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CONTENTS

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12. The Effect of the Plant on the Reaction of the Culture Solution, by D. R. Hoagland. November, 1923.
14. The Respiration of Potato Tubers in Relation to the Occurrence of Blackheart, by J. P. Bennett and E. T. Bartholomew. January, 1924.
16. The Moisture Equivalent as Influenced by the Amount of Soil Used in its Determination, by F. J. Veihmeyer, O. W. Israelsen and J. P. Conrad. September, 1924.
17. Nutrient and Toxic Effects of Certain Ions on Citrus and Walnut Trees with Especial Reference to the Concentration and Ph of the Medium, by H. S. Reed and A. R. C. Haas. October, 1924.
18. Factors Influencing the Rate of Germination of Seed of Asparagus Officinalis, by H. A. Borthwick. March, 1925.
19. The Relation of the Subcutaneous Administration of Living Bacterium abortum to the Immunity and Carrier Problem of Bovine Infectious Abortion, by George H. Hart and Jacob Traum. April, 1925.
20. A Study of the Conductive Tissues in Shoots of the Bartlett Pear and the Relationship of Food Movement to Dominance of the Apical Buds, by Frank E. Gardner. April, 1925.

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THE RESISTANCE OF VARIETIES AND NEW DWARF RACES OF TOMATO TO CURLY TOP (WESTERN YELLOW BLIGHT OR YELLOWS)[1]

J. W. LESLEY[2]

INTRODUCTION

Certain tomato varieties are known to be resistant to curly top,[3] formerly known as western yellow blight. Curly top is transmitted, in the United States, to beets, tomatoes, and a great variety of other host plants by the leafhopper *Euttetix tenellus* (Baker). As the absence of disease in some previous trials of resistance in tomato varieties was believed to be due to a lack of infective leafhoppers, viruliferous leafhoppers were confined on the plants in some of the experiments reported in this paper. However, trials under natural infestation were thought to be still necessary to test the value of natural resistance as a practical means of control. Accordingly, it was decided to make use of both natural and artificial infestation. An account of trials with natural infestation during three years, 1922–1925, has previously appeared in this journal.[(5)]

[1] Paper No. 234, University of California Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

[2] Assistant Plant Breeder in the Experiment Station.

[3] Since the disease is caused by the same virus as curly top of sugar beets, the name curly top, which was first used with the tomato by Carsner and Stahl[(4)] and subsequently by Severin,[(6)] is preferred to 'yellows.'[(8)] The name chosen has the additional advantage of avoiding confusion with yellows of asters, a disease caused by a different virus, which is transmissible to the tomato.

METHODS

The investigation was carried on at the Citrus Experiment Station, Riverside, California, and at the Cotton Field Station, United States Department of Agriculture, Shafter, California.[4] At Shafter in 1926–1929 and at Riverside in 1926 the plants were started in cold frames, but at Riverside in 1927–1930 they were started in paper pots in a heated greenhouse. Transplanting to the field was done late in April or in the first fortnight of May, which is about the usual time of planting when the crop is intended for the cannery. Santa Clara Canner, Stone, and Norton, important canning varieties susceptible to yellows, were planted as checks. Varieties which were less susceptible than the check varieties when exposed only to natural infestation in the field by the leafhoppers are termed resistant. In recording the condition of the plants, the first definite symptoms of curly top were denoted by *E,* signifying an early stage of the disease, and fully developed symptoms, especially yellowing, by *Y*. Only plants showing definite symptoms of curly top were counted as affected. The probable error of the percentage affected (tables 1 to 3) was obtained from the formula:

$$\text{P. E.} = 0.67 \times \sqrt{p \times q \div n}$$

where p is the observed percentage affected, and $q = 100 - p$. Since it is known that the standard deviation of the observed percentages may far exceed that of simple sampling[(5)] the probable error must be used with reserve, especially where p approaches its limiting values.

NATURAL INFESTATION

The results of the trials with plants exposed only to natural infestation are shown in tables 1 to 3. At Shafter in 1926 an extremely severe epidemic of curly top occurred early in the summer. As in some previous trials there, no variety had sufficient resistance to survive, and on June 23 only 4 plants out of over 800 remained healthy. Progeny tests of these plants indicate that they were not exceptionally resistant. At Shafter in 1928 and at Riverside in 1927 to 1929 less than 5 per cent of curly top occurred. At Shafter in 1927 and 1929 and at Riverside in 1926 moderate epidemics occurred. Selected

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[4] The writer is especially indebted to Dr. E. Carsner, and Mr. M. Shapovalov, Senior Pathologists, United States Department of Agriculture, for many helpful suggestions.

