VOL. 2 SEPTEMBER, 1926 NO. 3

HILGARDIA

A Journal of Agricultural Science

PUBLISHED BY THE

California Agricultural Experiment Station

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UNIVERSITY OF CALIFORNIA PRINTING OFFICE
BERKELEY, CALIFORNIA

HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE

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A STUDY OF RESISTANCE TO WESTERN YELLOW BLIGHT OF TOMATO VARIETIES*

JAMES W. LESLEY†

INTRODUCTION

Western yellow blight is an important disease of tomatoes prevalent in certain regions west of the Rocky Mountains. In California the loss from this disease is very heavy in certain years; for instance, in 1925 tomato growers in the interior valleys of central California lost from 75 to 95 per cent of their crop from this cause. In this paper, for brevity, "western yellow blight" is called "blight."

The practicability of controlling blight by the use of resistant varieties seems worthy of thorough consideration. The object of the present work is the discovery of varieties well adapted to the conditions where blight is severe or the development of such varieties by breeding. The present paper reports the reaction of certain varieties to blight, the results of three years' work on selection for blight resistance and some results of hybridization.

It was found that the varieties Dwarf Champion, Dwarf Aristocrat, Red Pear, and certain strains selected for blight resistance, are more resistant than the standard commercial varieties Stone and Santa Clara Canner. In a blight attack of moderate severity the resistant varieties and certain selected lines are about 25 per cent less susceptible than the standard varieties, but in attacks of extreme severity in early summer all of these have been nearly 100 per cent blighted. The dwarf character is closely associated with resistance to blight;

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this indicates that blight resistance is in this case conferred by the gene responsible for the dwarf character or by a gene or genes closely linked with it.

In the warmer interior sections of California where this work was conducted, the plant affected with blight ceases to grow, and the midribs of the leaves and leaflets become twisted, sometimes through as much as 180°. Owing to a combination of rolling and folding of the lamina the under surface of the leaves tends to be exposed to view and their texture becomes stiff and leathery. The whole plant assumes a pale sulfurous color which may first be seen

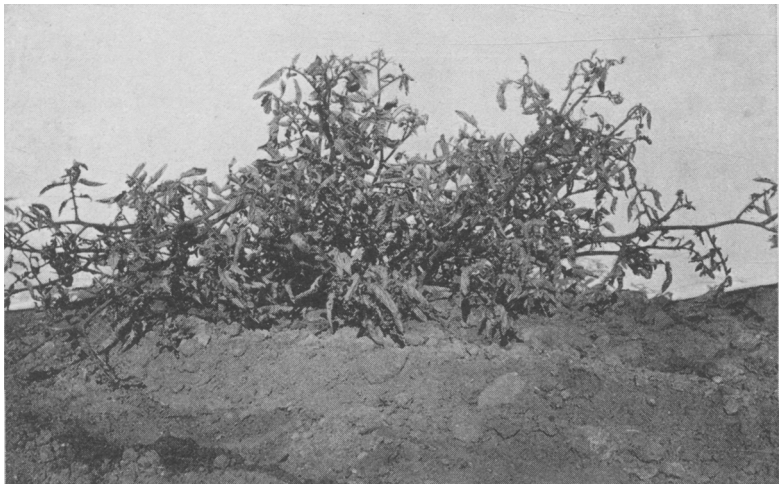

Fig. 1.—Tomato plant of standard habit with typical symptoms of western yellow blight.

in the mesophyll at the base of the young leaves. The veins often become purplish but this symptom is especially variable. The affected plant ceases to flower, the fruit stops growing but usually becomes prematurely colored, and the seeds cease to develop. Examination of the root system shows decay, especially of the smaller roots, the cortical tissue being shriveled and inclined to slough off. A photograph of a blighted plant is seen in figure 1. Occasionally such plants recover by sending up healthy shoots from the leaf axils. In the field the diseased and healthy plants usually appear to be scattered almost at random and may even grow side by side in the same hill.

The cause of blight is not known and as yet it has not been possible to induce the disease artificially. In California, blight usually

makes its appearance after the first warm period, but new cases may appear in the field at any time during the warmer part of the growing season, that is from April to October. Late-planted fields are often less affected than early ones. The severity of the disease is subject to very wide seasonal variation. Thus at Riverside, California, the season of 1923 was one of relatively little blight, while 1924 was emphatically a "blight year." The disease is also subject to regional variation. For instance, it is much more severe in the southern San Joaquin Valley of California than in coastal sections. On the basis of a study of the disease in California and of the weather records in the tomato-growing sections west of the Rocky Mountains, Shapovalov[11, 12] found a close correlation between the amount of blight and the rate of evaporation of moisture. Low relative humidity, high temperature and considerable wind movement regularly accompany severe outbreaks of blight. This conclusion is in keeping with many of the known facts concerning the remarkable seasonal and regional variation in the severity of blight and is a substantial contribution to our knowledge of a disease which has baffled pathologists for twenty-eight years.

Shapovalov[11] found that shading the plants with muslin was the most effective means of control; by this means the amount of blight was reduced more than two-thirds.

Several studies of the reaction of varieties and selected lines to blight in the western United States have been reported. In Idaho, Henderson[2] tested 13 varieties and reported that all of them were about equally susceptible. According to Hungerford[4], strains selected in the eastern states for resistance to *Fusarium* wilt were less resistant to blight in Idaho than local varieties, but certain other varieties and some selections from John Baer and Earliana showed marked indications of resistance. In Oregon, McKay[8] records that four varieties, including Norton, were all susceptible. In the State of Washington trials were initiated in 1903 and Humphrey[3] reports that certain varieties, Livingston's Dwarf Champion for example, were less susceptible to blight than others. Yaw[14] states that Dwarf Champion gives some indication of resistance when grown in California. Humphrey's and Hungerford's data, although not quantitative, suggest the feasibility of the control of blight by the use of resistant varieties.

