to separate the factor of differential winter hardiness from the factor for differential killing by fly by subtracting in each row of $F_4$ hybrids the percentage of survival at Springfield from the percentage of survival at Manhattan. The remainder, as evident from the above analysis, represents the amount of killing due to fly and may likewise be plotted in a frequency distribution (fig. 15). This gives a distribution resembling the "normal" curve and indicates that by selecting for low infestation and high winter survival in $F_2$ and $F_3$ there was no selection for

ability to exhibit high survival after a heavy infestation. If low infestation were governed by the same genetic factors as ability to survive fly infestation one would expect many Marquillo hybrids to have had higher survival at Springfield than at Manhattan. This was not true of the material studied.

The extremely heavy infestation in $F_4$ made possible a selection for this second type of mechanism of resistance. The importance of this factor in resistance is indicated by figure 16, in which the yields of culms and heads of single $F_4$ Marquillo rows (selection 35 FN 742) are compared with the similar yield of adjoining rows of ordinary fly susceptible winter wheat. The Marquillo hybrid population was still segregating for resistance to fly and to winter killing.

Further evidence of the lack of relation between killing of plants by Hessian fly and the inherited factors for low infestation has been obtained from another source. Four plots representing as many Marquillo hybrids were planted thinly as bulk $F_3$ populations at Manhattan and Springfield in the fall of 1935 (fig. 1). There was some winter killing at both stations. At Springfield, the $F_3$ plants were subjected to the heavy infestation described above. Seed obtained from the plots at Manhattan and Springfield was planted the following year and the percentage of infested plants recorded. Since more than 75 percent of the susceptible wheats were

TABLE 9.—*The comparison of subsequent infestation in bulk Marquillo hybrids from seed stocks surviving heavy infestation at Springfield, Mo., and those from Manhattan, Kan., which had not been exposed to killing by fly in 1935-1936.*

| VARIETY OR $F_4$ BULK HYBRID. | Percent of plants infested. | | | | Percent of culms infested. | |
|---|---|---|---|---|---|---|
| | Manhattan, Fall, 1936. | | Springfield, Fall, 1936. | | Springfield, Spring, 1937. | |
| | Seed from Manhattan (a) | Seed from Springfield (b) | Seed from Manhattan (a) | Seed from Springfield (b) | Seed from Manhattan (a) | Seed from Springfield (b) |
| Marquillo × Tenmarq | 30 | 17 | 40 | 20 | 28 | 8 |
| Marquillo × Oro | 27 | 9 | 32 | 26 | 14 | 28 |
| Kawvale × Marquillo | 19 | 4 | 26 | 36 | 19 | 16 |
| (Kanred × H. F.) × Marquillo | 15 | 7 | 52 | 28 | 22 | 28 |
| Tenmarq | 35 | 49 | 54 | 66 | 64 | 80 |
| Marquillo | 1 | ..... | 2 | ..... | 6 | ..... |

(a) No killing by Hessian fly of susceptible segregates from which seed was grown, Manhattan, Kan., 1935-'36.

(b) Some of susceptible segregates in rows producing this seed were killed by fly in fall of 1935. In space planted susceptible wheats 75 to 100 percent of plants were killed, Springfield, Mo.

killed at Springfield in the fall of 1935, a considerably lower infestation was expected on the bulk of the Marquillo hybrids saved from Springfield than those from Manhattan. This would be especially true if selections for resistance to killing by fly were also to result in selection for low larval survival. However, the results recorded in table 9 show surprisingly little difference between the two lots of seed which differed only in respect to plants that had been killed by fly in the fall of 1935. This is further evidence that no very close genetic relationship existed between resistance to killing by fly and low larval survival or infestation.

It is recognized that in susceptible plants the amount of killing by Hessian fly may be proportional to the intensity of infestation. Therefore, the segregates of Marquillo hybrids having low intensity of infestation might be expected to have somewhat higher survival regardless of any genetic differences for this factor. This relationship probably is partly responsible for the small difference in infestation recorded in table 9 for the bulk hybrids from the two sources.

In the nursery at Springfield the spring generation of fly gave a relatively light infestation, but a heavy infestation of joint worm *(Harmolita tritici* [Fitch]) occurred in the spring of 1936. The different lines of Marquillo hybrids showed considerable variation in respect to the amount of damage done by this insect. Since the parental winter wheat checks had been killed by the fly and many of the Marquillo hybrids reduced in respect to number of plants it was possible only to get an intimation that some of the hybrid lines may be of value in a program for the study of resistance to this insect.

In the Manhattan fly nursery, in addition to the information on winter hardiness, data were obtained on differences in infection by leaf rust and stem rust. Stem-rust infection in the fly nursery varied from a trace to 85 percent among the $F_4$ Marquillo hybrid lines. Marquillo had only a trace of stem rust and only slightly more than a trace of leaf rust. Among the hybrids 80 lines had an infection of less than 25 percent stem rust, while 60 lines out of a total of 265 were still segregating for resistance to this disease. The Kawvale parent had a stem-rust infection of 25 percent, Minturki 45, Tenmarq and Oro 65, and Kanred X Hard Federation 85 percent. Leaf-rust infection readings were taken only on the lines which exhibited considerable resistance to stem rust, but the range of infection by leaf rust varied from a trace to 65 percent among the various hybrids.

Unusually heavy infestations of the wheat jointworm *(Harmolita tritici* [Fitch]) occurred during the testing of the $F_4$ and $F_7$ generation plants at Springfield. Lighter, though appreciable, mfestations prevailed during the testing of the $F_5$ and $F_6$ plants. In the $F_4$ generation a number of clear-cut cases of resistance to jointworm were apparent in some families of each cross. Ranked in increasing order of susceptibility were selections of crosses of Marquillo

with Kanred X Hard Federation and with Oro, Minturki, Kawvale and Tenmarq.

In spite of some selection in the $F_5$ and $F_6$ generations for resistance to jointworm, the overwhelming abundance of this insect in 1939 gave infestations of practically 100 percent for all plants. However, it is of interest to note that of a series of 61 $F_7$ selections of Marquillo hybrids representing all 5 crosses, 31 of the selections

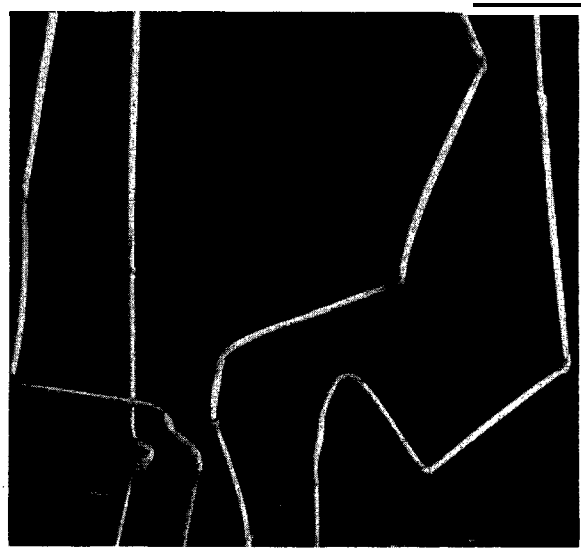


FIG. 17.—Typical galls and injury by wheat joint worm, *Harmolita tritici* (Fitch) to stems of susceptible wheats. Tolerant strains showed little distortion of wheat stems and no broken straws.

were not seriously injured, indicating a degree of tolerance to this insect not shown by 33 varieties and selections of winter wheats in the same test. Only one non-Marquillo selection showed any tolerance whatsoever. Injury was principally due to broken and distorted straws. All plants were infested (fig. 17.) It was observed that the stems of the severely injured plants generally appeared to be soft and weak and supported larger galls than plants of tolerant strains. No differential tolerance between crosses was noted. There was no apparent relationship between tolerance to jointworm and resistance to Hessian fly.

## OBSERVATIONS ON $F_5$ MARQUILLO HYBRIDS

The $F_4$ rows growing in the various fly nurseries in the spring of 1936 furnished an excellent opportunity for selecting lines with certain desired characteristics. The $F_4$ rows selected for harvesting had been mostly those which had fairly low stem-rust infection, less than 85 percent plant infestation by Hessian fly, and/or more than 50 percent spring survival following the fly infestation. The 85 percent fly infestation represented somewhat more than the maximum for any one row of Marquillo in the fall of 1935; while 50 percent survival was more than twice the spring survival of any winter wheat variety. It must be remembered, however, that these figures are based on plants grown in spaced sowings.

Infestations in the fall of 1936 on the $F_5$ Marquillo hybrids verified the correctness of the method used in making selections. Plantings of grain from each of the selected plants were made in single space-planted eight-foot rows in the Manhattan and in the Springfield fly nurseries, and in the Manhattan rust nursery. Samples from each of 326 hybrid lines were represented in each of the nurseries. A few of the $F_4$ plants also produced enough seed for sowing in winter hardiness tests at Lincoln, Neb., or in the Manhattan bunt nursery for a study of resistance to this disease.