TABLE 1

TOMATO CURLY TOP AT RIVERSIDE, CALIFORNIA, IN 1926; NATURAL INFESTATION*

	Number recorded	Per cent affected, June 28	Per cent affected, whole season	Probable error of sampling of percentage affected, whole season
Santa Clara Canner	39	23	64	5.2
Dwarf Aristocrat	86	5	34	3.4
Philippine Wild	39	18	56	5.3
Selected line from:				
Stone	41	29	66	5.0
Santa Clara Canner, series 73-1†	193	19	62	2.3
Santa Clara Canner, various	248	20	62	2 1
Dwarf Aristocrat × Red Pear F_3, dwarf	254	9	50	2.1
Dwarf Champion × Santa Clara Canner F_3, dwarf	151	9	53	2.7
Dwarf Aristocrat × Santa Clara Canner F_3, dwarf	172	5	38	2.5
(Dwarf Aristocrat × Red Pear, F_1)×(Dwarf Champion × Santa Clara Canner, F_1), standard	27	26	59	6.3
(Dwarf Aristocrat × Red Pear F_1) × (Dwarf Champion × Santa Clara Canner F_1), dwarf	17	6	30	7.4

* The following races were tested on a small scale and found to be susceptible: dwarf yellow pear; standard peach pear; dwarf compound; Manx Marvel X Santa Clara Canner F_1.

† Compare Hilgardia **2**:61, *table 5*, 1926.

TABLE 2

CURLY TOP AT SHAFTER, CALIFORNIA, IN 1927; NATURAL INFESTATION

	Sown February 25 Transplanted May 14				Sown Feb. 25 Transplanted June 2		Sown May 14 Transplanted July 6	
	Number recorded	Per cent affected June 16	Per cent affected whole season	Probable error of sampling of percentage affected whole season	Number recorded	Per cent affected whole season	Number recorded	Per cent affected whole season
Dwarf Aristocrat	63	44	52	4.2	20	5	148	1
Dwarf Yellow Pear	22	32	50	7.1	29	21	....	....
Red Pear	47	32	53	4 9	51	37	....	....
Yaquí Valley Wild*	29	14	48	6.2	....	....	....	....
Marglobe	17	12	18	6.2	7	29	....	....
Selected line from:								
Stone	27	33	48	6 4	....	....	....	....
Merced Stone	47	43	66	4.6	17	30	....	....
Santa Clara Canner, series 376	71	27	56	4.0	9	22	....	....
Santa Clara Canner, series 73-1	80	41	65	3.6	....	....	....	....
Dwarf Champion	5	20	20	......	10	10	....	....
Dwarf Aristocrat × Santa Clara Canner, F_4, dwarf	122	33	53	3.0	67	16	359	1
Red Pear × Dwarf, dwarf	20	40	60	7.4	....	....	....	....
Dwarf Aristocrat × Red Pear F_3, dwarf	92	25	38	3 4	48	19	....	....
Dwarf Aristocrat × Red Pear F_4, dwarf	68	12	38	3.9	29	7	....	....

* Collected by Mr. W. W. Mackie, Associate Agronomist, University of California.

lines from Santa Clara Canner, which were previously believed to be resistant, were as much affected as the parent variety (table 1) but Dwarf Aristocrat and most of the progenies of dwarf habit derived from crosses between Dwarf Aristocrat or Dwarf Champion and Santa Clara Canner were resistant. At Shafter in 1929, the difference between the per cent affected in the dwarf hybrid progeny of 2–7–1–3 and in Santa Clara Canner was 8.2 times the probable error (table 3). No variety of standard (nondwarf) habit was resistant except Red Pear, which in a single test at Shafter (table 2) seemed as resistant as Dwarf Aristocrat. Of the progenies of dwarf habit from Dwarf Aristocrat × Red Pear, none was clearly more resistant than Dwarf Aristocrat. Hitherto all dwarf varieties tested have appeared to be resistant, but a few dwarf progenies appear to be susceptible, in particular the F_6 from 2–7–1–5, which differed from Dwarf Aristocrat by 4.3 times the probable error (table 3).

TABLE 3

CURLY TOP AT SHAFTER, CALIFORNIA, IN 1929; NATURAL INFESTATION

	Pedigree number	Transplanted May 8				Transplanted May 14	
		Number recorded	Per cent affected May 31	Per cent affected whole season	Probable error of sampling of percentage affected whole season	Number recorded	Per cent affected whole season
Dwarf Aristocrat		200	24	71	2.1	....	....
Santa Clara Canner		83	46	94	1.7	16	100
Parana (Argentine)		61	26	93	2.2	32	81
Peru Wild*		46	24	96	1.9	....	....
Selected line from:							
Gigante liscio		90	29	94	1.7	12	92
Stone, series 52-1-1		367	25	88	1.1	32	75
Dwarf Aristocrat × Santa Clara Canner, F_6, dwarf	2–7–1–1	99	10	70	3.1	....	....
	2–7–1–3	100	14	64	3.2	....	....
	2–7–1–4	93	11	74	3.0	....	....
	2–7–1–5	97	15	85	2.4	....	....
	1–2–1–1	91	21	79	2.8	12	83
	1–2–1–3	52	6	62	4.5	....	....
	1–7–1–1	66	17	85	2.9	....	....
Dwarf Aristocrat × Red Pear, F_5, dwarf		93	10	70	3.2	10	40

* Collected by Mr. O. F. Cook, U. S. Dept. of Agriculture.