ACKNOWLEDGMENTS

It is with pleasure that the author tenders his thanks to Mr. Michael Shapovalov, Pathologist, Office of Cotton, Truck and Forage-crop Disease Investigations, U. S. Dept. Agric., for much help in this work. Acknowledgments are also gladly made to Professor E. B. Babcock, Division of Genetics, University of California, who initiated this work, to Dr. J. T. Barrett, Associate Director of the Citrus Experiment Station, for subsequent help and to Mr. W. B. Camp, Associate Agronomist, U. S. Dept. Agric., for facilities provided at Shafter.

METHODS

The present work which was begun in the summer of 1922 was conducted in California. It was decided to test first the reaction to blight of numerous varieties and the efficacy of selection for blight resistance, and subsequently if necessary to employ hybridization with a view to increasing resistance.

In testing resistance a serious difficulty had to be faced at the outset, namely, our inability to induce blight artificially and our dependence on the irregular and highly variable severity with which it appears in different years. This difficulty adds considerably to the labor and time involved in working with blight.

In 1922 variety trials were visited at Zelzah†, Manteca, San Jose and Santa Ana, but so little blight appeared at any of these places that no comparisons were possible and it could only be concluded that certain of the varieties grown were not entirely immune to blight. In other places large commercial plantings of three of the most widely grown varieties, namely, Stone, Santa Clara Canner* and Earliana were found to be, in many cases, 75 per cent blighted.

In all the trials conducted by the writer the seeds were sown in cold frames and the plants transplanted to the field and grown with irrigation at a spacing of about 6 by 6 feet. The vines were not pruned and no manure or fertilizer was applied. The amount of blight on the plots was usually recorded at intervals of from 3 to 4 weeks. The unit plot was one row of varying length extending in the same direction as the irrigation furrows. Some of the varieties

† The trial at Zelzah was conducted by the Division of Genetics, at Manteca by the Division of Plant Pathology, University of California; at San Jose by the California Packing Corporation; at Santa Ana by the Haven Seed Company.

* This name has been given to the variety sometimes known as "Jap Canner" by Mr. Frank Dixon with the authority of the Canners League of California.

and selected lines were planted in plots replicated 2 to 4 times and in tables 2, 3 and 4 the result of each plot is shown separately. The proportion blighted was obtained by dividing the number of plants blighted by the number of plants which survived transplanting and were definitely classified. Stone or Santa Clara Canner was planted in the check plots; these varieties are very susceptible to blight and to about the same degree. Varieties and selected lines which showed more resistance than the check varieties are termed resistant.

That large differences in the proportion blighted may arise from causes which are not genetic was evident from a comparison of replicate rows of the same variety.

Near San Jose, one field of 20 acres of the variety Santa Clara Canner was for the greater part about 10 per cent blighted, but over an area of 4 to 5 acres as much as 80 per cent was blighted. The healthy plants were, as usual, scattered among the blighted ones.

It was clearly necessary to know something of the distribution of blight in fields containing only one variety.

Blight counts were made in two fields of the variety Stone. The variant was the proportion blighted in a single row of a certain fixed length, the rows running parallel to the irrigation furrows as in the variety trials. The proportion rather than the number blighted was taken because a variable number of plants were missing. If the proportion blighted per row were subject only to the fluctuations of simple or random sampling, the distribution would be of the binomial type of which the standard deviation is $\sqrt{\frac{p\,q}{n}}$ where p and q are the proportion blighted and not blighted, respectively, and n is the number of plants.

In the field near Arlington, California, a blight count was taken on November 20, 1924, on a block of 40 rows. The mean number of plants per row was 46, and the mean proportion blighted was 17 per cent. The standard deviation of the proportion blighted was 5.4 per cent; with one exception all of the sample rows came within a range of four times the standard deviation and the frequency curve was unimodal and approximately symmetrical. The standard deviation of random sampling in a binomial series where $n = 46$, $p = 17$ per cent and $q = 83$ per cent, is 5.5 per cent, or practically the same as that derived from the field data.

The other field was at Norco, California, and blight counts were taken on August 6 and again on September 30, 1925. A mere glance at this field showed that the blighted plants were much less evenly distributed than in the Arlington field. The area counted contained

32 rows; the average number of plants per row was 44 or approximately the same as at Arlington. The mean proportion blighted was 57 per cent, the attack being much more severe than at Arlington. The standard deviation was 10.1 per cent while that of random sampling was only 7.5 per cent; the difference is significant being 2.8 times the standard error of the standard deviation of random sampling. Furthermore there was a progressive change in the proportion blighted from one row to the next. These data indicate that the distribution of blight differs in different fields, that the variance in some cases may be similar to that of random sampling or in other cases may exceed it; also that the proportion blighted may change systematically from one row to the next, resulting in an unequal distribution over the field. Thus in interpreting observed differences in the proportion blighted in any given trial the ordinary test of significance may be inadequate, especially where the number of plants is small and the plots are not replicated.

