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THRIPS RESISTANCE IN THE ONION

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THRIPS RESISTANCE IN THE ONION[1]

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INTRODUCTION

THE SELECTION and breeding of plants resistant to parasites had its inception chiefly in the field of plant pathology, more specifically in the development of cereals resistant to rust. While the breeding for resistance to insects is still in its infancy, the possibilities in this field appear to be almost unlimited. In certain cases, among which may be mentioned the control of onion thrips, breeding for resistance seems to offer promise. In this paper are presented data which show that in the case of the onion certain varieties do possess a definite resistance to thrips, and the characters thought to be responsible for this resistance are described in some detail.

Howitt,(22)[5] McColloch,(30) Martin,(29) and others have given excellent general reviews of the development of resistant crop plants; here only the more important papers concerned with resistance to sucking insects are reviewed.

The causes of resistance to insects have been grouped by Wardle and Buckle,(43) McColloch,(30) and Wardle(42) as physical, chemical, or physiological. The first category includes such characters as hairiness, thickness of epidermis, thickness of seed coat and rind, and habit of growth; the second, the presence of such compounds as acids, alkaloids, essential oils, and tannin together with the potash-phosphoric acid ratio; the third, such characters as vigor, seasonal adaptation, early maturity, ability to recover from injury, and positive or negative response to specific stimuli. In most instances, however, the characters, whether physical (morphological), chemical, or physiological, are probably genetic in nature and are therefore governed by the laws of inheritance. Resistance may result from one character, or from several combined; and the effectiveness of a character may vary with the soil condition and climate.

Among the physical or morphological characters that seem to be intimately associated with host resistance is hairiness. Hollowell, *et al,*(21) state that the English and Italian types of red clover, which are gla-

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[5] Superior figures in parentheses refer to Literature Cited, p. 230.

brous, suffer much more from the potato leafhopper, *Empoasca fabae* (Harris), than do the American strains, which are hairy. Pieters[34] maintained that the leafhopper was responsible for the development of the hairy American strain. This insect, native to the United States, has probably hindered the reproduction of the more glabrous plants so that only the hairy strains have survived. Fenton and Hartzell[12] thought that the hatching nymphs became entangled in the hairs, whereas Monteith and Hollowell[31] suggested that some character in addition to hairiness may be involved. About the same time Poos[35] found that, in the seedling stages, all varieties of red clover succumbed when injured by this leafhopper; in addition he observed no difference in the amount of injury to Kansas alfalfa and the more hairy Peruvian type. Poos and Smith,[36] and Jewett[23] also concluded that characters other than the amount and type of pubescence are, at least in part, responsible for resistance. Jewett[24] showed that more force is necessary to penetrate the leaf of the Kentucky than other varieties of red clover, a fact which may account in part for its being more resistant than the Italian. A report from South Africa by Worrall[45] stated that the hairy American Upland cotton is more resistant to the jassid, *Chlorita fascialis* Jacobi, than the more glabrous Sea Island and Egyptian varieties. The hairy types are sufficiently resistant to allow the plants to mature the bolls.

At the Kansas Agricultural Experiment Station, 100 species of grasses, comprising about 80 per cent of the native prairie grasses, were tested by Hayes and Johnston[20] for resistance to chinch-bug injury. The native, perennial species with harsh tissues (*Andropogon scoparious* in particular) proved best able to survive injury and recover.

Mumford,[33] discussing the curly-top disease of sugar beets, suggested that the thicker epidermis and cuticle in the resistant strain may indicate some external protection from the beet leafhopper, *Eutettix tenellus* (Baker). In studying the onion thrips on cotton, Wardle and Simpson[44] noted that the underside of the leaves is preferred, apparently because of a difference in epidermal thickness. Bailey[2] observed the same preference on the part of the bean thrips, *Hercothrips fasciatus* (Perg.), on its native hosts.