The fall infestation in $F_5$ was fairly uniform in each of the fly nurseries. On the basis of the infestation of susceptible parents the intensity was about twice as high at Springfield as at Manhattan (table 1), yet the same hybrids reacted in much the same way to fly in both nurseries, especially when the two levels of infestation are taken into consideration. At Manhattan the susceptible parents ranged from 24 to 80 percent with an average of 48 percent, Marquillo ranged from zero to four percent with an average of 0.6 percent, and the hybrids ranged from zero to 43 percent. At Springfield the susceptible parents ranged from 73 to 97 percent, with an average of 87 percent, Marquillo ranged from zero to eight percent, with an average of 0.8 percent, and the hybrids from zero to 80 percent. The extent to which selection for fly resistance in the preceding three generations had been successful may be gaged by the fact that only two hybrids at Manhattan and only two in the Springfield nursery had as heavy an infestation as did any row of any susceptible parent, while 56 percent of the hybrids had an infestation within the range of the Marquillo checks at both nurseries (table 10). On the other hand, only about 14 percent of the hybrids were above the range of the resistant parents in both nurseries. Some lines appeared to be still segregating at a low level of resistance.

Throughout the three years in which fly records were taken, certain lines appeared to be more susceptible at one nursery than at the other. As mentioned in the study of the $F_3$ generation, hybrids between Kawvale and Marquillo were frequently less resistant at Springfield than at Manhattan. This probably is correlated with

TABLE 10.—*The number of families out of 326 tested in $F_5$ which had various combinations of resistance to fly, leaf rust, stem rust and bunt, 1936-1937.*

| HYBRID. | Total $F_5$ strains studied. | Susceptible to fly (within ranges of susceptible checks in either or both nurseries). | Resistant to fly fall 1937 (within ranges of Marquillo checks in both nurseries). | Resistant to leaf rust (25 percent or below). | Resistant to stem rust (20 percent or below). | Resistant to bunt (0 to 1 percent). | Resistant to fly and leaf rust. | Resistant to fly and stem rust. | Resistant to fly, leaf rust, and stem rust. | Resistant to fly, leaf rust, stem rust, and bunt. |
|---|---|---|---|---|---|---|---|---|---|---|
| Marquillo × Tenmarq..... | 38 | 0 | 27 | 18 | 3 | ..... | 12 | 3 | 1 | ..... |
| Marquillo × Minturki and Minturki × Marquillo..... | 82 | 2 | 37 | 15 | 32 | 20 | 9 | 7 | 0 | 0 |
| Marquillo × Oro..... | 84 | 1 | 36 | 59 | 23 | 26 | 31 | 11 | 8 | 4 |
| Kawvale × Marquillo..... | 99 | 0 | 70 | 76 | 2 | ..... | 49 | 2 | 1 | ..... |
| (Kanred × Hard Federation) × Marquillo..... | 23 | 1 | 12 | 11 | 1 | ..... | 6 | 0 | 0 | ..... |
| Totals..... | 326 | 4 | 182 | 179 | 61 | 46 | 107 | 23 | 10 | 4 |
| Percentage of total lines studied in $F_5$..... | ..... | 1.2 | 56 | 55 | 19 | 43 (a) | 33 | 7 | 3 | 4 (a) |

(a) Only the progeny of Minturki and Oro crosses carry resistance to bunt and only 108 of these hybrids were tested in this generation.

the greater susceptibility of Kawvale at Springfield in the presence of the eastern strain of fly. In other cases some of the hybrids have had a lower relative infestation at Springfield than at Manhattan. Some hybrids have shown a tendency to have a different infestation rating in the fall than that recorded for the same strain in the spring. Subsequent studies have shown that some of these differences were the result of different distributions of resistant and susceptible segregates in the respective rows of the two nurseries or at the two times of count in the heterozygous rows. In other strains no such explanation has been available and it is possible that some of the segregates from the various crosses will eventually be found to differ in susceptibility in the two localities or at different times of infestation. Many of the strains which have shown such tendencies have been discarded because of that or other defects.

## RESISTANCE TO DISEASE IN $F_5$ GENERATION

Besides resistance to Hessian fly, it is obvious, from the varieties used, that some of the hybrid lines should have resistance to one or more important diseases of wheat. Disease resistance tests were made on many lines in $F_5$ and subsequent generations in special rust and bunt nurseries. Owing to the ease of obtaining uniformly heavy infections of leaf and stem rust on susceptible wheats, it was possible to test a large number of plant selections in rows about three feet in length. Bunt tests were made on selections sown in single eight-foot rows. Artificial inoculation was used to establish infections of all of the diseases except mildew, which developed from natural infection.

When the hybrid lines were sown in the rust nursery uniform checks of Turkey wheat were placed at fifteen-row intervals. This was done because the high susceptibility of Turkey furnished evenly distributed points throughout the nursery for the establishment of infection centers of both leaf and stem rust. Check rows of the winter wheat parent varieties also were included at appropriate intervals among the hybrid lines.

Cultures of leaf and stem rust were grown on seedling plants in the greenhouse and used to inoculate plants in the field. The culture of leaf rust included physiologic races 9, 15, and 5, all important races in the Plains area, as well as several less important races. Five or six races of leaf rust were used each year. The stem-rust culture was derived from field collections in which physiologic race 56 was the most abundant, although other races were present in small amounts.

Infection centers of both rusts were established in the nursery by hypodermic inoculations made on plants in the Turkey and parental check rows during May and early June of each year. Hundreds of such centers were established in a short time and overhead sprinkling favored a uniform spread of rust to all parts of the nursery. Infection produced in this manner was so heavy and so uniformly distributed that all Turkey check rows invariably were killed by

rust before the seed filled. Leaf rust inoculations were started about two weeks earlier than stem rust, thus making it possible to make leaf rust readings at the peak of infection before stem rust became sufficiently severe to cause confusion.

The above procedure resulted in uniformly heavy infections each year and satisfactory leaf and stem rust readings were obtained on all hybrid lines tested in $F_5$ and later generations. Sharp differences in rust reaction were noted in all of the crosses and it was easy to select resistant lines. In the case of leaf rust numerous resistant lines were observed in all five crosses as shown in table 10. This table also shows that there were more lines resistant to leaf rust than to stem rust in all except the Marquillo X Minturki cross. This is due partially to the fact that, in addition to the strong resistance of Marquillo, the winter wheat parents Tenmarq, Kawvale, and Kanred X Hard Federation also are resistant to leaf rust, although the resistance of Tenmarq is weak. Another factor that undoubtedly was partly responsible for the large number of leaf rust resistant lines was the rigid selection for resistance to leaf rust in $F_3$ and $F_4$. This was particularly true of the Marquillo X Oro and Kawvale X Marquillo crosses, which show a very high proportion of resistant lines in table 10.

A third factor that probably is partly responsible for the large proportion of leaf rust resistant lines shown in table 10 is the relatively high level (25 percent) chosen for the upper limit in classification as resistant. This figure is considerably higher than the amount of infection usually observed on Marquillo, Kawvale, and Kanred X Hard Federation, but is sufficiently low to furnish a satisfactory degree of field resistance. In breeding for resistance to Hessian fly, leaf rust, stem rust and bunt, it was necessary to select many lines with only a moderate degree of resistance to one or more pests in order to combine resistance to all or most of them.

It also must be kept in mind that the selection for leaf rust resistance was done under artificial epidemic conditions much heavier than infections usually encountered in the field. More physiologic races were present in the leaf rust nursery than under most field conditions. Under such conditions Kawvale and Tenmarq frequently are heavily infected. Kawvale usually exhibits strong resistance to leaf rust in fields on Kansas farms where physiologic race 9, to which it is highly resistant, usually is the predominant race. Tenmarq, on the other hand, shows only a moderate resistance even in general field plantings.

Although table 10 shows a high proportion of resistant lines with infections of 25 percent or less, it does not present a complete picture. Actually there were 127 out of 326 lines with infections of 15 percent or lower, which was the upper limit for the Marquillo and Kawvale checks in 1937. Most of these were in the Marquillo X Oro and Kawvale X Marquillo crosses. Forty-one out of 84 Marquillo X Oro lines and 67 out of 99 Kawvale X Marquillo lines fell within the range, 15 percent or lower. Many selections in all

crosses were intermediate in reaction, with infections falling between the upper limit of the resistant checks and the lower limit of the susceptible checks. Besides those lines, there were 30 lines among the five crosses that were evidently still segregating for leaf-rust resistance in $F_5$.