The influence of time of planting on the intensity of curly top was well illustrated at Shafter in 1927 (table 2). In Dwarf Aristocrat and a dwarf hybrid sown on February 25 and transplanted on May 14 over 50 per cent were affected, but in the same varieties sown on May 14 and transplanted on July 6, only 1 per cent.

It is evident from these and from previous trials that certain dwarf varieties and hybrids and also Red Pear are slightly resistant to curly top; resistance in the dwarfs is recessive and is due to the *d* (dwarf) gene or to a gene or genes closely linked with it. Although the resistance of the dwarf varieties is not sufficient to withstand very severe attacks of curly top, it will help to moderate the loss due to this disease. The percentage losses of plants due to curly top in field trials at Riverside in 1923 to 1926 and 1929 in the susceptible varieties, Stone, Norton, and Santa Clara Canner were 2, 52, 44, 62, 4; the corresponding losses in resistant dwarf varieties were 0, 32, 21, 34, 3. At Shafter in 1923 to 1929 the losses in the susceptible varieties were 14, 100, 100, 99, 58, 9, 94, and in the resistant varieties 8, 99, 99, 100, 50, 6, 72. In five epidemics of moderate severity the mean loss of stand due to curly top was 62 per cent in susceptible varieties as against 42 per cent in resistant dwarf varieties.

In order to make practical use of resistance, the attempt has been made to breed dwarf varieties resistant to curly top and at least equal in other respects to the standard varieties now in cultivation. Some of the F_6 progenies of dwarf habit obtained from Dwarf Aristocrat × Santa Clara Canner, such as those from 2–7–1–3 and 1–2–1–3 (table 3) seem to combine resistance equal to that of the dwarf parent with large size and good quality of fruit for canning, sufficient vine to shade the fruit, and earlier maturity than Santa Clara Canner. These dwarf varieties may be planted more closely than standards and may prove useful in sections where curly top is prevalent.

ARTIFICIAL INFESTATION

Artificial infestation consisted in confining a number of the leafhoppers, *Eutettix tenellus* (Baker), for two days in a celluloid cage attached to the tip of a tomato shoot. The cage was of the type used by Shapovalov[9] and consisted of a cylinder of celluloid 10 cm long and 6.5 cm in diameter with cheesecloth ends. As a rule one cage was attached to a plant. For maintaining and increasing the supply of leafhoppers, sugar beets were used as host plants. For two days preceding their use the leafhoppers were kept on severely diseased leaves of susceptible beets. If, after two days' confinement on tomato, one or more insects survived, as was usually the case, the plant was counted as having been artificially infested or as 'treated.' In many cases tomato plants which had been artificially infested did not become diseased, although they were certainly not all genetically resistant. Apparently the virus was either not introduced into them at all or not in such a manner as to cause disease. At Riverside where the artificial infestations were made, in all four seasons, 1927 to 1930, not more than 5 per cent of the plants became diseased through natural infestation.

Shapovalov[7] has observed that young tomato plants are more susceptible to curly top than larger and older plants, and Shapovalov and Beecher[10] found that the development of curly top in infected plants is influenced by environmental conditions. Carsner and Lackey[3] reported that, with curly top of sugar beets, the chance of infection and the incubation period are influenced by the number of leafhoppers per plant. Evidence is presented below (p. 40) that in the tomato similar effects are produced by variation in the number of leafhoppers. Consequently, in judging resistance, only plants of the same age infested on the same days and exposed to the same number of leafhoppers are directly comparable.

In 1928 about 850 plants were artificially infested, including progenies of plants which had survived natural or artificial infestation in the previous year and a rather large number or varieties not previously tested. The results are shown in tables 4 and 5. The first infestation was made 21 days after transplanting and other infestations as late as August 15 when the vines had probably attained their maximum size. As a rule, 5 leafhoppers were used to a plant. The mean percentage affected from infestations with 5 leafhoppers on June 7, June 13, and June 27 (table 4) was less in Dwarf Aristocrat, the dwarf hybrids, and Red Pear than in Santa Clara Canner. A few plants of some of these varieties subjected to 5 hoppers on July 20 (table 4) and to repeated infestations (table 5) behaved in a similar manner. The progenies of series 73–1 seemed to be fairly susceptible under artificial infestation just as those of closely similar origin were susceptible under natural infestation (table 2). On the other hand, after infestation with 15 hoppers on August 1 (table 4), the proportion affected in Santa Clara Canner was less than in the dwarf races. The progeny of series 52–1–1 seemed to be resistant when artificially infested, although under natural infestation (table 3) the progenies of its derivatives were clearly susceptible. On the whole, the results of the artificial infestation in 1928, while somewhat conflicting, indicate that varieties resistant in natural infestation are also resistant when artificially infested.