Staniland[40, 41] found the Northern Spy apple practically resistant to the woolly aphid (*Eriosoma lanigerum* Haus.), but the same degree of resistance did not exist in roots and branches. According to the evidence, the resistance of apple stocks aboveground depends somewhat upon a high per cent of sclerenchyma encircling the stem and preventing penetration. The middle lamella, however, can be dissolved by the saliva of the aphid, so that the check formed by the sclerenchyma may be overcome eventually. He concluded that resistance cannot be explained wholly by mechanical considerations. *Aphis rumicis* Linn. was found on stocks resistant to woolly aphid. Apparently, then, resistance to these two aphids is associated with different characters. Davidson[8] reported that the saliva of *A. rumicis* can dissolve a passage for the piercing organ but that the presence of a thick cuticle may prevent the *young* aphid from piercing certain tissues. Monzen[32] in Japan thought that a greater pH concentration in the sap or a "specific repellent ingredient" caused resistance of apple stocks to the woolly aphid. Salman[37] considered the Zuccalmaglio-Reinette variety of apple to be resistant to attacks of woolly aphids. Resistance was most noticeable in grafted trees, the stock being infested while the scion was comparatively free. Lepelley,[27] conducting some tests with seedlings derived from crossing the Northern Spy with susceptible varieties, concluded that this variety was heterozygous for resistance.

Even less clearly understood are the chemical factors that are thought in some way to control resistance. Comes[6] stated that acidity of the plant sap caused by organic acids afforded protection and that malic was considered the most toxic. Gernert[15] stated that F_1 hybrids of teosinte and yellow dent corn resembled teosinte and were resistant to attacks of *Anuraphis maidi-radicis* (Forbes) and *Aphis maidis* Fitch. The tougher leaves and more bitter sap of the teosinte parent and the hybrid probably account for their being more resistant than corn.

Andrews[1] showed that a high ratio of potash to phosphoric acid in the tea plant acted inimically to *Helopeltis theivora* Waterh. (a mirid). Though the normal ratio (potash to phosphoric acid) is about 2 to 1, the resistant plants had a ratio of 4 to 1. Attempts to increase the normal ratio gave variable results. Direct injection of potash was not effective. The results of Dementiev[11] on the control of woolly aphid after the injection of barium chloride (1 to 350) into the roots of apple trees were variable. Sanford[38] controlled cottony cushion scale (*Icerya purchasi* Maskell) on Spanish broom by filling with potassium cyanide crystals a hole bored in the trunk.

Although the field of physiological resistance is exceedingly complex, we may well discuss some of the scattered references in the literature.

Harland[16] found that certain native Indian strains of cotton were resistant to leaf-blister mite, *Eriophyes gossypii* Banks. Flint and Hackleman[13] observed that Champion White Pearl, Democrat, and Black Hawk varieties of corn were able to grow vigorously under the same infestation of chinch bugs that killed the more susceptible varieties. Davidson[7] found that the eighteen varieties of *Vicia faba* that he studied were much more susceptible to *Aphis rumicis* than is *V. narbonensis*, the probable prototype of *V. faba*. Resistance seemed to be associated with the "general physiology of the plant." Searls[39] observed that the degree of aphid infestation (*Illinoia pisi* Kalt.) was less severe on the yellow than on the greener plants or varieties of peas. The same held for alfalfa and sweet clover infested with *Empoasca fabae* Harris.

According to Lees,[26] a mite (no species mentioned) that infests currants and normally feeds on the products of the hypertrophied tissue (the plant's response to the wound stimulus) cannot maintain itself on the red currant *Ribes vulgare,* which develops no hypertrophied tissue. Seabrook's Black, a variety of *Ribes nigrum,* is resistant because the mite kills the growing point and thus starves itself. Harland,[18] reporting that certain varieties of cotton are resistant to the leaf-blister mite (*Eriophyes gossypii* Banks), suggests that resistance results from lack of the gall formation that occurs in susceptible varieties.

In many instances the nature of resistance has not been suggested. Such a case is that of the grape phylloxera, among the first to receive consideration because of its great practical importance. Certain species indigenous to the Mississippi Valley were found to be resistant and have been used successfully as root stocks in infested regions. This subject has been thoroughly discussed by Davidson and Nougaret,[9] Bioletti, *et al,*[4] and Börner.[5]

Beach and Maney[3] secured resistant hybrids by crossing the sand cherry, *Prunus besseyi* Bailey, which is resistant to aphids (no species given), with Montmorency cherry (*Prunus cerasus*) and with Wyant plum (*Prunus americana*), both of which are susceptible. Resistance was found to be inherited as a simple dominant, but its nature was not determined.