In the statistical treatment of the data, each variety is compared with another variety, usually the check variety, and the probability that the difference in the proportion blighted might arise as a fluctuation of simple sampling was determined by Pearson's χ^2 method, the usefulness of which has recently been emphasized by Fisher[1]. This was equivalent to the application of this method to test the independence of variety and condition with relation to blight. Thus the number of blighted and not blighted plants expected in each of the two varieties to be compared was first ascertained assuming independence. Since the difference between the observed and the independence value was the same in each there is one degree of freedom. The value of P was taken from tables given by Yule[15] (p. 386) and in Pearson's Tables[13] (p. 30, Table XV C). The value of P then is the probability that a difference in the proportion blighted as great or greater than that observed might arise on random sampling assuming independence of variety and condition as to disease. As a rule, for a single experiment, a value of P exceeding .0027 ($\chi^2 = 9$) was not considered significant, and doubtless this rule excludes some significant differences. In tables 2, 4 and 6 the value of P attached to a given variety, unless having superscript,* refers to a difference in the direction of less susceptibility than the check variety.

In those cases where repeated trials clearly indicated resistance an attempt was made to measure its degree by another method, since the χ^2 method tests only the significance of an association and not its amount. For this purpose the standard error of the difference com-

puted from the binomial formula was compared with the observed difference in the proportion blighted. Thus if n_1, n_2 are the numbers of plants in the two varieties compared, p_0 is the proportion blighted and q_0 the proportion not blighted in the two varieties together, the standard error of the proportions in each variety is given by:

$$e_1^2 = \frac{p_0\ q_0}{n_1} \qquad e_2^2 = \frac{p_0\ q_0}{n_2}$$

and that of the difference is

$$e_{12}^2 = p_0\ q_0\ \left(\frac{1}{n_1} + \frac{1}{n_2}\right)$$

Assuming a normal distribution and that the direction of the difference was known, the probability of the observed difference arising as a fluctuation of simple sampling was taken from Pearson's Tables.[13]

TRIALS WITH VARIETIES AND SELECTED LINES

Experience in the year 1922 had emphasized the importance of choosing for trials localities where blight was as regular and severe as possible in its occurrence. With this in view the plots were planted in 1923 at the Citrus Experiment Station, Riverside, and at Shafter near Bakersfield. In 1922 a field of the variety Stone near Riverside and one near Bakersfield were respectively 30 per cent and 75 per cent blighted. Reports of previous years also indicated that as a rule the losses from blight at the latter place were especially severe.

Since the object of the trials in 1923 was the detection of resistance rather than its measurement a comparatively large number of varieties and progenies of single plants were included. Practically the same set of varieties and selected lines were set out at Riverside and Shafter. Stone was planted as the check variety.

At Riverside 33 varieties and 23 progenies of single plants selected in 1922 at Bakersfield, Fresno and San Jose were set out and an almost perfect stand was obtained. Out of 2475 plants recorded only 31 or 1.3 per cent blighted, so that this trial gave no comparative data and merely served to show that many of the varieties were not immune.

At Shafter the transplanting was done on May 11 and 12 in two separate fields (fields A and B in Table 1). Unfortunately many plants failed to become established and on June 6 much replanting was done in both fields. The blight attack was moderately severe but varied widely in plantings made in different fields or on different dates. The numbers are too small to permit the use of the χ^2 test and only permit conclusions of a most tentative kind.

TABLE 1

WESTERN YELLOW BLIGHT OF TOMATOES AT SHAFTER, CALIFORNIA, IN 1923
(Whole Season)

	Place	Date of trans-planting	Total number of plants recorded	Total number blighted	Per cent blighted
Stone	Shafter Field A	May 12	27	14	52
Selection 52	Shafter Field A	May 12	40	19	48
Selection 58	Shafter Field A	May 12	18	10	56
Selection 60	Shafter Field A	May 12	35	21	60
Selection 66	Shafter Field A	May 12	29	15	52
Selection 73	Shafter Field A	May 12	12	4	33
Selection 77	Shafter Field A	May 12	21	14	67
Selection 78	Shafter Field A	May 12	10	7	70
Selection 81	Shafter Field A	May 12	26	18	69
Selection 82	Shafter Field A	May 12	21	12	57
Stone	Shafter Field A	June 6	21	3	14
Dwarf Champion	Shafter Field A	June 6	39	3	8
Globe	Shafter Field A	June 6	10	3	30
Stone	Shafter Field B	May 11	23	1	4
du P. L. M.	Shafter Field B	May 11	14	3	21
Dwarf Aristocrat	Shafter Field B	May 11	21	0	0
King Humbert	Shafter Field B	May 11	16	7	44
Matchless	Shafter Field B	May 11	13	1	8
Magnus	Shafter Field B	May 11	10	3	30
Norduke	Shafter Field B	May 11	31	6	19
Perfection	Shafter Field B	May 11	16	3	19
Red Pear	Shafter Field B	May 11	10	0	0
Red Plum	Shafter Field B	May 11	26	3	12
Yellow Cherry	Shafter Field B	May 11	10	1	10
Yellow Peach	Shafter Field B	May 11	16	5	31
Yellow Plum	Shafter Field B	May 11	28	6	21
No. 213 (from Mexico)	Shafter Field B	May 11	15	2	13
Selection 53	Shafter Field B	May 11	21	0	0
Selection 55	Shafter Field B	May 11	10	0	0
Selection 75	Shafter Field B	May 11	15	2	13
Idaho Selection 3/2-1	Shafter Field B	May 11	17	3	18
Idaho Selection 3/2-2	Shafter Field B	May 11	13	0	0
Stone	Shafter Field B	June 6	66	2	3
Burwood	Shafter Field B	June 6	40	1	2
Dwarf Stone	Shafter Field B	June 6	46	3	7
Globe	Shafter Field B	June 6	48	2	4
Golden Dwarf Champion	Shafter Field B	June 6	33	2	6
Matchless	Shafter Field B	June 6	32	0	0
Norduke	Shafter Field B	June 6	40	1	2
Norton	Shafter Field B	June 6	36	5	14
Morse's San Jose Canner	Shafter Field B	June 6	39	7	18

In field A none of the selections were outstanding in blight resistance. Selection 66, the progeny of a healthy plant which had grown in the same hill, intertwined with a blighted plant, was as much blighted as the check. The smallest proportion blighted was in selection 73, from Santa Clara Canner. Further selections were made in this strain and seed was saved for the next year's trial.