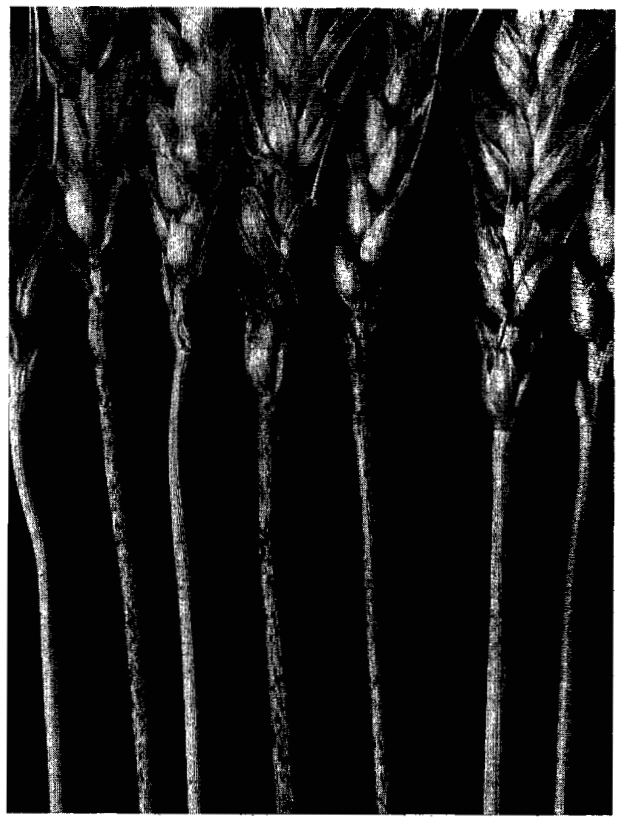


FIG. 18.—Individual stems and heads of wheat showing differences for susceptibility to stem rust in the Hessian fly nursery at Manhattan, Kan., 1936. Left to right: Imuillo, Marquis, Marquillo, Oro, Kawvale, Marquillo × Oro Sel., and Kawvale × Marquillo Sel.

Stem-rust infection in the portion of the rust nursery devoted to the Marquillo hybrids has been heavy each year (fig. 18). Satisfactory readings were obtained on hybrid lines in $F_5$, $F_6$, and $F_7$, and it was possible to select plants from rows with relatively low percentages of infection. The stem-rust readings on $F_5$ rows in 1937 revealed that in the five crosses 234 of the 326 lines tested exhibited more resistance than the winter wheat parents, while 80 lines

fell within the range of susceptibility of the susceptible parents. More strongly resistant lines were found in the Marquillo X Minturki and Marquillo X Oro crosses than in the other three crosses as shown in table 10. The reason for this is clear in the case of the Marquillo X Minturki cross, since both parent varieties usually exhibit considerable resistance in Kansas. Marquillo is highly resistant and Minturki moderately so under ordinary field conditions. In the rust nursery where many physiologic races are present and epidemic conditions are produced early in the season, Minturki often fails to exhibit any resistance. From the results obtained in these tests, however, it seems that the combined resistance of Minturki and Marquillo results in the production of many resistant hybrid lines. Under field conditions in Kansas, Kawvale shows considerable tolerance to stem rust. It is typically a late-rusting variety on which infection frequently does not develop until the plant is nearly mature. Under rust nursery conditions, however, it does not show that character so consistently. It is not surprising, therefore, that Kawvale X Marquillo lines were less resistant than Marquillo X Minturki strains.

The occurrence of the large number of stem rust resistant lines in the $F_5$ of the Marquillo X Oro must be explained on another basis. Although many selections were studied in $F_3$ and $F_4$ most of them traced back to only three $F_2$ plants. Selection for stem rust resistance in $F_3$ and subsequent generations resulted in the saving of many closely related lines. Despite their close relationship, it is interesting to note that some of the lines of the Marquillo X Oro cross have combined resistance to Hessian fly, leaf rust, stem rust, and bunt, a combination of resistances not achieved in the other crosses.

Thirty-two (39 percent) of the Marquillo X Minturki lines and 23 (27 percent) of the Marquillo X Oro lines had stem rust infections of 20 percent or less, as shown in table 10. As in the case of leaf rust, the limit chosen is a purely arbitrary one and is somewhat higher than the upper limit of the Marquillo checks, which in this case was 10 percent. However, an infection of only 20 percent in the presence of such a heavy rust epidemic indicates a satisfactory degree of resistance. If the upper limit of the Marquillo checks (10 percent) had been chosen as the line of demarcation for resistance, only one line of Marquillo X Minturki, nine lines of Marquillo X Oro, and none of the other three crosses would have achieved that level.

Besides the lines showing strong resistance to stem rust there were many lines exhibiting a moderate degree of resistance. In fact, one of the features of the stem rust studies on these Marquillo hybrids has been the preponderance of lines showing a moderate degree of resistance. The rust readings on $F_5$ lines revealed that 114 of the 326 lines (34.6 percent) had infections ranging between 25 and 50 percent, while the winter wheat parental varieties had infec-

tions ranging from 80 to 100 percent. Tests of hybrid lines with a moderate degree of resistance in 1938 and 1939 proved that many of them maintained that degree of resistance. There is evidence, therefore, that more than one factor governs the strong stem rust resistance of Marquillo and its highly resistant hybrids. Apparently desirable lines with a moderate degree of resistance can be selected with the expectation that they will be genetically stable for this resistance.

Conditions that favored a heavy development of rust in the 1935 rust nursery also favored a heavy and fairly uniform natural infection of mildew *(Erysiphe graminis* DC.). Differences in susceptibility were noted among the hybrid lines with Marquillo parentage as well as among named varieties of wheat. The amount of infection was recorded in terms of a scale having five degrees of severity, viz., 0, 1, 2, 3, and 4, with 0 representing the highest type of resistance and 4 complete susceptibility. Infection was so heavy on completely susceptible lines that even the glumes and awns were mildewed. Lines with type 3 infection were moderately susceptible, as shown by heavy infection on leaves and leaf sheaths in the lower half of the plant, but, very few mildew sori on upper leaves and none on glumes or awns. Infections of type 2 denote low-grade resistance, and are characterized by a moderate development of mildew sori on leaves near the ground and but few elsewhere. Type 1 infections denote strong resistance characterized by the occurrence of small scattered mildew sori on leaves near the bases of the plants. In this system of disease classification freedom from infection is indicated by zero.

In general, more resistance to mildew was observed among (Kanred X Hard Federation) X Marquillo and Marquillo X Oro lines than among strains of the other three Marquillo crosses. Some detailed data illustrating this point will be presented later under discussion of certain families.

The bunt-resistant winter wheat varieties Minturki and Oro were used as parents in combination with Marquillo in two of the crosses in an effort to combine resistance to Hessian fly and bunt. Since the crosses Marquillo X Minturki and Marquillo X Oro were the only crosses involving resistance to bunt, selections of those crosses only have been tested for bunt resistance. Seed of 57 lines of Marquillo X Minturki and 51 lines of Marquillo X Oro, both in $F_5$, was available for bunt tests in 1937. Before sowing, the seed of all lines was heavily inoculated with spores of *Tilletia levis* Kühn, the bunt of the Plains area. A composite of bunt collected in 30 localities in Kansas was used as inoculum. This composite is considered representative of the bunt flora of Kansas and is known to contain physiologic races L-1 and L-7 [Rodenhiser and Holton *(17)*].

Planting was delayed until late October to assure soil temperatures and moisture favorable for maximum bunt infection. Heavy infections of 51.3 and 47 percent were obtained on susceptible Kanred and Tenmarq check rows sown at the same time. The Oro

and Minturki parental checks exhibited strong resistance, having average infections of 3.4 and 5.4 percent, respectively. When all rows were fully headed and bunt was easily distinguishable, smut counts were made. Total heads and number of bunted heads were recorded and percentages of infection calculated on that basis.

Although much selection had been done for Hessian fly resistance in both crosses before any bunt tests were made, it was clear that there was a preponderance of bunt-resistant lines in both crosses. If the two crosses are considered together, 56 of the 108 selections, or 51.1 percent, were as resistant as the resistant parents. Such a large proportion of the lines exhibited resistance that only those lines with extremely low percentages of bunt or no bunt have been kept on the basis of bunt resistance. Only the number of lines with zero or one percent bunt are recorded in table 10. On this basis 20 lines (35 percent) of Marquillo X Minturki and 26 lines (50.9 percent) of Marquillo X Oro were extremely resistant to bunt.

The highest infection shown by any of the hybrid lines was 34 percent. This was considerably below the level of the susceptible checks and may have been due to elimination of many lines by selection in earlier generations. Various degrees of infection between zero and 34 percent were observed, but the frequency was low in all classes except in the zero class, which had frequencies of 14 and 26 for the Marquillo X Minturki and Marquillo X Oro crosses, respectively.