TABLE 4

CURLY TOP AT RIVERSIDE, CALIFORNIA, IN 1928*

Date of artificial infestation is followed by number of insects used, in parentheses.

	June 7 (3)		June 7 (5)		June 13 (5)		June 27 (5)		June 30 (5)		July 20 (5)		July 25 (10)		Aug. 1 (15)		Mean per cent affected of plants treated June 7, 13, and 27	Mean per cent affected of plants treated June 7 and June 30
	Number treated	Number affected	Number treated	Number affected	Number treated	Number affected	Number treated	Number affected	Number treated	Number affected	Number treated	Number affected	Number treated	Number affected	Number treated	Number affected		
Santa Clara Canner	....	....	6	5	16	10	12	6	....	....	10	5	....	....	6	1	65	....
Dwarf Aristocrat and Dwarf Champion	6	1	9	6	16	7	8	4	8	1	13	5	....	....	14	7	47	....
Red Pear	....	....	6	5	14	4	15	4	....	....	....	....	....	....	10	3	46	....
Selected line from:																		
Stone, series 52-1-1	....	....	5	1	14	4	11	1	....	....	10	5	....	....	7	2	19	....
Stone, various	....	....	11	9	....	....	....	....	16	4	....	....	....	....	....	....	....	53
Marglobe	....	....	4	2	....	....	....	....	8	3	....	....	10	4	....	....	....	44
Santa Clara Canner, series 73-1	....	....	7	5	12	5	10	6	8	2	....	....	....	....	....	....	58	....
Santa Clara Canner, series 400-4	....	....	4	2	4	2	....	....	10	5	....	....	....	....	....	....	....	50
Dwarf Aristocrat × Santa Clara Canner, F_4, dwarf	20	10	27	17	46	17	40	5	18	4	11	2	....	....	13	8	35	....
Dwarf Aristocrat × Red Pear, F_4, dwarf	8	3	26	15	30	13	27	8	20	6	10	1	....	....	12	5	42	....

* The following varieties were also artificially infested and were found to be susceptible: Précose Trophy, Nano e frutto grossissimo, Re Umberto, Meraviglia, di S. Marzano, Vittorio Emanuele, Dwarf Giant.

On June 2, 1930, 16 days after transplanting into the field, plants of a resistant dwarf race and of a susceptible variety were infested with 5 insects each, and other plants of similar varieties with 10 insects. When 5 leafhoppers were used 17 out of 24 plants of a resistant dwarf race and 20 out of 25 plants of a susceptible variety became diseased. When 10 insects were used, 22 out of 27 plants of a resistant dwarf race and all 27 plants of a susceptible variety became diseased. The proportion affected therefore was slightly less in the resistant races whether 5 or 10 insects were used for infestation.

TABLE 5

CURLY TOP AT RIVERSIDE, CALIFORNIA, IN 1928; REPEATED ARTIFICIAL INFESTATION

Date of infestation is followed by number of insects used, in parentheses.

	June 7 (3 to 5) or June 13 (5) or June 18 (5) and July 20 (10) or July 25 (10)		June 27 (5) and August 15 (25)	
	Number treated	Per cent affected	Number treated	Number affected
Santa Clara Canner	6	83	6	1
Dwarf Aristocrat	15	47	3	2
Dwarf Aristocrat, regenerated plant	1	100	....	....
Red Pear	10	40	....	....
Selected line from:				
Stone, series 52-1-1	14	64	8	4
Stone, regenerated plant	1	100	....	....
Santa Clara Canner, series 73-1	7	86	....	....
Dwarf Aristocrat × Santa Clara Canner, F_4, dwarf	31	52	16	4
Dwarf Aristocrat × Red Pear, F_4, dwarf	29	59	....	....

Very similar results were obtained from artificial infestation with 5 leafhoppers per plant on May 20, 1931, 20 days after transplanting to the field. On July 27, in a resistant dwarf race 79 per cent of the 56 plants treated were affected and in Norton 88 per cent of the 57 plants treated. In Grape Cluster, a small-fruited variety of standard habit, 69 per cent of the 32 plants treated were affected which indicates that it is at least as resistant as the dwarf race.

In 1927 artificial infestation was begun on July 18, when the plants were about six weeks older than those treated on June 5, 1928. The results are shown in table 6. As in the artificial infestations in June, 1928, as a rule, 5 leafhoppers were used per plant.