Harland[17] observed that two types of Seredo cotton were resistant to the black scale (*Saissetia nigra* Nietn.), but did not suggest the cause of resistance.

Wardle and Buckle[43] stated that the Leconte and Kieffer varieties of *Pyrus,* which are F_1 hybrids between the Chinese pear (*Pyrus sinensis*), resistant to San Jose scale, and the susceptible *Pyrus communis,* resemble *P. sinensis* in resistance.

In none of the cases cited above has the exact nature of resistance been determined. With such a complex condition presenting itself, detailed and highly technical experiments must precede any definite conclusions regarding the exact nature of resistance. Obviously, too, even though the feeding process in the sucking insects mentioned is very similar, the characters causing resistance are not at all comparable, and each problem must be treated individually.

STUDIES ON RESISTANCE TO THRIPS

For three-quarters of a century or more, investigators have sought a satisfactory method of controlling thrips (*Thrips tabaci* Lind) on the onion (*Allium cepa* L.). Although thrips are readily killed by various contact insecticides, usually a number of rather costly applications are necessary. Satisfactory chemical control, indeed, has thus far been impossible for several reasons: A large number of thrips are always protected between the inner leaves of the onion plant, the pupal stage is spent in the soil, the species is very prolific, the generations overlap, natural parasites are lacking, and other host plants are numerous. The enormous damage to the onion crop in California and the unsatisfactoriness of chemical control have necessitated a mode of attack different from that made in the past upon this insect.

Growers who have compared different varieties planted side by side have observed that the Spanish types are somewhat more resistant to thrips injury than are such varieties as Australian Brown and Southport Yellow Globe. The Spanish types do suffer less under conditions of moderate infestation than the so-called American types; but under conditions of extreme infestation as occurred in Davis, California, in 1931 they also were killed prematurely. This difference in the susceptibility of onion varieties suggested the possibility of developing resistant ones, and this work has now been under way for several years at the California Agricultural Experiment Station.

Throughout this investigation, the Division of Foreign Plant Introduction of the United States Department of Agriculture has closely coöperated with the present authors. It has secured seed from many countries, which were tested in the breeding plots at Davis, along with most of the varieties commonly grown in this country. Of chief interest were the introductions from countries of western Asia, especially the area extending from Palestine to India which De Candolle[10] assigned as the probable native home of the onion. In this region, then, we should expect to find the greatest diversity of form, and perhaps a variety with a high degree of resistance.

Comparison of Thrips Population on Different Types of Onions.—In a study of thrips resistance MacLeod[28] in New York State, classified varieties of onions as susceptible, average, and resistant, according to the number of thrips present on the plant. As susceptible, he lists Southport Red Globe, Extra Early Barletta, Red Wethersfield, Mountain Danvers, Ebenezer, and Yellow Globe Danvers; as average, Crystal White Wax, Yellow Strasburg, Prizetaker, and Southport White Globe; as resistant, Utah Valencia, Utah White Sweet Spanish, Valencia, Riverside

Sweet Spanish, Sweet Spanish, Extra Early Red Flat, White Portugal, and Yellow Danvers Flat. The results secured at Davis have not coincided exactly with these. The last three varieties, especially, cannot be classified as resistant here, either as to number of thrips or as to freedom from injury (table 2).

Fig. 1.—The three rows in the foreground to the left are the variety White Persian; the others are Australian Brown. Note the serious damage done by thrips to the latter variety and the freedom of the White Persian from injury. Photographed, June 26, 1931.