In the second planting in field A Dwarf Champion was somewhat less affected than Stone.

In field B (Table 1) blight was much less prevalent than in field A, only four miles distant, and its distribution over the field was more uneven, possibly owing to soil differences resulting from the recent grading of the land. While most of the varieties and selected lines in the first planting (May 11) were affected by blight, Dwarf Aristocrat, Red Pear and line 53 from Stone and a few others were free from it.

In 1924 duplicate trials were again planted at Riverside and Shafter, including the more promising varieties, some progenies of single plants in the more promising selected lines of the previous year, and a few F_1 and F_2 hybrid progenies from crosses between standard and dwarf varieties. Excellent stands were obtained and in these trials over 3000 plants came under observation. Stone and Santa Clara Canner were used as check varieties. At Riverside the variety, Stone, which in 1923 was only 1.3 per cent blighted during the whole season, on July 3, 1924, was 21 per cent blighted. The disease continued to increase, on the whole with diminishing rapidity, until the middle of October. In the final count Stone was 50 per cent and Santa Clara Canner 55 per cent blighted. None of the varieties or selected lines were immune but notable differences were seen in the proportion blighted in different varieties and selected lines.

Table 2 shows the results at Riverside when each variety is compared with the check variety Stone as to numbers of healthy and blighted plants at the close of the first part of the season, up to July 3 inclusive, and as to the corresponding numbers for the whole season.

On July 3, in accordance with the indications at Shafter in the preceding year Dwarf Champion and Dwarf Aristocrat, the former especially, seemed to be resistant. When the figures for all three dwarf varieties, Dwarf Champion, Dwarf Aristocrat and Dwarf Giant, are compared with the check variety the resistance of dwarf varieties is emphasized. Red Pear, of standard habit, while again less affected than the checks, gave only a vague indication of resistance. Selected line 73–1, also of standard habit and derived from Santa Clara Canner, gave an indication of resistance in accordance with the record of 1923 (Table 1).

At the end of the season, corresponding with the increase of blight, the differences among varieties and strains were greater than on July 3. Indications of resistance seen earlier in the season were confirmed. Dwarf Champion again showed the most significant difference when compared with the check variety, and Dwarf Aristocrat continued to give an indication of resistance. Selection 73–1 still appeared to be resistant and 73–2 gave some such indication, but it

should be noted that the data in both cases are derived from single plots. Red Pear now gave more definite evidence of resistance than in the first period, whereas a single plot of Yellow Cherry which reacted much like Stone in the first period now gave evidence of even

TABLE 2

BLIGHT AT RIVERSIDE, CALIFORNIA, IN 1924

	Whole season							July 3			
	Per row		Total					Total			
	Number recorded	Per cent blighted	Number recorded	Number blighted	Per cent blighted	Compared with Stone	Probability that the difference from Stone is *not* significant.	Number blighted	Per cent blighted	Compared with Stone	
						χ^2	P			χ^2	P
Stone	56	55									
	43	53									
	36	39	135	68	50			28	21		
Burwood			53	21	40	2	.16	8	15	1	.32
Dwarf Aristocrat	53	34									
	42	40	95	35	37	5	.02	10	11	5	.02
Dwarf Champion	53	23									
	28	39									
	42	29	123	35	29	13	.0003	10	8	8	.005
Dwarf Giant			18	6	33			1	6	2	.16
Dwarfs (3 combined)			236	76	32	13	.0003	21	9	10	.002
Globe			25	9	36	2	.16	2	8	3	.08
Manx Marvel	52	65	78					20	26	0	1.00
	26	42		45	58	1	.32*				
Matchless			47	27	58	0	1.00	16	34	4	.04*
Norton			53	28	53	0	1.00	13	25	0	1.00
Red Pear	29	24									
	45	38	74	24	33	7	.01	10	14	1	.32
Santa Clara Canner	48	54									
	44	55	92	50	55	0	1.00	25	27	2	.16*
Yellow Cherry			56	36	65	4	.04*	10	18	0	1.00
Selection 52-1			44	19	43	0	1.00	8	18	0	1.00
Selection 52-2			47	22	47	0	1.00	11	23	0	1.00
Selection 52-3a			49	25	51	0	1.00	9	18	0	1.00
Selection 73-1			52	14	28	9	.003	7	13	2	.16†
Selection 73-2			51	18	35	4	.04	8	16	1	.32
Selection 267			36	13	36	2	.16	7	19	0	1.00

† Compared with Santa Clara Canner July 3 $\chi^2=4$, $P=.04$; whole season, $\chi^2=10$, $P=.002$.
* In the direction of *greater* susceptibility.

greater susceptibility. Norton, a selection from Stone resistant to *Fusarium* wilt, showed no greater resistance to blight than the parent variety. On the whole the data of Table 2 confirm the observations of the previous year. They also indicate in most cases a similarity in the reaction of a variety in these two overlapping periods.