In 1929 over 1,000 plants were treated (table 7), beginning on May 25 when the plants were approximately of the same age as the youngest plants treated in 1928. As a rule in 1929 a greater number of plants of a variety received the same treatment and more leafhoppers were applied per plant than in 1927 or 1928. Tables 6 and 7 show that both in 1927 and 1929 Dwarf Aristocrat and practically all the dwarf hybrids and perhaps also Red Pear were as much affected with curly top as susceptible varieties such as Santa Clara Canner and the progenies of series 52–1–1. Simple trisomic (triplo-A) dwarf plants containing an extra *d* (dwarf) gene were slightly less affected than diploids in the same F_2 population (table 7), but no variety was clearly better able to survive artificial infestation than the susceptible checks. In 1929 some plants which survived the first infestation and were thought to be resistant were reinfested, but all became diseased.

TABLE 6

CURLY TOP AT RIVERSIDE, CALIFORNIA, IN 1927

Five leafhoppers were used per plant.

	Date of transplanting	Date of artificial infestation			
		July 20, 22, 24, and 26		July 28, 29, 30, 31, and August 1	
		Number treated	Per cent affected	Number treated	Per cent affected
Dwarf Aristocrat	May 20 and 25	40	78	11	36
Red Pear	May 20	....	....	14	50
Selected line from:					
Stone	May 25	....	....	10*	30
Morse's Santa Clara Canner	May 20	20	45	5	80
Selected line from:					
Santa Clara Canner series 73-1	May 20	....	....	10†	30
Dwarf Aristocrat × Red Pear, F_3, dwarf	May 20	20	60	15	33
Dwarf Aristocrat × Red Pear, F_4, dwarf	June 6	....	....	14*	50
Dwarf Aristocrat × Santa Clara Canner, F_4, dwarf	May 25	20	85	1	100

* 4 leafhoppers per plant. † 2 leafhoppers per plant.

Apparently when varieties and races known to be resistant under natural infestation were artificially infested in 1928, 1930 and 1931 they showed resistance, but in 1927 and 1929 they failed to do so and behaved like susceptible varieties.

As a smaller number of insects per plant was used in artificial infestations in 1928 than in 1929, it seemed probable that these differences in varietal response might be due to variations in the number of leafhoppers used. But in 1930 some resistance was evident even in young plants of the dwarf races whether 5 or 10 leafhoppers were used for infestation. It appears, therefore, that variations in the number of insects used do not account for the differences in varietal response in 1928, 1930 and 1931 compared with 1927 and 1929. Moreover, in 1927 only 5 leafhoppers per plant were used and the plants were relatively old when treated, yet the resistant varieties were as much affected as the susceptible checks. Shapovalov and Beecher[10] have shown that climatic conditions, especially the intensity of light, influence the development of symptoms of curly top in infected plants. Possibly the climatic conditions were less favorable for curly top in 1928, 1930 and 1931 and so resistance was evident, whereas in 1927 and 1929 the conditions were more favorable for the disease and resistance was obscured.

Resistance in these tomato varieties is weak and evidently is overcome if the number of viruliferous leafhoppers is sufficiently large and other conditions are favorable to the disease. The sequence of symptoms, namely, cessation of growth, progressive yellowing, and death is the same in the resistant and susceptible varieties, and, as will appear (p. 40), there is very little difference in the incubation periods. Recovery occurs with nearly the same frequency in resistant and susceptible varieties. Moreover, Shapovalov and Jones[11] found that the chemical changes in plants affected with curly top were the same in resistant dwarf and in susceptible strains.

The resistance of sugar beets to curly top which was found in certain selected lines by Carsner,[1] is evidently much greater than in the tomato. Beet plants of the highly resistant strains generally show mild symptoms and plants of less resistant strains more pronounced symptoms of the disease. According to Carsner and Lackey[2] attenuation of the virus occurs in the most resistant strains. Evidently these strains of beets are resistant not only to infection, but to the virus after they become infected. In beets resistance is strong and tolerance of the virus is a main factor, but in tomatoes resistance is weak and probably due to a tendency to escape infection. The dwarf varieties of tomato have a small, darker green vine, more rigid foliage, and a more compact habit of growth than susceptible standard varieties. Red Pear, however, which is resistant, is standard in habit, although distinct in vine from other standard varieties. Apparently these varieties offer some slight mechanical or other barrier to infection, which is overcome when viruliferous leafhoppers feed on them and climatic conditions are favorable to the disease.

TABLE 7

CURLY TOP AT RIVERSIDE, CALIFORNIA, IN 1929*

Date of artificial infestation is followed by number of insects used, in parentheses.