In 1931, at Davis, occurred an exceptional opportunity to observe the resistance to thrips of a number of domestic onion varieties and foreign introductions. As conditions were ideal for the rapid increase of thrips, infestation was very severe, and most of the varieties were killed early in the season. The leaves dried from the tips down, causing the premature death of the plants. One introduction, however, FPI 86279 from Persia (fig. 1), remained green throughout the season and showed no injury. This variety, which is here called White Persian, was outstanding in its resistance. The Spanish types, while showing somewhat less injury than the American, were also killed prematurely.

In 1932 a daily count of the thrips population was made on several varieties (table 1) from May 11 to June 1. In some instances there were only a few plants available for observation. The data, being very interesting, are included here; they agree closely with the results obtained in 1933 (table 2).

In 1933 a more comprehensive test of thrips resistance was made. This included varieties and strains of onions commercially important in the

TABLE 1

VARIETIES OF ONIONS ARRANGED ACCORDING TO THE NUMBER OF THRIPS (ADULTS AND LARVAE) PER PLANT; DAVIS, CALIFORNIA, MAY 11 TO JUNE 1, 1932

Variety	Number of plants	Average number of thrips
White Persian	16	8.0
California Early Red (21-22-1)	38	20.3
Early Grano	4	26.5
Sweet Spanish	68	29.3
Denia	6	31.1
Australian Brown	28	33.2
Italian Red	26	38.3
Yellow Danvers Flat	4	39.2
Red Wethersfield	12	40.0
Southport Red Globe	24	42.0

United States, as well as all the foreign introductions. The seed was sown in the coldframe the last of November. The seedlings were transplanted to the field on March 29 and were spaced 3 inches in rows 27 feet long and 18 inches apart. A plot consisted of ten plants of a strain, and these were replicated five times (except FPI 101113 and FPI 101533). Irrigation water was applied in furrows between the rows. The plants were not treated with insecticides.

In 1933 only the larvae present were counted. These represent rather accurately a definite proportion of the entire thrips population, which is composed of overlapping generations. They cannot fly, are not difficult to count, and remain on the same plant throughout the larval stage.

At each count, the mean number of larvae per plant was determined for each lot of ten plants. These averages were used to determine the frequency distribution.

Counts were begun on May 9 and were repeated at five-day intervals on each strain, until the first plant matured. A plant was considered mature when the top fell. Counts on Nebuka (*Allium fistulosum*) or

Japanese onion were stopped on July 8, although this is a perennial and continues to grow as long as conditions are congenial. The varieties in

TABLE 2

Varieties and Strains of Onions Arranged According to the Average Number of Thrips Larvae per Plant; Davis, California, 1933

Variety	Mean number of larvae per plant	Period of counting, May 9 to date indicated
White Persian	4.14±0.09	July 8
Nebuka (37-1-1)	5.99±0.23	July 8
39-4	6.43±0.16	June 23
FPI 101460; Poona, India	6.68±0.20	June 13
FPI 101499; Poona, India	6.85±0.21	June 13
44-2	6.99±0.20	June 28
Yellow Bermuda	7.00±0.24	June 13
California Early Red (21-22-1)	7.03±0.19	June 23
Australian Brown (5-317-5); light-green foliage	7.06±0.15	July 13
Crystal White Wax	7.23±0.26	June 13
FPI 101461; Poona, India	7.25±0.26	June 13
Italian Red (13-20-3)	7.39±0.16	June 28
Early Grano	7.66±0.18	June 13
Southport White Globe	7.74±0.17	June 18
Prizetaker	7.86±0.18	June 23
Sweet Spanish	8.14±0.16	June 28
White Sweet Spanish	8.16±0.19	June 23
51-3	8.41±0.25	June 28
FPI 101113; Nanking, China	9.08±0.29	June 28
FPI 101112; Nanking, China	9.17±0.24	June 18
FPI 101533; Burma, India	9.28±0.43	June 23
FPI 101575; Pashawar, India	9.38±0.34	June 18
41-8	9.40±0.35	June 18
FPI 101171; Pusa, India	9.41±0.32	June 13
Extra Early Yellow	9.55±0.19	June 18
Australian Brown (commercial)	9.65±0.24	June 23
42-8	9.78±0.24	July 3
White Portugal	9.91±0.31	June 18
Yellow Strasburg	10.02±0.29	June 18
Extra Early Red Flat	10.32±0.28	June 18
FPI 101224; Punjab, India	10.35±0.28	June 23
Australian Brown (5-222)	10.39±0.25	June 23
Mt. Danvers	10.40±0.29	June 18
Yellow Danvers Flat	10.54±0.30	June 23
Red Wethersfield	11.05±0.29	June 23
Ohio Yellow Globe	11.17±0.26	June 23
Ebenezer	11.35±0.25	June 28
Australian Brown (combined pure lines)	11.60±0.25	June 28
Southport Red Globe	11.69±0.26	June 28
Yellow Globe Danvers	12.05±0.26	June 23
Australian Brown (5-16)	12.62±0.31	June 28
Yellow Bottleneck	12.76±0.39	June 28
Australian Brown (5-24)	12.84±0.33	June 23
Southport Yellow Globe	12.90±0.36	June 23