At Shafter on May 7, 1924, 1200 plants were transplanted and of these 92 per cent became established. The incidence of blight was remarkable for earliness and severity. As early as June 3, 67 per cent of the check variety Stone had blighted. The younger leaves of affected plants in some cases showed wilting, presumably due to the extraordinarily dry, hot weather associated with this attack. In Table 3 the number of plants healthy and blighted on June 3 and on July 31 are compared with the corresponding number in the check variety Stone. As in previous trials, the data indicate that Dwarf Champion and Dwarf Aristocrat are more resistant than Stone. On the contrary, except for 73–1, the data for the selected lines conflict with the data of Table 2. As at Riverside, data derived from single small plots are of course inconclusive but the high proportion blighted in 73–2 in Table 3 indicates that this line is not resistant. If the onset of blight had been checked on June 3 (and according to Shapovalov,[11] such a check might be expected as a result of a suitable change in the climatic conditions), the difference between varieties observed on that date would probably have persisted throughout the season. For, as previously noted, the data at Riverside (Table 2) indicate that as a rule a positive correlation may be expected between the proportions blighted in the earlier and in the later portions of the season.

On June 30, out of 1107 plants recorded in all, 1091, or 98.6 per cent, were blighted and the differences so apparent at the earlier date were then negligible. Most of the survivors were dwarfs. A month later all but five of the plants were blighted. These survived throughout the season but one of them for some reason produced little fruit and scarcely any viable seed. It was evident that no variety or selection included in this trial could withstand an attack of such severity as occurred in this test. Dwarf Champion, which had shown resistance on June 3 and which has been reported resistant by Humphrey in the State of Washington was 99 per cent blighted on July 31.

In 1925 trials were again planted practically in duplicate at Riverside and Shafter. Many of the selected lines were derived from selections for blight resistance made in 1922, reselected in 1923 and 1924. Santa Clara Canner was used as a check. Field observations had indicated that this variety was about as susceptible as Stone and the data at Riverside (in Tables 2 and 4) confirmed this.

The trial at Riverside was planted in the same field as in 1924 but covered a larger area. Unfortunately, a comparison of replicate plots showed that those on the new land taken in developed con-

siderably more blight than corresponding plots on the old ground, although the whole trial was planted on the same day and received similar treatment. As a rule the plots were repeated serially in the same order: this proved to be by no means an ideal disposition but certainly tended to correct the error arising from the marked

TABLE 3

BLIGHT AT SHAFTER, CALIFORNIA, IN 1924

	June 3							July 31	
	Per row			Total				Total	
	Number recorded	Per cent blighted	Number recorded	Number blighted	Per cent blighted	Compared with Stone	Probability that the difference from Stone is *not* significant.	Number blighted	Per cent blighted
						χ^2	*P*		
Stone	46	63							
	50	72							
	49	63							
	50	68	195	130	67			195	100
Burwood			49	31	63	0	1.00	49	100
Dwarf Aristocrat	41	61							
	41	27	82	36	44	12	.0005	81	99
Dwarf Champion	43	51							
	49	33							
	46	41							
	47	36	185	74	40	26	4×10^{-7}	183	99
Dwarf Giant			15	6	40			15	100
Dwarfs (3 combined)			282	116	41	29	10^{-7}	279	99
Manx Marvel			49	31	63	0	1.00	49	100
Norton			49	30	61	0	1.00	49	100
Red Pear			48	23	48	5	.02	48	100
Yellow Cherry			47	16	34	16	.00006	47	100
Selection 52–1			43	19	44	8	.005	42	98
Selection 52–2			27	7	26	18	.00002	27	100
Selection 52–3a			48	18	37	13	.003	48	100
Selection 73–1			44	14	32	20	8×10^{-6}	44	100
Selection 73–2			40	26	65	0	1.00	40	100
Selection 267			45	17	38	14	.0002	44	98

inequality in the distribution of blight. In Table 4, the upper part shows the results at Riverside and Shafter for the whole season of 1925.

Previous evidence of resistance in Red Pear is greatly strengthened by this trial. Line 310, the progeny of a first-year selection from Dwarf Champion, seems resistant, thus tending to confirm previous experience with this variety. All the four selected lines (73–1–2,

73–1–4, 73–1–5, 73–1–6) derived from 73–1, which gave evidence of resistance in both of the 1924 trials, gave evidence of resistance in 1925 also. Line 52–1–1, which was the progeny of the only standard plant in the whole trial which survived and set seed at Shafter in 1924, also gave an indication of resistance. Two short rows (only 49 plants) of the so-called Red Currant tomato (*L. pimpinellifolium*) were