### COMBINATIONS OF INSECT AND DISEASE RESISTASCE IN $F_5$

The distribution of seed from the same plant to the several nurseries for special tests has made possible the tabulation of various combinations of resistance to fly, leaf rust, stem rust., and bunt, as indicated in table 10. The limits set for resistance in each case are arbitrary and somewhat beyond the range of the resistant parent for leaf and stem rust. The percentage of $F_5$ hybrid lines among the total 326 resistant to fly has been mentioned previously. The proportion of lines resistant to leaf rust is almost as great (55 percent). This is perhaps due in part to the greater opportunity for selection for leaf rust resistance along with resistance to insects in early generations in the fly nursery and partly to the fact that three of the winter parents are somewhat resistant to leaf rust. Thus it will be noted that about a third of the total number of strains studied in $F_5$ were resistant to both fly and leaf rust. Only 19 percent of all the strains studied were resistant to stem rust and 43 percent were resistant to bunt, while seven percent combined resistance to fly and stem rust and three percent combined resistance to fly with resistance to both rusts. In 1937 four strains, or slightly less than four percent of the total studied, showed resistance to fly, leaf rust, stern rust, and bunt combined. These four strains were closely related, all of them being derived from one Marquillo X Oro $F_3$ selection, 35 FN 742.

This relatively low number of strains that had the combined resistance to fly and the three diseases is partly due to the fact that in 1937 the reaction to bunt was known for only two-thirds of the available strains. Later information on bunt resistance and studies in selections from 30 strains which were segregating for leaf rust and 12 strains which were segregating for stem rust have added to the number of strains which have combined resistance to fly and the three diseases. Coupled with the large number of strains resistant to both fly and leaf rust is the fact that approximately 72 percent of the $F_5$ Marquillo hybrids had greater resistance to stem rust than any of the commercial winter wheats. This latter fact is especially true of most of the strains which were promoted to the agronomy nursery for yield and other tests.

Grain from the $F_5$ plants was disposed of in accordance with a study of the records of the $F_5$ rows. In a few cases seed from a single $F_5$ row was bulked and grown in three eight-foot rows in the agronomy nursery. In most cases seed from individual plants was drilled in single eight-foot rows if sufficient seed was available, otherwise kernels were space planted for study and possible selection in the following season. A total of 611 selections were advanced to the agronomy nursery for study, including yield tests in 1938. Seed from 113 selected plants from rows segregating for rust was planted in the rust nursery in 1938. In the same way 202 selections from rows that appeared to be still segregating for fly resistance were replanted in spaced rows in the fly nursery.

Bulk seed from 46 different Marquillo hybrid rows was used for "doughball" (wheat meal time fermentation) tests for gluten quality. All of the hybrids have a good record with only four selections below 100 minutes, a "time" considered satisfactory for hard wheats.

## OBSERVATIONS ON $F_6$ HYBRIDS

The fly records were rather unsatisfactory in this generation. Drought at Manhattan in 1938 prevented an infestation by fly, and grasshoppers injured the nursery. White grubs, moles, and wireworms were abundant at Springfield and greatly reduced the accuracy of the results obtained there. Enough information on fly infestation was available at Springfield, however, to give an approximate resistance rating for most of the hybrids studied.

In the agronomy nursery at Manhattan satisfactory preliminary yield records were obtained. After discarding a number of rows in the field for various reasons, the remaining strains made a fairly good showing. The good yield records may have been due in part to a season that was favorable to these hybrids. The leaf rust epidemic was severe and the infection of stem rust was moderate to severe on the susceptible varieties of winter wheat with which these hybrids were compared. Data regarding the number of strains and the yield of the different hybrid groups are given in table 11. The 26 strains harvested from the three eight-foot row

TABLE 11.—*The number and average yield of Marquillo hybrid lines grown in yield tests compared with yields of parental and uniform check rows, Manhattan, 1938-1939.*

| HYBRID OR VARIETY. | Strains. | | | | | | |
|---|---|---|---|---|---|---|---|
| | In 1937-1938. | | | | | | Continued in agronomy nursery 1938-1939 (d) |
| | Planted in agronomy nursery (a) | Harvested from SR8 (b) | Average yield in SR8 (b) | Harvest from 3R8 (c) | Average yield in 3R8 (c) | Above 30 bushels in 3R8 and SR8 | |
| | Number | Number | Bushels | Number | Bushels | Number | Number |
| Marquillo × Tenmarq | 152 | 65 | 28.9 | 5 | 33.0 | 31 | 84 |
| Marquillo × Minturki and reciprocal | 64 | 13 | 28.0 | 0 | ..... | 8 | 46 |
| Marquillo × Oro | 306 | 74 | 31.6 | 11 | 31.0 | 45 | 136 |
| Kawvale × Marquillo | 77 | 28 | 27.3 | 9 | 30.1 | 14 | 67 |
| (Kanred × Hard Federation) × Marquillo | 12 | 0 | ..... | 1 | 36.0 | 1 | 7 |
| Turkey | ..... | 14 (e) | 30.9 | 10 | 23.9 | ..... | ..... |
| Tenmarq | ..... | 14 (e) | 35.2 | 9 | 27.6 | ..... | ..... |
| Oro | ..... | 1 | 16.2 | 1 | 25.0 | ..... | ..... |
| Kawvale | ..... | 1 | 26.0 | 2 | 38.4 | ..... | ..... |
| Minturki | ..... | 1 | 20.4 | 1 | 19.6 | ..... | ..... |

(a) In three eight-foot rows, single eight-foot rows, and space planted rows.
(b) Single eight-foot rows.
(c) Three eight-foot row plots.
(d) Including new selections from fly, rust and bunt nurseries.
(e) Grown among group of Marquillo hybrids.

series ranged in yield from 15 bushels to 39.8 bushels with all except one strain above 24 bushels. The average yield in the different groups of hybrids in all cases was above 30 bushels. This may be compared with the average yield of 27.6 for Tenmarq and 23.9 for Turkey in this section of the nursery.

Although the yields from single rows are admittedly unreliable, they often indicate definite trends. Yields of 180 rows harvested in the single eight-foot-row series ranged from 13.6 bushels to 53.0 bushels with most of the rows yielding above 23 bushels. The 53-bushel yield for the Marquillo X Oro selection was the highest recorded in this series in competition with a number of other wheat varieties and non-Marquillo hybrids. The average for the 180 rows harvested was 29.7 bushels, but 34 of the strains were above the average of the Tenmarq checks and 64 above the average of the Turkey checks in this series. These data appear to indicate that some of the Marquillo hybrids may be expected to give yields at least equal to standard varieties such as Turkey and Tenmarq.

One of the undesirable characteristics of Marquillo is the creamy color of the flour, due to the presence of carotene. Eight of the best of the Marquillo X Oro and the Marquillo X Tenmarq hybrids from the agronomy nursery were analyzed for the presence of this pigment and all eight appeared to be as good as or better than their winter wheat parents.

## DISCUSSION

### STUDY OF SELECTED HYBRID LINES

A study of the different hybrid lines that have been saved and which are the progeny of individual $F_2$ plants is of interest, not only in indicating the method of selection, but also typical of results obtained throughout this experiment. The principal records obtained from the progeny of four $F_2$ plants that proved to be among the best for different characters are given in tables 12, 13, 14 and 15. The various combinations and characters carried by these four $F_2$ families may be discussed separately.

Selection 35 FN 742, Marquillo X Oro, is the family that has given rise to selections which in some respects carry the best available combination of characters. A study of the records for the selections from this line as given in table 12 will indicate that the original $F_2$ plant may have been heterozygous for fly resistance. While all selections are fairly resistant (figs. 10, 12), they are not equally so and it is possible that they may have differed in such characters of resistance as the tendency to induce different oviposition rates. It is evident that the three selections grown in $F_4$ were all highly resistant to killing by fly. The original $F_2$ plant was evidently highly resistant to leaf rust but heterozygous for resistance to stem rust and to bunt.