table 2 that bear numbers only, such as 39–4 and 44–2, are selections from foreign introductions that have been selfed for one generation. Of the introductions listed in the table, only White Persian had characters that would make its further propagation desirable.

All varieties were compared with the White Persian, on which the lowest mean number of larvae per plant (4.14) were found. The difference between this number and that of all other varieties and strains is significant. The varieties fall in practically the same order in 1933 (table 2) as in 1932 (table 1), so that certain of their characters evidently in-

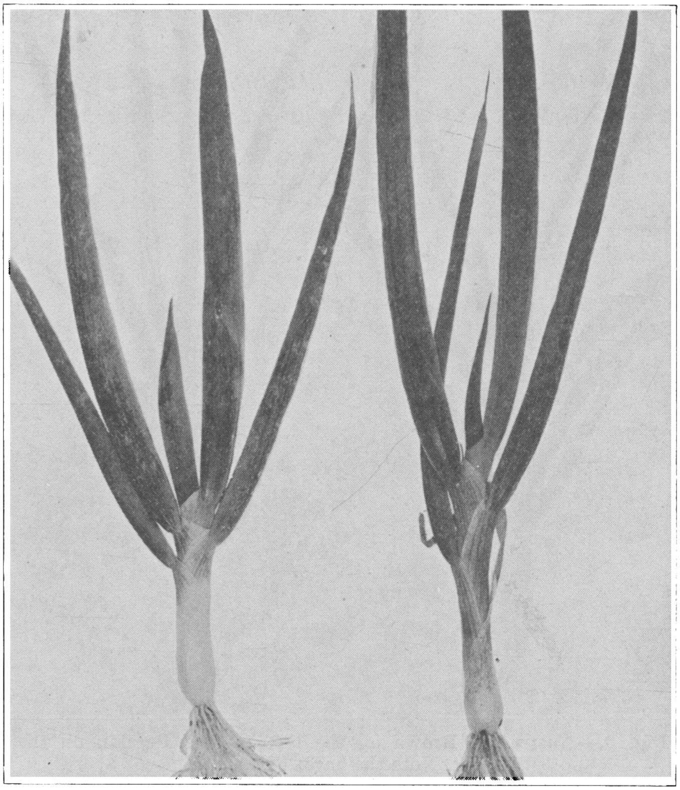

Fig. 2.—Nebuka (*Allium fistulosum*) or Japanese onion. The habit of leaf growth in this species helps to restrict the thrips population.

fluenced the size of the thrips population. The Nebuka, figure 2, which has foliage somewhat like that of White Persian has a thrips population nearly as low, but its leaf tissue is much more severely injured where the thrips have fed.

Most of the Australian Brown strains are severely injured by thrips and, as shown by table 2, support a large population. There is, however, one exception—namely, Australian Brown 5–317–5, which has been inbred for two generations and has foliage similar in color to that of Sweet Spanish.