	Date of transplanting	May 25 (5)		May 25 (10)		May 29 (5)		May 29 (10)		June 7 (10)		June 12 (10)		June 12 (20)		June 21 (20)	
		Number treated	Per cent affected	Number treated	Per cent affected	Number treated	Per cent affected	Number treated	Per cent affected	Number treated	Per cent affected	Number treated	Per cent affected	Number treated	Per cent affected	Number treated	Per cent affected
Dwarf Aristocrat	April 30	....	....	....	....	25	40	....	....	25	28	12	67	17	47	....	....
Santa Clara Canner	April 30	25	64	25	48†	....	....	....	....	12	33	....	....	....	....	....	....
Selected line from:																	
Stone, series 52-1-1	April 30	25	40	....	....	25	60	25	60	8	62	....	....	....	....	....	....
Santa Clara Canner, series 400-4	April 30	11	36	....	....	25	72	....	....	....	....	....	....	....	....	....	....
Dwarf Aristocrat × Santa Clara Canner, F_5, dwarf	April 30	50	64	25	44†	25	64	27	48	33	55	22	77	....	....	10	100
Dwarf Aristocrat × Red Pear, F_4, dwarf	April 30	25	36	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Dwarf Aristocrat	May 13	....	....	....	....	....	....	....	....	25	24	....	....	....	....	....	....
Selected line from:																	
Stone, series 52-1-1	May 13	....	....	....	....	....	....	....	....	18	39	....	....	....	....	....	....
Dwarf Aristocrat × Santa Clara Canner, F_6, dwarf	May 13	....	....	....	....	....	....	....	....	24	62	....	....	....	....	....	....
Dwarf Aristocrat × Red Pear:																	
Diploid, dwarf	May 13	....	....	....	....	....	....	24	62	....	....	....	....	....	....	....	....
Triplo-A, dwarf	May 13	....	....	....	....	....	....	25	40	....	....	....	....	....	....	....	....

* The following varieties were also artificially infested and found to be susceptible: Institute of Applied Botany, U.S.S.R., Nos. 748 and 759 (from Peru, collected by Dr. Juseptschuk); F. P. I. Nos. 55575 and 55841; Uitenhage (South Africa) Wild; *Solanum tomatillo* (Red Currant); Gigante liscio; *S. Humboldtii* (Yellow Cherry).

† Up to June 18.

RECOVERY

Recovery of plants even from an advanced stage of disease sometimes occurs, especially in the late summer and fall. The change is usually accomplished by a process of regeneration in which new shoots grow out from the leaf axils, so that a healthy plant is reproduced, which may even yield a crop of fruit. Of the 400 plants which became diseased owing to artificial infestation in 1928, over 11 per cent recovered. The percentage of plants which recovered was slightly greater in the resistant than in the susceptible varieties, but the difference was not significant. A few plants raised from seed of fruits produced by regenerated plants were artificially infested, but they seemed to be as susceptible as seedlings from healthy parents of the same stock. One plant which regained its normal color after reaching an advanced stage of curly top was artificially infested with 80 leafhoppers. It again developed symptoms of curly top and did not recover. The new shoots produced in the regeneration of affected plants often develop symptoms of curly top. This was especially common at Riverside in 1929. Evidently a tomato plant which recovers is not rendered immune, and probably it is not more resistant than a plant which has not previously been affected.

INCUBATION PERIOD

The incubation period in the plant or the length of time between the removal of the hoppers and the appearance of symptoms, in 1928 and 1929, is shown in tables 8 and 9. The plants were examined at intervals of about a week throughout the period from May to August in which most cases of disease occurred, and at longer intervals during September and October. The incubation period in tables 8 and 9 is therefore approximately correct to the nearest week. Many of the minor fluctuations in the frequency distribution are due to irregularities in the interval between observations. The incubation period was very variable, however, especially after artificial infestations made late in the season when the plants were large. In 1930 the mean incubation period in 49 young plants infested on June 2 with 5 leafhoppers was 20 days and in 54 similar plants treated on the same date with 10 leafhoppers 19 days, but in 14 of the 59 cases of curly top following artificial infestation on June 27 and 30, 1928 (table 8), the

TABLE 8

FREQUENCY DISTRIBUTION OF INCUBATION PERIOD OR NUMBER OF WEEKS FROM ARTIFICIAL INFESTATION TO APPEARANCE OF SYMPTOMS OF CURLY TOP AT RIVERSIDE IN 1928