The records for resistance to mildew were taken in four grades, from 1 (most resistant) to 4 (susceptible). This particular family

TABLE 12.—*Records of Marquillo × Oro $F_3$ family 35 FN 742 containing lines most highly resistant to Hessian fly, stem rust, leaf rust, bunt and mildew.*

| $F_3$ 1934–1935. | | | $F_4$ 1935–1936. | | | | | $F_5$ 1936–1937. | | | | | | | $F_6$ and $F_7$ 1938. | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Row No. | Manhattan. | | Springfield. | | Manhattan. | | | Row No. | Springfield. | | Manhattan. | | | | 1937 FN and BN (c) | Springfield. | Manhattan. | Kansas selection number |
| | Plants infested | Spring survival | Plants infested, fall | Survival after fly infestation | Survival after winter killing | Stem rust | Leaf rust | | Plants infested, fall | Culms infested, spring | Plants infested, fall | In disease nurseries. | | | | Fly infestation fall 1938, $F_7$ | Yield in bushels in agronomy nursery | |
| | | | | | | | | | | | | Stem rust | Leaf rust | Bunt | Mildew reaction | | | |
| | Per-cent | Per-cent | Per-cent | Per-cent | Per-cent | Per-cent | Per-cent | | Per-cent | Per-cent | Per-cent | Per-cent | Per-cent | Per-cent | | | | |
| | | | | | | | | 634 | 0 | 3 | 6 | 5 | Tr | 0 | 3 (b) | 634 | | |
| | | | | | | | | 635 | 3 | 0 | 0 | 5 | Tr | 0 | 3 | 2635–5 | | (a) 384118 |
| | | | | | | | | | | | | | | | | –6 | | (a) 384119 |
| | | | | | | | | | | | | | | | | BN2771–3 | | (a) 385008 |
| | | | | | | | | | | | | | | | | –6 | | (a) 385009 |
| | | | 41 | 59 | 89 | Tr+ | Tr | | | | | | | | | 636–B | | 27.0 383244 |
| | | | | | | | | | | | | | | | | 636–1 | | 26.0 383433 |
| | | | | | | | | | | | | | | | | 2636–9 | 0 | (a) 384135 |
| | | | | | | | | 636 | 4 | 0 | 6 | 5 | 5 | 0 | 3 | BN2772–1 | | (a) 385012 |
| | | | | | | | | | | | | | | | | –2 | | (a) 385013 |
| 742 | 16 | 88 | | | | | | | | | | | | | | –3 | | (a) 385014 |
| | | | | | | | | | | | | | | | | –4 | | (a) 385015 |
| | | | | | | | | | | | | | | | | –5 | | (a) 385016 |
| | | | | | | | | 637 | 3 | 0 | 0 | 5 | 5 | 0 | 3 | 637–2 | | 30.0 383436 |
| | | | | | | | | 638 | 0 | 0 | 0 | 5 | 5 | 0 | 2 | 638–3 | 0 | 30.6 383442 |
| | | | | | | | | | | | | | | | | 2638–3 | | (a) 384146 |
| | | | | | | | | 639 | 9 | 6 | 4 | 5 | 5 | ..... | 2 (b) | 2638–7 | 0 | (a) 384148 |
| | | | 57 | 74 | 75 | 15 MR | 5 | 640 | 5 | 0 | 0 | 10 | 5 | 13 | 1 | 640–2 | | 31.2 383448 |
| | | | | | | | | | | | | | | | | –4 | 0 | 34.8 383451 |
| | | | | | | | | 641 | 6 | ..... | 0 | 80 | 5 | ..... | 1 (b) | 2640–1 | | (a) 384152 |
| | | | 90 | 60 | 72 | 25 | 5 (b) | | | | | | | | | | | |
| **Parental varieties** | | | | | | | | | | | | | | | | | | |
| Marquillo | 9 | 0 | 44 | 0 | 0 | Tr | Tr | | 0.8 | 6 | 0.6 | Tr to 5 | 10–15 | ..... | 2–3 | | 5 | |
| Oro | 87 | 93 | 100 | 13 | 84 | 65 | ..... | | 88 | 75 | 61 | 100 | 85 | 3.4 | 1–2 | | 96 | |

(a) Strains for which yield is not given were grown in short rows or rows of spaced plants.
(b) Line discontinued.
(c) Fly nursery and bunt nursery 1937 row and plant number.

gave selections falling in the three more resistant grades. At least some strains in the family have shown less injury by *Harmolita tritici* (Fitch), the wheat jointworm, than have many wheat varieties with which they have been compared. Thus, selections from this family combine resistance to fly and probably tolerance to jointworm with high resistance to leaf rust, stem rust, bunt and mildew. Since most selections so far made are not very winter hardy, however, this family is not likely to give rise directly to wheats of commercial possibilities. The selections are, however, a valuable source of parental material, since they combine resistance to two insects and four diseases with such desirable agronomic characters as dark hard grain, stiff straw, and at least fair yield.

Selection 35 FN 743, Marquillo X Oro, is the $F_3$ family in this cross which has given rise to the best agronomic types. Many of the strains of this cross now being studied in the agronomy nursery were derived from this same $F_2$ plant. Most of the strains have given excellent yields of dark hard grain. The principal records for only those strains which had yields above 30 bushels in the 1938 agronomy nursery are given in table 13.

It is interesting to note that the $F_2$ plant from which this 35 FN 743 family was derived apparently was heterozygous for practically all characters being studied, including winter hardiness and awn type. It was certainly heterozygous for resistance to fly, especially in respect to low larval survival, some derived lines giving plants with fairly high infestation even in $F_5$. All lines appear to be resistant to killing by fly. Most of the lines derived from this $F_2$ plant were resistant to leaf rust, although one line apparently still was segregating in $F_5$. The family was segregating for resistance to stem rust from moderate resistance to susceptibility with two lines still segregating in $F_5$. The family was segregating for resistance to bunt and mildew, but most lines were resistant to these two diseases. Some strains in this family have been less injured by the wheat jointworm than others. Thus, although the original plant was heterozygous for many characters, selections have been made which combine resistance to fly and tolerance to jointworm with resistance to leaf rust, bunt, mildew and moderate resistance to stem rust. Therefore, while not so good as family 35 FN 742 in resistance to stem rust, selections in this group of 35 FN 743 hybrids may have promise as commercial wheats since they are more winter hardy and have higher yield than do selections from the previously mentioned family.

Selection 35 FN 677, Marquillo X Tenmarq, has given rise to strains which as a group show the best record of any $F_3$ family in this cross (table 14). The original $F_2$ plant was evidently heterozygous for resistance to fly, leaf rust and stem rust. All the strains have fairly good winter hardiness and most of them also have good survival after severe infestation by fly. While all of the strains are at least as resistant to leaf rust as is Tenmarq, they are only moderately resistant to stem rust and were segregating for this character in $F_4$. Most of the strains were rather susceptible to mildew, but

TABLE 13.—*Records of Marquillo × Oro $F_3$ 35 FN 743 which has furnished most of the strains giving good yield records in the agronomy nursery which are resistant to Hession fly, leaf rust, and bunt, and are moderately resistant to stem rust.*

| $F_3$ 1934–1935. | | | $F_4$ 1935–1936. | | | | | $F_5$ 1936–1937. | | | | | | | $F_6$ and $F_7$ 1938. | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Springfield. | | Manhattan fly nursery. | | | | Springfield. | | Manhattan. | | | | | | | |
| Row No. | Plants infested, average for three stations | Manhattan, spring survival | Plants infested | Survival after fly infestation | Survival after winter killing | Stem rust | Leaf rust | Row No | Plants infested, fall | Culms infested, spring | Plants infested, fall | In disease nurseries. Stem rust | Leaf rust | Bunt | Mildew reaction | 1937 fly nursery | Springfield. Fly infestation, fall | Manhattan. Yield in bushels in agronomy nursery | C. I. Kansas, or selection number |
| | Percent | Percent | Percent | Percent | Percent | Percent | Percent | | Percent | Percent | Percent | Percent | Percent | Percent | | | Percent | | |
| | | | | | | | | 642 | 3 | 0 | 0 | 45 | 5 | 0 | 2 | 642–B | 0 | 39.4 | CI 11851 |
| | | | | | | | | | | | | | | | | 642–5 | | 34.0 | 383452 |
| | | | | | | | | 643 | 3 | 0 | 0 | 40 | 5 | 0 | 1 | 643–B | 0 | 39.8 | CI 11955 |
| | | | | | | | | | | | | | | | | 643–2 | | 32.0 | 383453 |
| | | | | | | | | 644 | 0 | 3 | 0 | 50 | 5 | –(b) | 2 | 644–B | | 34.3 | 382957 |
| | | | | | | | | | | | | | | | | 644–1 | | 33.0 | 383455 |
| | | | 54 | 79 | 84 | Tr | Tr | 645 | 0 | 0 | 0 | 40 | 10 | 0 | 2 | 645–1 | | 36.8 | 383456 |
| | | | | | | | | 646 | 19 | 0 | 11 | 40 | 10 | 9 | 2 | 646 | | | |
| | | | | | | | | 647 | 0 | 0 | 6 | 20 | 10 | 10 | 1 | 647 | | | |
| | | | | | | | | 648 | 3 | 0 | 0 | 40 | 10 | – | 1 | 648 | | | |
| | | | | | | | | | | | | | | | | 649–B | 0 | 39.2 | CI 11957 |
| | | | | | | | | 649 | 3 | 0 | 0 | 50 | 10 | –(b) | 1 | 649–1 | | 35.6 | 383457 |
| | | | | | | | | | | | | | | | | 649–4 | | 40.6 | 383458 |
| | | | | | | | | 650 | 4 | 6 | 0 | 50 | 20 | 0 | 1 | 650–2 | | 30.2 | 383462 |
| | | | | | | | | 653 | 3 | 12 | 3 | 60 | 10 | 0 | 2 | 653 | | | |
| | | | | | | | | 654 | 3 | 0 | 8 | 60 | 10 | –(b) | 3 | 654–1 | | 36.0 | 383464 |
| | | | | | | | | 655 | 46 | 31 | 29 | 85 | 10 | – | 2 | 655 | | | |
| | | | | | | | | 656 | 3 | 8 | 0 | 65 | 10 | 0 | 3 | 656 | | | |
| | | | | | | | | 657 | 3 | 4 | 3 | 20–80 | 25 | – | 3 | 657 | | | |
| | | | | | | | | 658 | 5 | | 0 | 40 | 10 | 0 | 2 | 658 | | | |
| | | | | | | | | 659 | 0 | 11 | 0 | 45 | 20 | 0 | 3 | 659 | | | |
| | | | | | | | | 660 | 0 | 15 | 0 | 25 | 5 | 0 | 3 | 660 | | | |
| | | | | | | | | 661 | 0 | 0 | 0 | 40 | 5 | –(b) | 3 | 661–4 | | 31.2 | 383474 |
| 743 | 30 | 75 | 79 | 84 | 88 | Seg | Tr | 662 | 6 | 10 | 0 | 45 | 5 | 0 | 2 | 662 | | | |
| | | | | | | | | | | | | | | | | 663–1 | | 44.2 | CI 11978 |
| | | | | | | | | | | | | | | | | 663–2 | | 40.0 | KS 2753 |
| | | | | | | | | | | | | | | | | 663–4 | | 44.4 | 383477 |