Nature of Resistance in the White Persian.—The resistance of the White Persian to thrips seems to be determined by two groups of factors: one, probably, controls those characters that hold the thrips population to a minimum; the other helps the plant to withstand injury. Two, or perhaps three, characters apparently tend to restrict the thrips popu-

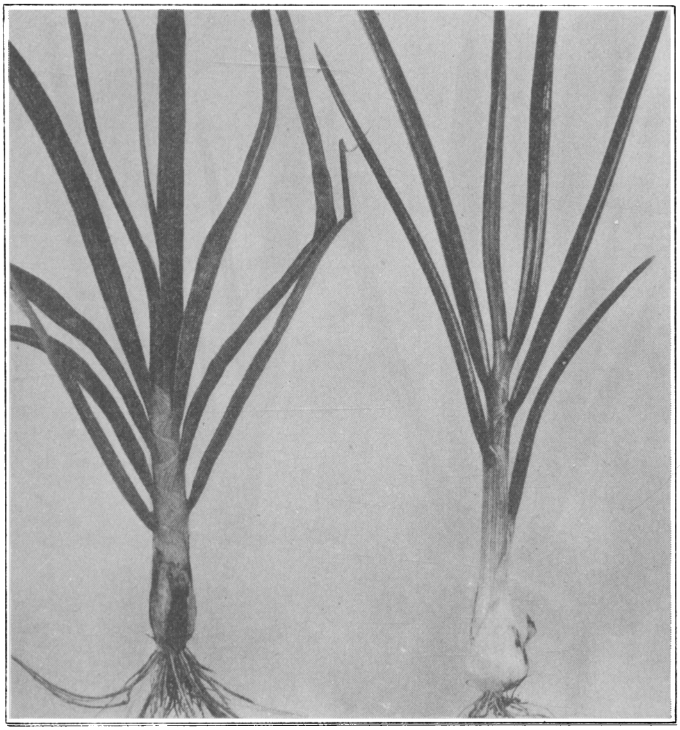

Fig. 3.—Australian Brown on the left; White Persian on the right. Note the habit of growth.

lation—namely, the shape of the leaves, the angle of divergence of the two innermost leaves, and the distance apart of the leaf blades on the sheath column. Probably of considerable importance is the difference in shape of the leaves. In most varieties the leaf blades have a flat side; these sides are face to face and, in the young leaves, closely appressed, protecting the larvae against insect enemies and adverse weather conditions. In White Persian the leaves are almost circular in cross section (fig. 3), reducing protection to a minimum.

The leaf blades of ten White Persian plants were pulled together and tied in order to increase the amount of contiguous leaf surface and thus determine whether the greater protective area formed would cause an increase in the thrips population. Ten plants of the Denia variety were handled in the same manner. Ten other plants of each variety not tied, were used as checks. Before tying and at about seven-day intervals thereafter, the number of larvae per plant was determined. The counts are presented in table 3.

The marked increase in the number of thrips on the plants whose tops were tied shows that closely bunched leaves make a very favorable environment for this insect. This also indicates that resistance in the White Persian is probably not caused by some toxic component within the plant, since the percentage increase in the number of larvae per plant

TABLE 3

MEAN NUMBER OF LARVAE PER PLANT WITH FOLIAGE TIED AND UNTIED; 1932

	Number of thrips on date tied, July 14	Number of thrips after		
		8 days	15 days	21 days
Denia, leaf blades tied	78.7	139.3	122.8	37.4
Denia, leaf blades not tied (check)	115.0	81.5	44.8	16.8
White Persian, leaf blades tied	19.3	60.5	80.4	20.3
White Persian, leaf blades not tied (check)	26.1	25.7	3.6	0.9

after the leaves were tied was more rapid in White Persian than in Denia. The later downward trend of the population was caused by the maturing of the plants.

The wide angle between the two innermost emerged leaves (fig. 3), especially in the young plant, is another White Persian character that helps to restrict the thrips population by reducing the protective environment to a minimum. Still another character, probably of some importance, is the greater vertical distance between the leaf blades. Each new leaf extends its sheath farther beyond the one encircling it than in other commonly cultivated varieties (fig. 3). This habit of growth produces an extremely long sheath column. If commercial varieties of onions had these leaf characters, one might secure a more efficient control by spraying or dusting than at present, because practically all of the foliage could be covered.