TABLE 4

BLIGHT AT RIVERSIDE, SHAFTER AND DAVIS IN 1925

	Place and period	Per row		Total					Probability that the difference from the check variety is *not* significant.
		Number recorded	Per cent blighted	Number recorded	Number blighted	Per cent blighted	Check variety	Compared with check variety	
								χ^2	P
Santa Clara Canner	Riverside,	46	35						
	whole season	39	36						
		31	48						
		22	50	138	56	41	Santa Clara Canner		
Dwarf Champion, Selection 310	"	50	22						
		44	18						
		37	22	131	27	21	"	12	.0005
Norton	"			25	10	40	"	0	1.00
Red Currant (L. pimpinelli folium)	"	28	79						
		21	67	49	36	73	"	16	.00006*
Red Pear	"	50	12						
		43	14						
		37	24	130	21	16	"	19	.00001
Stone	"			61	32	52	"	2	.16*
Selection 52–1–1	"	48	21						
		41	28	89	22	25	"	7	.01
Selection 73–1–2	"	45	18						
		39	38						
		27	45	111	35	32	"	2	.16
Selection 73–1–4	"	44	23						
		39	41	83	26	31	"	2	.16
Selection 73–1–5	"	46	24						
		40	32	86	24	28	"	4	.04
Selection 73–1–6	"	43	14						
		42	33	85	20	24	"	7	.01
Santa Clara Canner	Shafter, to June	72	97						
	22	75	95	147	141	96			
Dwarf Champion, Selection 310	"	73	78						
		72	89	145	121	83	"	12	.0005
Red Pear				73	65	89		3	.08
Stone	Davis,								
	whole season			104	86	83			
Earliana	"			915	828	91	Stone	6	.01*
Globe	"			75	53	71	Stone	14	.0002
	"						Earliana	72	Less than 10^{-7}

* In the direction of greater susceptibility.

planted; one of these came from seed kindly sent by Dr. Weberbauer* and collected by him in Peru. This small fruited wild tomato seems to be more susceptible to blight than the cultivated *esculentum* variety used as a check.

As a result of three seasons' trials, the resistance of Dwarf Champion, Dwarf Aristocrat, Red Pear and selected lines 73–1–2, 73–1–4, 73–1–5 and 73–1–6 is considered to be well established.

Table 4 includes the records of three varieties grown at Davis, California, in 1925.† Blight was exceedingly prevalent. Earliana showed greater susceptibility than Stone or Globe. The latter appeared to be somewhat less susceptible than Stone, but further trial is needed.

In the Shafter trials of 1925 the transplanting was done on April 28 and a little replanting on May 4. About two weeks later a series of dust storms swept the field. On May 28 there was undoubtedly some blight but the little plants were so coated with dust that classification was difficult. On June 22 out of 1300 plants transplanted, only 63 were not blighted. As Table 4 shows, the check variety Santa Clara Canner was 96 per cent blighted, and again Dwarf Champion and Red Pear gave some indication of resistance. Selection 73–1–2, 73–1–4, 73–1–5, 73–1–6 and 52–1–1, which were more resistant than Stone at Riverside in the same year, showed no appreciable resistance under these conditions. On August 8, in the whole planting only 2 plants remained healthy; both of these were dwarfs. As in the previous year no variety was able to survive in the blight epidemic at Shafter. Thus under one set of conditions significant differences in the reaction of varieties were apparent, but under other and more severe conditions these differences were obliterated.

The degree of resistance has been estimated in cases where the evidence of resistance was considered to be well established. Table 5 was prepared from the data at Riverside in 1924 and 1925 using the method described above (p. 53). Thus in 1924 Stone was 50 per cent and Dwarf Champion 29 per cent blighted. The difference is 21 per cent and its standard error 6.1 per cent. The odds are 19 : 1 that the true difference equaled or exceeded 12 per cent, or in other words that Dwarf Champion was at least 24 per cent less susceptible than Stone. In 1924 selection 73–1 appeared to be 24 per cent less susceptible than its parent variety Santa Clara Canner. In 1925 the

* Dr. Weberbauer writes, "Die Pflanze wächst zwischen Lima und Ancon, am Meerestrand, auf steinigem und natürlich auch salzigem Boden. Bekanntlich giebt es in diesem Gebiet niemals wirklich Regen nur feine Nebel befeuchten das Land während die Monate Juni bis October."

† The writer is indebted to Dr. J. T. Rosa, University of California for these data.

most resistant of the five selections from it, namely 73–1–6, appeared to be 15 per cent less susceptible than Santa Clara Canner, indicating a loss rather than a gain in resistance by a second year of selection. A comparison of the reaction of Red Pear in 1924 and 1925 suggests that this variety may be characteristically more variable in its behavior than Dwarf Champion. No significant differences were found in the reaction of Dwarf Champion and Red Pear or of Dwarf Champion and the most resistant selections of 1924 and 1925. It is

TABLE 5

CALCULATED MEAN DIFFERENCES IN SUSCEPTIBILITY TO BLIGHT AT RIVERSIDE

	Year	Compared with	Observed difference per cent blighted.	Standard error of observed difference, per cent.	By 19 to 1 odds (one direction) mean difference exceeded this per cent.	On same basis of odds mean difference, stated as per cent less susceptible than check, exceeded this per cent.
Dwarf Champion	1924	Stone	21	6.1	12	24
Dwarf Champion	1925	Santa Clara Canner	20	5.6	11	27
Red Pear	1924	Stone	18	7.2	6	12
Red Pear	1925	Santa Clara Canner	25	5.6	16	39
Selection 73-1	1924	Santa Clara Canner	27	8.6	13	24
Selection 73-1-6	1925	Santa Clara Canner	17	6.5	6	15

evident that no variety or selection has shown a very high degree of resistance to blight. For the present it may be assumed that, in a moderate blight epidemic, for every four blighted plants in Stone or Santa Clara Canner not more than three would be found blighted in the resistant varieties.

TRIALS WITH PROGENIES OF HYBRIDS

At the beginning of the present study Dwarf Champion was the only variety which had been reported to be resistant. Since this is not a desirable commercial variety, because the fruit is rather small and too soft for commercial purposes, the study of blight resistance in hybrid progenies was clearly desirable. Accordingly F_1 and F_2 progenies between Dwarf Champion or Dwarf Aristocrat and three commercial varieties of standard habit, Norton, Santa Clara Canner and Globe, were planted at Riverside and Shafter in 1924 and

1925. The F_1 progenies were all standard in habit of growth, showing the well-known dominance of standard over dwarf. At Riverside for the whole season of 1924 the proportion blighted in two such families combined was about the same as in the check variety Stone.