*Continued on page 46*

TABLE 13—CONCLUDED

| $F_3$ 1934–1935. | | | $F_4$ 1935–1936. | | | | | $F_5$ 1936–1937. | | | | | | | $F_6$ and $F_8$ 1938. | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Springfield. | | Manhattan fly nursery. | | | | Springfield. | | Manhattan. | | | | | | | |
| | | | | | | | | | | | | In disease nurseries. | | | | | | |
| Row No. | Plants infested, average for three stations | Manhattan, spring survival | Plants infested | Survival after fly infestation | Survival after winter killing | Stem rust | Leaf rust | Row No. | Plants infested, fall | Culms infested, spring | Plants infested, fall | Stem rust | Leaf rust | Bunt | Mildew reaction | 1937 fly nursery | Fly infestation, fall | Yield in bushels in agronomy nursery | C. I. Kansas, or selection number |
| | Percent | Percent | Percent | Percent | Percent | Percent | Percent | | Percent | Percent | Percent | Percent | Percent | Percent | | | Percent | | |
| | | | | | | | | 663 | 5 | 0 | 0 | 40 | 10 | –(b) | 2 | 663–5 | | 43.2 | 383478 |
| | | | | | | | | | | | | | | | | 663–6 | | 34.4 | 383479 |
| | | | | | | | | | | | | | | | | 663–7 | | 36.2 | 383481 |
| | | | | | | | | | | | | | | | | 663–8 | 0 | 47.8 | 383482 |
| | | | | | | | | | | | | | | | | 663–9 | 0.4 | 53.0 | CI 11979 |
| | | | | | | | | | | | | | | | | 663–15 | | 46.8 | 383484 |
| | | | | | | | | | | | | | | | | 663–16 | | 42.0 | 383485 |
| | | | | | | | | 664 | 10 | 6 | 0 | 45 | 10 | –(b) | 3 | 664–2 | 0 | 47.6 | CI 11980 |
| | | | | | | | | | | | | | | | | 664–4 | | 43.2 | 383488 |
| | | | | | | | | 665 | 6 | | 8 | 40 | 10–60 | 0 | 2 | 665 | | | |
| | | | | | | | | | | | | | | | | 666–B | 0 | | 382951 |
| | | | | | | | | | | | | | | | | 666–1 | | 32.8 | 383492 |
| | | | | | | | | 666 | 0 | 3 | 17 | 30 | 10 | 0 | 3 | 666–2 | 0 | 44.4 | 383493 |
| | | | | | | | | | | | | | | | | 666–3 | | 34.8 | 383494 |
| | | | | | | | | | | | | | | | | 666–4 | | 33.0 | 383495 |
| | | | 84 | 79 | 87 | 1 | Tr | 667 | 10 | | 3 | 30 | 10 | –(b) | 2 | 667 | | | |
| | | | | | | | | | | | | | | | | 668–B | | 30.8 | 382984 |
| | | | | | | | | 668 | 7 | 0 | 7 | 40 | 10 | – | 2 | 668–1 | | 38.6 | 383496 |
| | | | | | | | | | | | | | | | | 668–6 | | 34.4 | 383499 |
| | | | | | | | | 669 | 13 | | 4 | 40 | 10 | 0 | 3 | 669 | | | |
| | | | 88 | 19 | 47 | Seg | 5 (a) | 670 | 6 | 5 | 0 | 25–90 | 10 | – | 2 | 670 | | | |
| | | | | | | | | 671 | 3 | | 0 | 45 | 10 | 0 | 2 | 671 | | | |
| | | | 88 | 6 | 0 | – | – (a) | 672 | 10 | | 0 | 45 | 10 | 0 | 2 | 672 | | | |
| | | | | | | | | 673 | 3 | | 11 | 50 | 20 | 0 | 2 | 673 | | | |
| | | | | | | | | 674 | 3 | 0 | 7 | 45 | 20 | – | 1 | 674 | | | |
| | | | | | | | | 675 | 3 | | 6 | 45 | 40 | 0 | 1 | 675 | | 37.6 | 383503 |
| **Parental varieties** | | | | | | | | | | | | | | | | | | | |
| Marquillo | 6 | 0 | 44 | 0 | 0 | Tr | Tr | | 0.8 | 6 | 0.6 | Tr to 5 | 10–15 | | 2–3 | | 5 | | |
| Oro | 77 | 93 | 100 | 13 | 84 | 65 | | | 88 | 75 | 61 | 100 | 85 | 3.4 | 1–2 | | 96 | | |

(a) Line discontinued.
(b) Resistant to bunt in later tests.

some were less injured by the jointworm than was Tenmarq. Despite the fact that some strains of this cross possess only moderate resistance to stem rust, they hold promise as commercial wheats. This is due to the combination of strong resistance to Hessian fly, and leaf rust with good yield and high grain quality.

Selection 35 FN 660 Marquillo X Tenmarq contains lines which in general have given the best records for resistance to Hessian fly. The various lines have given high yields of grain that appears of good quality, but, the resistance to disease has not been so promising (table 15). The original $F_2$ plant was possibly heterozygous for fly resistance, but most of the lines saved have carried high resistance. The family was segregating for leaf-rust reaction from 10 to 90 percent and for stem-rust reaction from 60 to 90 percent, but a few strains combining moderate resistance to stem rust with high resistance to fly and leaf rust have been obtained. All lines except two were susceptible to mildew.

In the course of the study of this material numerous strains have been discarded even though highly resistant to fly when they did not carry resistance to disease and desirable agronomic characters. A study of the records, especially of the four families mentioned above, emphasizes the fact that if the final combination of characters is to be secured, it often is necessary to consider and use some selections which in early generations are segregating for the various desirable characters being studied. Since resistance to Hessian fly tends to be recessive, this has meant that some apparently susceptible plants and lines had to be continued with the expectation that they would give rise to resistant segregates. Evidence given above clearly indicates that the carrying of lines apparently susceptible but actually heterozygous for fly resistance has permitted the successful selection of desirable combinations in the absence of impractically large $F_2$ populations. It also is entirely possible that it may be necessary to accept a slightly lower level of resistance to fly or to stem rust in order to secure a commercial wheat carrying at the same time resistance of some economic importance to these two pests.

### PRESENCE OF INFESTATION ON MARQUILLO AND ITS HYBRIDS

It has been mentioned frequently that a varying amount of infestation occurs on Marquillo and on the hybrids derived from it. The larvae and flaxseed maturing on Marquillo and its resistant hybrids are often small in size and not normal in color, but apparently normal flaxseed are sometimes present.

A consideration of possible explanations for the presence of this infestation in some of these resistant plants, in some of the tests, will aid in the understanding of the nature of resistance and of the economic possibilities of Marquillo hybrids in Hessian fly control. Several possible explanations are offered below and it is possible that one or more of them apply under the conditions of different experiments.