	Date of infestation	Number of leaf-hoppers used	Incubation period in weeks from date of last infestation to early stage of curly top*														Mean incubation period in weeks to E stage of curly top	Mean incubation period in weeks to Y stage of curly top
			1	2	3	4	5	6	7	8	9	10	11	12	13	14		
All varieties	June 7	5 or 3	0	3	15	19	13	4	2	2	0	0	0	1	0	—	4	5
	June 13	5	2	2	17	14	10	4	0	0	0	0	0	0	—	0	4	5
	June 27	5	0	2	4	11	4	2	1	3	1	0	—	1	—	1	5	6
	June 30	5	—	4	—	12	5	1	3	2	—	1	—	1	—	1	5	6
	July 20	5	0	0	0	0	—	5	6	—	2	—	0	—	0	....	7	8
	June 7 or 13 and July 20	5 10	5	2	2	4	—	16	6	—	2	—	1	—	0	....	5	7
	July 25	10	1	0	0	1	5	5	—	5	—	1	—	3	....	....	7	8
	August 1	15	0	0	0	0	5	—	10	—	5	—	1	....	....	....	7	8
	June 7 or 13 and July 25	5 10	0	0	0	0	2	7	—	5	—	0	—	0	....	....	7	9
Resistant varieties	June 7	5 or 3	0	1	13	13	10	3	2	1	0	0	0	0	0	—	4	5
	June 13	5	0	0	11	10	7	3	0	0	0	0	0	0	—	0	4	5
	June 27	5	0	1	2	5	2	2	1	3	1	0	—	0	—	1	6	7
	July 20	5	0	0	0	0	—	4	1	—	1	—	0	—	0	....	7	8
Susceptible varieties	June 7	5 or 3	0	1	1	4	1	1	0	0	0	0	0	0	0	—	4	5
	June 13	5	0	2	7	4	2	1	0	0	0	0	0	0	—	0	4	4
	June 27	5	0	1	2	6	2	0	0	0	0	0	—	1	—	0	4	6
	July 20	5	0	0	0	0	—	1	5	—	1	—	0	—	0	....	7	9

* Dash (—) indicates that no observation was made during this period.

incubation period was 7 weeks or more. During the period August 20 to October 17, when these cases occurred, among 438 plants not artificially infested 8 at the most became affected, so that probably not more than 1 or 2 of those 14 cases were due to natural infestation. Evidence of a long incubation period is also given by the frequency distribution for plants first treated June 7 or 13, 1928, and again treated July 20 (table 8). Seven of the 38 affected plants showed early symptoms 1 to 2 weeks after reinfestation, only two plants 3 weeks after and the majority 4 to 7 weeks after. The discontinuity of this distribution suggests that the earliest cases were due to the *first infestation* on June 7 or 13, so that the incubation period for these cases was at least 6 weeks.

On account of the difference in color and texture of the leaves it is diffcult to determine when plants of dwarf and standard varieties have reached precisely the same stage of disease. The incubation period in 1928 and 1929 in groups of varieties resistant and susceptible to natural infestation is also shown in tables 8 and 9. In 1930, the incubation period in 16 plants of a resistant dwarf race treated on June 2 with 5 leafhoppers was 23 days and in 21 plants of a susceptible variety it was 17 days; in 21 plants of another resistant dwarf race treated on June 2 with 10 insects it was 19 days and in 27 plants of a susceptible variety it was 18 days. In most cases the mean incubation period of both stages of curly top was longer in the resistant than in the susceptible group, but the differences may not be significant. The fact that the incubation period in resistant and susceptible varieties was so similar is some evidence of a negative kind that, in this tomato material, resistance to the virus is unimportant. In the present work no very young plants were artificially infested, but in 1928 (table 8) plants of several varieties treated June 7 had a shorter incubation period than plants treated June 30, in accordance with expectation. In 1929 (table 9), when the number of leafhoppers caged on plants of the same age varied, as a rule the incubation period was shorter when the number of leafhoppers was greater.

TABLE 9

FREQUENCY DISTRIBUTION OF INCUBATION PERIOD OR NUMBER OF WEEKS FROM ARTIFICIAL INFESTATION TO APPEARANCE OF SYMPTOMS OF CURLY TOP AT RIVERSIDE IN 1929