TABLE 6

BLIGHT IN HYBRIDS BETWEEN STANDARD AND DWARF VARIETIES

	Year, place and period	Habit	Number recorded	Number blighted	Per cent blighted	Check variety	Compared with check variety	Probability that the difference from the check variety is *not* significant.
							χ^2	*P*
C46, C59b. Fl. Dwarf Aristocrat x Santa Clara Canner, and Dwarf Champion x Norton, combined.	1924, Riverside, whole season		35	21	60	Stone.....	1	.32*
C46, C59b. Fl. Dwarf Aristocrat x Santa Clara Canner, and Dwarf Champion x Norton, combined.	1924, Shafter, to June 3		62	39	63	Stone.....	0	1.00
C42-2b, C46-1b, C49-1a. F2. Norton x Dwarf Champion, Dwarf Aristocrat x Santa Clara Canner, Dwarf Aristocrat x Globe, combined.	1924, Riverside, whole season	Standard....	44	16	36	Standard....		
		Dwarf.....	24	2	8		5	.02
C58-1. F2. Dwarf Champion x Santa Clara Canner.	1925, Riverside, whole season	Standard....	79	32	40	Standard....		
		Dwarf.....	23	2	9		9	.003
C46-1b. F2. Dwarf Aristocrat x Santa Clara Canner.	1925, Riverside whole season	Standard....	37	11	30	Standard....		
		Dwarf	11	1	9		2	.16
C95-1. F2. Dwarf Aristocrat x Red Pear.	1925, Riverside, whole season	Standard....	75	13	17	Standard....		
		Dwarf.....	27	0	0		4	.04
C58-1, C46-1b, C95-1. F2. Progenies combined.	1925, Riverside, whole season	Standard....	191	56	29	Standard....		
		Dwarf.....	61	3	5		15	.0001
C58-1. F2. Dwarf Champion x Santa Clara Canner.	1925, Shafter, to June 22	Standard....	150	149	99	Standard....		Less than 10^{-7}
		Dwarf.....	62	44	71		39	

* In the direction of greater susceptibility.

The same two families were planted at Shafter in the same year and up to June 3 also appeared to be about as susceptible as Stone (Table 6, C46, C59b). Apparently the blight resistance of the dwarfs is recessive. Three small F_2 families were planted at Riverside in 1924. Together they contained 44 standard and 24 dwarf plants* (Table 6). The plants of each F_2 population were set out indiscriminately so that standard and dwarf plants grew in the same row; this probably gives a more accurate comparison with reference to blight than if the two types had been planted in separate rows as with two different varieties. In their reaction to blight these families were not comparable with the check variety Stone, as they were planted a month later. Within the F_2 families the dwarf plants were less blighted than those of standard habit and it was decided to test this association with larger progenies in the following year.

At Riverside in 1925 three F_2 progenies were planted (Table 6). The same association between the dwarf character and resistance to blight was more or less pronounced in all of these, and in C58–1 there can be little doubt of its significance. Again, in F_2 progenies at Shafter in 1925 up to June 22, when blight was very prevalent, a similar difference was observed and the association therefore seemed to be well established. The indication of resistance shown by all three dwarf varieties tested (e.g., Table 2) is in harmony with this conclusion. The data are not sufficient to test the degree of association.

The dwarf and standard characters depend on a single pair of allelomorphic genes, *d* and *D* as Price and Drinkard[9] have shown, the dwarf character being a simple recessive to standard. If the association observed between the dwarf character and resistance is complete and if, as it appeared, resistance vanished together with the dwarf character in F_1 of dwarf $\times$ standard, it seems probable the resistance is in some way bound up with the dwarf character and that some quality peculiar to the dwarf plants better enables them to resist blight. If so, dwarfness and resistance have a common genetic basis in the dwarf gene *d,* or else the resistance of dwarfs depends on some gene or genes completely linked with the dwarf gene. Thus recent work by Lindstrom[7] indicates a complete linkage between the genes for smooth (i.e., not peach) skin and dwarf. But if resistance and dwarfness depend on distinct genes that are not completely linked, then some resistant standard and non-resistant dwarf plants should appear in F_2 as a result of crossing over, and the proportions of blighted plants among the F_2 standards and dwarfs

* The excess of dwarfs over the expected proportion of 25 per cent was due to trisomic inheritance in the family C49–1a.

should differ from those in respective standard and dwarf parental races. It is proposed to plant several F_3 progenies in the coming season. That resistance is not conferred exclusively by the dwarf gene is shown by the resistant character of Red Pear and of selections of standard habit. This fact appears to support the hypothesis of partial linkage. It may be, however, that resistance in these standard varieties depends on genes other than those which produce it in the dwarfs. If so, it may be possible by hydridization to breed types with increased resistance. This is being attempted.

Jones[5] has pointed out that incomplete linkage exists between the dwarf gene and the gene or genes which cause the constriction of fruit as in Red Pear. Further evidence of such linkage was provided by an F_2 population from Dwarf Aristocrat $\times$ Red Pear grown at Riverside in 1925 with the following result:

Standard		Dwarf	
Unconstricted	Constricted	Unconstricted	Constricted
46	21	27	0

These data also indicate that the constricted character behaves as a simple recessive. If dwarf and resistance to blight are partially linked and if resistance in Dwarf Aristocrat and Red Pear is of the same nature a similar linkage should exist between resistance to blight and constricted fruit. In this F_2 family there was not much blight and only 7 blighted plants fruited. Of these six were unconstricted and one constricted (pear) and the result was inconclusive.