It has been shown by Powers *(16)* that Marquillo has a greater variability than some other wheats. This variety also has a more

TABLE 14.—*Records of Marquillo × Tenmarq $F_3$ family 35 FN 677 which contains lines with good agronomic records, resistant to fly and leaf rust, and more resistant to stem rust than are commercial wheats.*

| $F_3$ 1934–1935. | | | $F_4$ 1935–1936. | | | | | $F_5$ 1936–1937. | | | | | | $F_6$ and $F_7$ 1938. | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Row No. | Manhattan. | | Springfield. | | Manhattan fly nursery. | | | Row No. | Springfield. | | Manhattan. | | | 1937 fly nursery | Springfield. | Manhattan. | Kansas selection number |
| | Plants infested | Spring survival | Plants infested, fall | Survival after fly infestation | Survival after winter killing | Stem rust | Leaf rust | | Plants infested, fall | Culms infested, spring | Plants infested, fall | In disease nurseries. Stem rust | Leaf rust | Mildew reaction | | Fly infestation, fall | Yield in bushels in agronomy nursery | |
| | Percent | Percent | Percent | Percent | Percent | Percent | Percent | | Percent | Percent | Percent | Percent | Percent | | | Percent | | |
| | | | | | | | | 521 | 3 | — | 0 | 45 | 40 | 4 (a) | 521B | | | |
| | | | | | | | | 522 | 0 | 9 | 4 | 65 | 25 | 3 | 522B | 0 | 31.2 | 383208 |
| | | | | | | | | | | | | | | | 2522–3 | | —(b) | 384024 |
| | | | 72 | 72 | 90 | 85 | —(a) | | | | | | | | 523–B | 2 | 35.8 | 382879 |
| | | | | | | | | 523 | 3 | 0 | 0 | 50 | 25 | 3 | 523–2 | 7 | 29.6 | 383353 |
| | | | | | | | | | | | | | | | 2523–5 | | —(b) | 384028 |
| | | | | | | | | 524 | 7 | — | 8 | 60 | 25 | 4 | 524–B | | 28.4 | 382885 |
| | | | | | | | | | | | | | | | 524–3 | | 33.2 | 383361 |
| | | | 41 | 69 | 100 | Seg | — | 527 | 2 | 0 | 0 | 60 | 40 | 3 | 527–B | | 29.4 | 383212 |
| | | | | | | | | 528 | 0 | 0 | 0 | 60 | 25 | 3 | 528–B | 0 | 35.4 | 382888 |
| | | | | | | | | 529 | 6 | 0 | 0 | 45 | 20 | 3 | 529–B | | 33.8 | 382894 |
| | | | | | | | | | | | | | | | 529–2 | | 31.6 | 383367 |
| 677 | 21 | 82 | | | | | | | | | | | | | 530–B | 0 | 30.0 | 383214 |
| | | | | | | | | | | | | | | | 530–1 | | 30.2 | 383372 |
| | | | | | | | | | | | | | | | 530–8 | | —(b) | 384058 |
| | | | | | | | | 530 | 0 | 3 | 0 | 45 | 40 | 3 | 2530–1 | | —(b) | 384059 |
| | | | | | | | | | | | | | | | 2530–2 | | —(b) | 384061 |
| | | | | | | | | | | | | | | | 2530–3 | | —(b) | 384062 |
| | | | | | | | | | | | | | | | 2530–4 | | 34.0 | 383373 |
| | | | 96 | 56 | 92 | Seg | — | 531 | 3 | — | 0 | 45 | 40 | 2 (a) | 531 | | | |
| | | | 75 | 57 | 92 | 70 | —(a) | 532 | 16 | | 8 | 50 | 10 | 3 (a) | 532 | | | |
| | | | | | | | | 533 | 5 | 50 | 12 | 60 | 10 | 4 | 533–B | | 30.0 | 383216 |
| | | | 82 | 52 | 88 | 45 | — | 534 | 10 | — | 9 | 60 | 10 | 4 (a) | 534 | | | |
| | | | 97 | 33 | 50 | 45 | —(a) | 535 | 3 | 28 | 6 | 60 | 20 | 4 (a) | 535 | | | |
| | | | 97 | 71 | 88 | Seg | —(a) | 536 | 5 | 14 | 0 | 60 | 10 | 4 (a) | 536 | | | |
| **Parental varieties** | | | | | | | | | | | | | | | | | | |
| Marquillo, | 9 | 0 | 44 | 0 | 0 | Tr | — | | 0.8 | 6 | 0.6 | Tr to 5 | 10–15 | 2–3 | | 5 | | |
| Tenmarq | 97 | 86 | 100 | 0 | 85 | 65 | — | | 80 | 65 | 35 | 90 | 40 | 2 | | 100 | | |

(a) Line discontinued. (b) Strains for which yield is not given were grown in short rows or rows of spaced plants.

TABLE 15.—*Records of Marquillo × Tenmarq 35 FN 660 which gave lines that had highest resistance to fly, good agronomic records and resistance to leaf rust, but most of which were susceptible to stem rust.*

| $F_3$ 1934–1935. | | | $F_4$ 1935–1936. | | | | | $F_5$ 1936–1937. | | | | | | $F_6$ and $F_7$ 1938. | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Manhattan. | | Springfield. | | Manhattan fly nursery. | | | | Springfield. | | Manhattan. | | | | | | |
| | | | | | | | | | | | | In disease nurseries. | | | | | |
| Row No. | Plants infested | Spring survival | Plants infested, fall | Survival after fly infestation | Survival after winter killing | Stem rust | Leaf rust | Row No. | Plants infested, fall | Culms infested, spring | Plants infested, fall | Stem rust | Leaf rust | Mildew reaction | 1937 fly nursery | Springfield. Fly infestation, fall | Manhattan. Yield in bushels in agronomy nursery | Kansas selection number |
| | Percent | Percent | Percent | Percent | Percent | Percent | Percent | | Percent | Percent | Percent | Percent | Percent | | | Percent | | |
| | | | | | | | | 1157 | 3 | — | 7 | | 90 | | 36FN605–B | 0 | 27.0 | 35FN660–1 |
| | | | | | | | | | | | | | | | 508–B | 4 | 27.0 | 383204 |
| | | | | | | | | | | | | | | | 2508–2 | | 35.2 | 383344 |
| | | | | | | | | 508 | 3 | 0 | 0 | 65 | 10 | 4 | 2508–4 | | — (b) | 384011 |
| | | | | | | | | | | | | | | | 2508–5 | | — (b) | 384012 |
| | | | | | | | | 509 | 6 | — | | 70 | 25 | 4 (a) | 509 | | | |
| | | | 50 | 67 | 97 | 80 | — | 1503 | — | — | 0 | — | — | — | 1503–1 | | 30.8 | 383393 |
| | | | | | | | | | | | | | | | 1503–3 | | 31.0 | 383395 |
| | | | | | | | | | | | | | | | 1505–1 | | 30.2 | 383396 |
| | | | | | | | | 1505 | — | — | 0 | — | — | — | 1505–3 | 0 | 39.6 | 383397 |
| | | | | | | | | | | | | | | | 1505–4 | | 35.8 | 383398 |
| | | | | | | | | | | | | | | | 1505–6 | | 42.2 | 383399 |
| 660 | 8 | 97 | | | | | | 1037 | 0 | 3 | 11 | 80 | 65 | 4 | 36FN606–B | 0 | 40.0 | 35FN660–2 |
| | | | | | | | | 510 | 5 | — | 3 | 60 | 20 | 4 (a) | 510 | | | |
| | | | | | | | | 511 | 0 | — | 3 | 65 | 40 | 4 (a) | 511 | | | |
| | | | 38 | 100 | 91 | 80 | — | 512 | 0 | — | 3 | 70 | 20 | 4 (a) | 512 | | | |
| | | | | | | | | | | | | | | | 1507–B | 1 | | |
| | | | | | | | | 1507 | — | — | 0 | — | — | — | 1507–1 | | 34.6 | 383403 |
| | | | 54 | 92 | 92 | 80 | -- | 1513 | — | — | 0 | — | — | — (a) | 1507–5 | | 34.6 | 383407 |
| | | | 88 | 50 | 96 | 80 | — (a) | 513 | 9 | 0 | 0 | 60 | 40 | 2 | 513 | | | |
| | | | 62 | 54 | 90 | 70 | — | 514 | 0 | 6 | 0 | 60 | 20 | 2 | 514–2 | | 30.4 | 383347 |
| | | | | | | | | 515 | 10 | — | 13 | 60 | 25 | 3 (a) | 515 | | | |
| | | | 93 | 67 | 97 | 80 | — | 516 | 0 | — | 9 | 90 | 80 | 4 (a) | 516 | | | |
| | | | 84 | 58 | 90 | 80 | — | 517 | 3 | — | 0 | 70 | 60 | 3 (a) | 517 | | | |
| | | | | | | | | 518 | 3 | | 0 | 65 | 10–80 | 4 (a) | 518 | | | |
| **Parental varieties** | | | | | | | | | | | | | | | | | | |
| Marquillo, | 9 | 0 | 44 | 0 | 0 | Tr | — | | 0.8 | 6 | 0.6 | Tr to 5 | 10–15 | 2–3 | | 5 | | |
| Tenmarq.. | 97 | 86 | 100 | 0 | 85 | 65 | — | | 80 | 65 | 35 | 90 | 40 | 2 | | 100 | | |