As stated above, the shape and habit of leaf growth in the White Persian probably help to restrict the number of thrips. Other characters help the plants to withstand injury, but these are as yet not well understood.

As has often been observed, thrips injury becomes most conspicuous following the first hot days of summer when there is a desiccation and dying back of the foliage; but it is not known just how high temperatures accentuate thrips injury. This typical injury is most prominent in varieties with dark-green foliage; less so in the Spanish types which have lighter-green foliage, and is apparently absent in White Persian which has foliage that is even lighter green than that of the Spanish types. Leaf color may be a factor in resistance to injury, because the temperature in the White Persian leaf tissues is possibly lower than in those varieties having darker-green foliage. Similarly, in the tomato fruit, Harvey[19] found dark-green areas to be more subject to injury by sunscald than light-green areas, because of the greater absorption of light with a consequent higher temperature in these areas.

In the White Persian one can determine the exact location where the thrips have fed because these areas are somewhat lighter green in color than the surrounding tissue but they do not seem to dry out. As a thicker leaf tissue might conceivably help to prevent desiccation of the cells surrounding the injured areas, measurements were made to find whether there was a difference between leaves of varieties showing different degrees of resistance. The varieties used were White Persian, Sweet Spanish, and Australian Brown. Sections were taken of the entire circumference at the widest part of mature leaf blades. These were killed, sectioned, stained, and made into permanent slides in the usual manner. The image of the section was projected with a Zeiss microprojector upon a screen, and at each bundle the thickness of the tissue was measured. Leaves of about fifty plants of each variety were so studied. If the thickness of the Australian Brown is taken as 1, then the Sweet Spanish has a value of 1.13; the White Persian 1.32. Analyzed statistically, the differences between the mean thickness of the Australian Brown and White Persian, and Sweet Spanish and White Persian were found to be significant. The difference between Australian Brown and Sweet Spanish may, however, be unimportant. Leaf thickness alone probably does not account for resistance to injury, because certain White Persian plants had leaves about the thickness of Australian Brown but still without typical injury.

History of the White Persian.—The White Persian variety of onion was obtained by Dr. W. E. Whitehouse of the United States Department of Agriculture, Division of Foreign Plant Introduction, in 1929, while he and H. L. Westover were traveling through Europe and Asia Minor to study and collect the forage, fruit, and vegetable crops indigenous to that part of the world. A number of varieties of onions were secured in Persia; but there, according to Dr. Whitehouse, the peasants considered the best onion to be a large white one grown under irrigation in Kashan, a village situated in the hills about 3,000 feet above sea level. Seed of this variety was distributed from Washington as FPI 86279. It was later named White Persian by the California Agricultural Experiment Station.

Characteristics of the White Persian.—Three crops of White Persian bulbs and two crops of the seed have now been grown at Davis. Although selections have been made within the variety for certain leaf characters, very little attention has been given to the isolation of desirable bulbs. Probably the best use of this variety at present is to cross it with the existing important commercial types, thus incorporating in them the resistant characters.

The chief objections to the variety as a commercial onion are its tendency to split badly and its poor keeping quality. Its strong tendency to bolt is no worse than that of some other varieties. When seeded in coldframes on September 4, 1931, and transplanted to the field on December 17, about 98 per cent of the plants bolted the following spring. Very little bolting occurred when seeding was done in the coldframe in late November and the transplanting was done in March.

As stated previously, the foliage is of a lighter green than that of any other variety ever grown in the plots at Davis. The innermost leaf, as it emerges, bends away somewhat from the next oldest leaf; and the sheath of the new leaf extends considerably beyond the one encircling it, causing the mature onion to have a conspicuously long sheath column. The leaf blades of the young plant are round in cross section, but those that arise later are more flattened.

The plants mature very late. The bulbs are white and oblate. The flavor is exceptionally mild—probably milder than that of any of the commercial varieties now grown in this country—and unlike that of any other onion variety known to us.

Breeding for Resistance.—An effort is now being made to incorporate the resistance characters of White Persian into susceptible varieties. At present, F_2 and first back-cross generations are being grown in the field and in the greenhouse. In order to expedite the work, the plants are being handled so that one generation is grown each year. If the seed is sown in July, the plants have a longer growing season, and most of them go to seed the following spring.