Triploid tomato plants have recently been discovered (Lesley[6]) and among the progeny of these, a simple trisomic type has been obtained in which the extra chromosome appears to be that associated with the *d D* pair of genes. If the *d* gene confers resistance, a simple trisomic plant of the constitution *Ddd*, although it is predominantly standard in habit, might well be more resistant than a *dD* diploid, and a *ddd* trisomic plant more resistant than a *dd* (diploid) dwarf. It is possible that the reaction of these types might throw light on the genetic basis of blight resistance, especially if a reliable method of testing the reaction of single plants could be devised.

On the whole perhaps the evidence indicates that the resistance of Dwarf Champion and Dwarf Aristocrat in some way depends on their dwarf character, and therefore that their resistance to blight is a recessive character dependent on the dwarf gene.

SUMMARY

The reaction to western yellow blight of tomatoes, shown by various varieties and progenies of single plants selected for resistance and also by some hybrid populations has been tested in two different localities during three seasons. The incidence of the disease varied widely according to the season and place of trial. The standard deviation of the proportion blighted per row varies in different fields and may considerably exceed the standard deviation of random sampling. This emphasized the desirability of a suitable arrangement of replicate rows containing an adequate number of plants and of a uniform field. Against an attack of moderate severity in which about half of the plants of the check varieties Stone and Santa Clara Canner blighted in the whole season, Dwarf Champion, Red Pear and Dwarf Aristocrat showed a fair degree of resistance; they were probably at least 25 per cent less susceptible than the checks. They also showed resistance to a more severe attack if the first part of the blight period only was taken into account. The Globe variety appears somewhat resistant, while Norton is about as susceptible to blight as Stone. The currant tomato, *L. pimpinellifolium,* seemed to be somewhat more susceptible to blight than Santa Clara Canner. None of the varieties had sufficient resistance to survive an attack of extreme severity in the early part of the season. Three years' selection for blight resistance in the commercial variety Santa Clara Canner resulted in strains with resistance about equal to that of the dwarfs and Red Pear.

The resistant character of the dwarfs behaves as a recessive and appears to depend on the gene for dwarf or possibly on a gene or genes more or less closely linked with it. The reaction of Red Pear and the standard selection showed that resistance may be obtained without the gene for dwarf. If resistance is genetically of more than one kind, it may be possible by crossing to breed a variety with increased resistance to blight.

LITERATURE CITED

[1] FISHER, R. A.
1925. Statistical methods for research workers. 1–239, 6 tables. Oliver and Boyd, Edinburgh.

[2] HENDERSON, L. F.
1905. Idaho Agr. Exp. Sta. Ann. Rept. (1904) 28–32.

[3] HUMPHREY, H. B.
1914. Studies on the relation of certain species of Fusarium to the tomato blight of the Pacific Northwest. Washington Agr. Exp. Sta. Bul. **115**: 1–22. pl. 1–5.

[4] HUNGERFORD, C. W.
1923. Report of Director. Idaho Agr. Exp. Sta. Bul. **131**: 51.

[5] JONES, D. F.
1917. Linkage in Lycopersicum. Amer. Nat. **51**: 608–621.

[6] LESLEY, J. W., and MARGARET M.
1925. Triploidy in the tomato. Science n.s. **61**: 208.

[7] LINDSTROM, E. W.
1925. Inheritance in tomatoes. Genetics **10**: 305–317.

[8] MCKAY, M. B.
1921. Third crop pest and horticultural report. Oregon Agr. Exp. Sta. 174–178.

[9] PRICE, H. L., and A. W. DRINKARD
1908. Inheritance in tomato hybrids. Virginia Agr. Exp. Sta. Bul. **177**: 17–53.

[10] ROGERS, S. S.
1913. The culture of tomatoes in California with special reference to their diseases. California Agr. Exp. Sta. Bul. **239**: 591–617.

[11] SHAPOVALOV, M.
1925. Ecological aspects of a pathological problem (western yellow blight of tomatoes). Ecology **6**: 241–259.

[12] ———
1925. High evaporation: a precursor and a concomitant of western yellow blight. Phytopathology **15**: 270–278.

[13] PEARSON, KARL, Editor
1914. Tables for statisticians and biometricians. Cambridge University Press. LXXXIII, 1–143.

[14] YAW, F. L.
1924. Report on survey of the canning tomato industry with suggestions for improvements. California Agr. Exp. Sta. Circular **280**: 1–30. fig. 1–12.

[15] YULE, G. U.
1922. An introduction to the theory of statistics, 6th ed. xv, 1–415. C. Griffin and Company, London.

The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

1. The Removal of Sodium Carbonate from Soils, by Walter P. Kelley and Edward E. Thomas. January, 1923.
3. The Formation of Sodium Carbonate in Soils, by Arthur B. Cummins and Walter P. Kelley. March, 1923.
4. Effect of Sodium Chlorid and Calcium Chlorid upon the Growth and Composition of Young Orange Trees, by H. S. Reed and A. R. C. Haas. April, 1923.
5. Citrus Blast and Black Pit, by H. S. Fawcett, W. T. Horne, and A. F. Camp. May, 1923.
6. A Study of Deciduous Fruit Tree Rootstocks with Special Reference to Their Identification, by Myer J. Heppner. June, 1923.
7. A Study of the Darkening of Apple Tissue, by E. L. Overholser and W. V. Cruess. June, 1923.
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