(a) Line discontinued. (b) Strains for which yield is not given were grown in short rows or rows of spaced plants.

marked tendency to form field hybrids. As has been shown above, $F_1$ plants involving Marquillo resistance tend to be susceptible. At times the susceptibility of these occasional field hybrids would explain the presence of a small infestation in Marquillo. This explanation is of limited application, since it does not apply in those cases where Marquillo carried a fairly high infestation, nor will it apply to infestation in Iumillo from which Marquillo derives its resistance. It is highly probable that this explanation will not apply to all winter-type Marquillo hybrids, since it did not, apply to one spring wheat hybrid involving a parent related to Marquillo [Powers (16)].

The presence of strains of fly which differ in infestation capacities on different wheat varieties has been demonstrated in previous publications *(12) (20).* The occurrence of biotypes of fly capable of feeding on Marquillo may be suggested as a possible explanation of the presence of larvae which are able to mature on this variety and its hybrids. Such strains of fly, normally occurring in the general population, would be sorted out in increasing numbers with each increase in the intensity of the infestation. This increase has been observed in series of field tests (fig. 2). Such strains of fly, if present, might take the form, either of types definitely associated with certain varieties and resistant factors transmitted to their hybrids, or they may be merely more vigorous individuals or strains capable of higher infestation on any resistant variety.

Under high intensities of infestation many larvae reach the feeding position on the resistant Marquillo, and later die there (figs. 10, 12). The mass secretions from many live larvae or enzymes and other products of the decaying larvae might operate to break down resistance to some extent, allowing a few larvae, arriving later, to reach maturity. Such an effect if present would give increasing numbers of larvae maturing on Marquillo with increasing intensity of field infestation, as has been observed (fig. 2). This explanation would hardly apply, however, to flaxseed formed on Marquillo under tests with low intensities of infestation,

The data in table 2 suggest that disproportionately larger populations of fly occurred on Marquillo in the spring at times when the plants were growing rapidly. Thus, there appears to be a difference in the strength of resistance related to stage of plant growth. This explanation will account for some of the higher infestation records on Marquillo and its hybrids. Its occurrence is of economic importance, since the lower infestation in the fall in Marquillo hybrids would mean a smaller source of infestation for the spring generation at a time when the resistant plants were relatively more susceptible. The explanation of stage of growth will not account for a differing infestation of two seedling Marquillo plants, side by side in the same row.

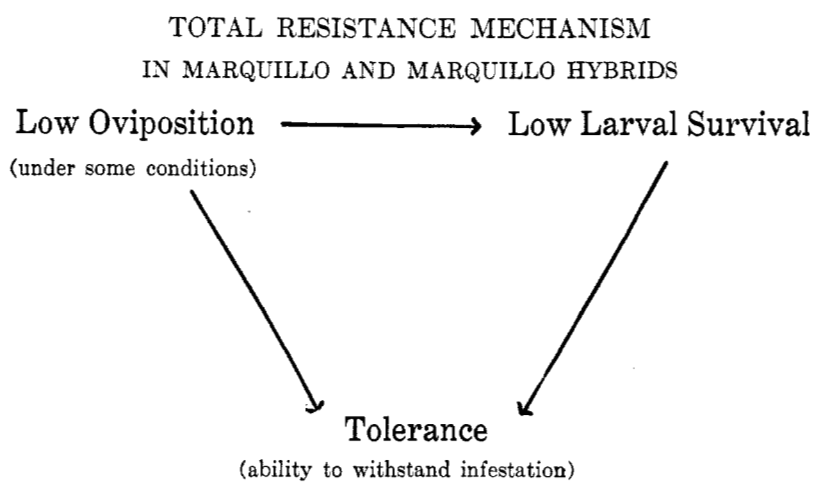
In many of the tests Marquillo has appeared to be more resistant than the winter type hybrids derived from it. An examination of young plants that are beyond the seedling stage and especially those at the time of development of the spring brood of fly will indicate the presence of many more tillers and leaves on the winter

type hybrids. Thus, these hybrids have more leaf surface available for oviposition and more tillers available for infestation. In these older plants a culm or tiller infestation count is a better basis for comparison between Marquillo and its hybrids than is a plant count.

Experimental studies of these and other possible explanations of the mechanism of resistance and of infestation on resistant hybrids are being continued.

### NATURE OF THE MECHANISM OF RESISTANCE IN MARQUILLO AND MARQUILLO HYBRIDS

Many of the data on Hessian fly presented in this paper are concerned with the low infestation on Marquillo and its hybrids which comes about primarily as a result of low larval survival after the larvae reach the feeding position. A study of the total fly resistance of Marquillo and its hybrids shows at least two other mechanisms which make these strains more desirable economically than susceptible wheats. Little is known concerning the way they operate,




but both appear more sensitive to environmental conditions than is the character of larval survival. The mechanism of tolerance, or ability to withstand infestation was particularly evident in the $F_4$ Marquillo hybrids, but has been observed in several subsequent tests. The resistance mechanism for receiving low oviposition is present in Marquillo under some conditions and there is a little evidence that this mechanism has been transferred to at least some of the winter type Marquillo hybrids. The first two mechanisms mentioned and possibly the third also appear to be the result of separate genetic factors, although they are clearly interrelated in their final effects as indicated in the above diagram. These three mechanisms then make up the total difference between Marquillo or some of its hybrids and susceptible winter wheats and collectively represent the characteristic called Hessian fly resistance in these strains.

## SUMMARY

1. Marquillo spring wheat, which resulted from an interspecific cross made at the Minnesota Agricultural Experiment Station, has been found to possess marked resistance to Hessian fly in both hard and soft wheat belts. The fly resistance of Marquillo is probably derived from its Iumillo durum wheat parent.

2. The fly resistance of Marquillo which was incidentally carried over from the durum parent along with the stem rust resistance, for which the cross was made, has now been transferred to winter wheats by means of crossing.

3. The fly resistance derived from Marquillo tends to be recessive, although it appears to be due to more than a single genetic factor.

4. In these hybrids there was no evidence of linkage between fly resistance and resistance to disease, winter hardiness, spring or winter habit of growth, or other visible agronomic characters on which records were taken.

5. These hybrids also represent a marked advance over their parents in ability to survive and produce grain under extremely heavy fly infestations. This tolerance, as exhibited by the winter type Marquillo hybrids, is often less evident than the type of resistance resulting from low larval survival. It is nevertheless of considerable importance, especially in combination with low larval survival.

6. The different Marquillo hybrid lines showed wide differences in the amount of damage done by wheat jointworm. Although all lines were sometimes heavily infested, some had badly twisted and broken straws at the point of infestation, while other lines gave no such evidence of the presence of the insect, thus possessing a type of tolerance.

7. The various winter type Marquillo hybrids have given several different combinations of resistance to fly, tolerance to jointworm, resistance to leaf rust, stem rust, bunt and mildew.

8. Preliminary data indicate that Marquillo hybrids, particularly various lines of Marquillo X Oro and Marquillo X Tenmarq, may equal or excel the yield of standard varieties of winter wheats such as Turkey and Tenmarq.

9. Several possible explanations, based on available information, are given for the small infestation present on Marquillo and its hybrids.

10. The total difference in fly resistance between Marquillo or its hybrids and susceptible winter wheat varieties appears to be the result of the interaction between three or more separate heritable mechanisms; low larval survival, ability to withstand infestation, and under some conditions low oviposition.

11. The most important contribution from this cooperative study has been the gathering together of resistance to Hessian fly and tolerance to wheat jointworm with resistance to leaf rust, stem

rust, bunt, and mildew into each of several strains of promising hard red winter wheat. This combination of insect and disease resistance is not found in any other winter wheat so far reported. The presence of these resistant qualities in strains which closely approach the commercial types of winter wheat represents an important advance in plant breeding and in potential insect contnol.

12. These Marquillo hybrids are the first winter wheats to show marked resistance to the Hessian fly in experimental tests in both hard and soft wheat belts wherever so far tested.

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