The first crosses between White Persian and other varieties were made by intermingling under muslin cages. Flies were introduced to do the pollinating, as described elsewhere (Jones and Emsweller[(25)]). Seed from these White Persian parents was sown in the coldframe; and the F_1 plants having a darker foliage color could be selected from among the seedlings. Some of them were selfed; others were back-crossed to commercial types. Selfing was accomplished by enclosing each umbel within a one-pound manila paper bag; back-crossing, by emasculating an inflorescence of the plant to be used as the female parent, tying to it one from the pollen parent, and enclosing both within a small cheesecloth cage. In some cases the plants that were to be crossed were grown side by side (fig. 4). In other cases the flower stem of the pollen parent was severed near the base and placed in a bottle of water, where it re-

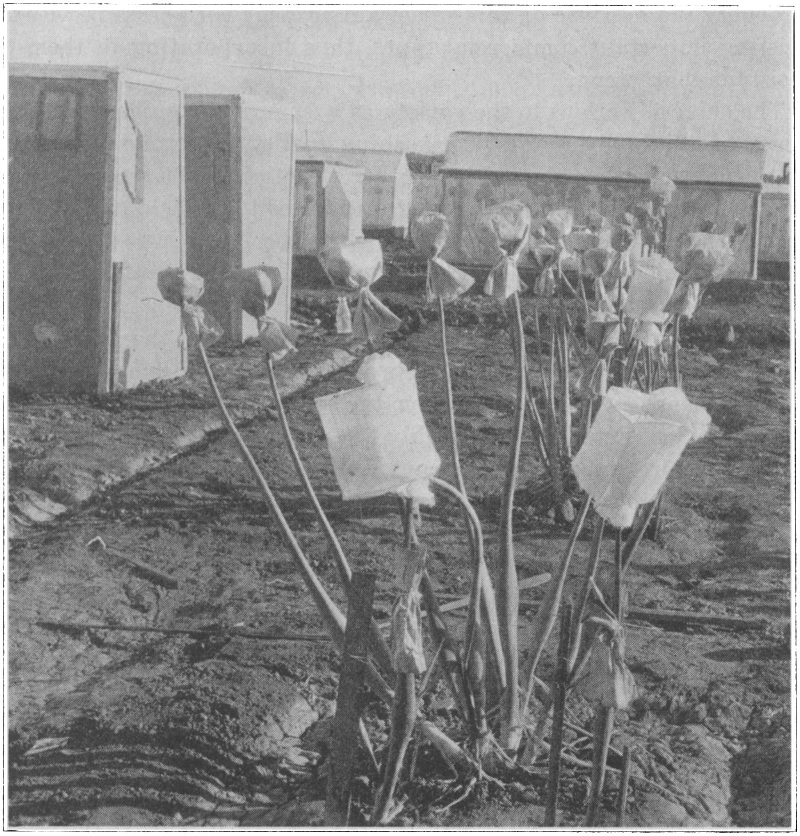

Fig. 4.—The two small cages in the foreground are made of a wire framework and covered with cheesecloth. Flower heads of the male and female parents are enclosed within, and flies are added to carry on pollination.

mained fresh and produced pollen for more than a week. Flies, hatched artificially, were placed within the small cages enclosing the two umbels; and a set of from 700 to 800 hybrid seeds was often secured. Crossing by means of flies is much more efficient than crossing by hand.

As stated previously, the bulbs are very poor keepers; as a rule they rot and sprout soon after being placed in storage. If set in the field, they usually make a good growth until about the time the plants start to bloom, but often die from various bulb rots before much of the seed is mature. Fair results have been secured by disinfecting the bulbs shortly after they have been harvested and then planting them in sterile soil before they begin to sprout. This method is used only for plants that are needed for breeding. For the production of large quantities of seed, the plants are not permitted to bulb. If seeding is done in July or in early August, the plants become large and are then set in the field some time during the winter. At Davis these plants produce a good yield of seed and remain in a healthy condition until practically all the seed is mature.

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