	Date of infestation	Number of leaf-hoppers used	Incubation period in weeks from date of last infestation to appearance of early symptoms												Mean incubation period in weeks to E stage of curly top	Mean incubation period in weeks to Y stage of curly top
			1	2	3	4	5	6	7	8	9	10	11	12		
All varieties	May 25	5	....	....	24	2	11	3	5	1	1	5	—*	0	5	6
	May 25	10	....	....	17	2	3	3	1	0	0	0	—	0	4	5
	May 29	5	....	0	4	17	11	—	3	6	5	2	2	—	6	6
	May 29	10	....	0	5	16	32	—	3	5	3	1	0	—	5	6
	June 7	10	0	1	31	5	—	9	4	4	1	0	—	4	5	7
	June 7	20	0	1	6	1	—	3	0	0	0	0	—	0	4	6
	June 12	10	0	0	13	—	3	1	1	1	0	—	1	—	4	7
	June 12	20	0	0	7	—	0	1	1	1	0	—	1	—	5	6
	May 25 and June 21	5 or 10 20	1	0	—	5	0	0	1	0	—	0	—	—	4	5
	May 25 June 21 and June 29	10 20 40	2	3	2	1	0	—	0	0	—	—	0	—	2	6
	June 21	5	0	1	—	3	2	1	0	0	—	0	—	—	4	8
	June 21	20	0	0	—	10	3	1	0	1	—	0	—	—	5	6
Resistant varieties	May 25	5	....	....	16	2	5	2	4	1	0	4	—	0	5	6
	May 25	10	....	....	8	1	1	0	0	0	0	0	—	0	3	6
	May 29	5	....	0	3	5	3	—	0	3	1	1	2	—	7	6
	May 29	10	....	0	2	11	22	—	3	2	3	1	0	—	5	7
	June 7	10	....	0	25	2	—	7	1	4	0	0	—	2	5	7
Susceptible varieties	May 25	5	....	....	8	0	3	1	1	0	1	0	—	0	4	5
	May 25	10	....	....	8	0	2	2	0	0	0	0	—	0	4	5
	May 29	5	....	0	1	3	2	—	1	0	0	0	0	—	4	5
	May 29	10	....	0	0	5	9	—	0	3	0	0	0	—	5	6
	June 7	10	....	1	6	3	—	2	3	0	1	0	—	2	5	7

* Dash (—) indicates that no observation was made during this period.

INFLUENCE OF THE NUMBER OF LEAFHOPPERS

The data in table 10 show the effect of the number of leafhoppers used in artificial infestation on the probability of infection. In seven of the nine tests with different tomato varieties in 1928, 1929, and 1930, the percentage affected with curly top increased with the number of leafhoppers used. In only one test the opposite was the case, and in one there was no difference. The conclusion seems justified that in tomatoes, as in sugar beets,[3] the probability of infection is partly determined by the number of infesting leafhoppers. Whether this effect is due to variations in the quantity of inoculum introduced or in the infectivity of the individual leafhoppers or to some other cause, is at present uncertain.

TABLE 10

THE EFFECT OF VARIATIONS IN THE NUMBER OF LEAFHOPPERS USED ON THE INCIDENCE OF CURLY TOP AT RIVERSIDE, CALIFORNIA. IN EACH COMPARATIVE TEST THE SAME VARIETY OF TOMATO WAS USED

1928				1929				1930			
Date of infestation	Number of leafhoppers used	Number treated	Per cent affected	Date of infestation	Number of leafhoppers used	Number treated	Per cent affected	Date of infestation	Number of leafhoppers used	Number treated	Per cent affected
June 7	3	34	38	May 29	5	25	60	June 2	5	49	75
June 7	5	34	56	May 29	10	25	60	June 2	10	54	89
June 30	5	13	38	June 7	10	57	25				
June 30	15	13	46	June 7	20	15	87				
July 2	5	11	27	June 12	10	12	67				
July 2	10	9	44	June 12	20	17	47				
July 25	5	9	0	June 21	5	10	70				
July 25	25	8	50	June 21	20	10	100				

SUMMARY

As in previous trials, some tomato varieties of dwarf habit and also Red Pear, a variety of standard habit, proved to be resistant to curly top when exposed to natural infestation by leafhoppers (*Eutettix tenellus* Baker). In epidemics of moderate severity, the mean loss of plants from curly top in five trials in four seasons, at two places, was 42 per cent in resistant dwarf varieties and 62 per cent in the susceptible varieties—Santa Clara Canner, Norton, and Stone. In epidemics of extreme severity all varieties became nearly 100 per cent diseased. Attempts to isolate resistant lines from commercial varieties of standard habit have failed. No increase in resistance has been obtained by crossing a resistant dwarf with Red Pear. By hybridization, improved dwarf varieties have been obtained which may prove useful for localities where curly top is a serious menace.

When resistant and susceptible varieties were artificially infested, the results were variable. In three seasons the resistance of the dwarf races was evident as in natural epidemics of moderate intensity, but in the other two seasons no resistance was apparent, although a considerable proportion of the plants of resistant and susceptible varieties did not become diseased. Consequently artificial infestation, at least with small numbers of plants, has not proved reliable as a means of testing the resistance of tomato varieties under natural infestation. The variation in the response under artificial infestation was probably not due to variations in the number of insects used but may have been due to differences in climatic conditions.

The resistance is weak and seems to be due not so much to tolerance of the virus as to a tendency to escape infection. The chance of infection is influenced by the number of leafhoppers used in artificial infestation. The incubation period of the disease after artificial infestation of plants not less than 3 weeks after transplanting varied from 2 to at least 7 weeks. No significant difference was found in the length of the incubation period or in the frequency of recovery in resistant and susceptible varieties, and resistance was not increased in plants which had recovered or in their progeny.

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