Levels, Dependability, and Usefulness of Resistance to Tomato Curly Top Disease

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ABSTRACT

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Disease losses caused by beet curly top virus (BCTV) in lines of tomato (*Lycopersicon esculentum*) derived from interspecific hybridization with wild *Lycopersicon* species ranged from essentially none to almost complete destruction over a 3-yr period. Exposure to large populations of viruliferous leafhoppers in transplanted field disease nurseries caused disease incidence ranging from a low of 2–14% in the most resistant group through several intermediate levels to 70–100% in the most susceptible commercial cultivars. The various levels of resistance were consistent from year to year and were accurately determined throughout the season when the disease was prevalent. Disease incidence was more strongly influenced in some lines than others by plant age at time of disease exposure. Fields transplanted in May and interplanted with sugar beets provided the severe disease exposure needed to screen and compare hybrid progenies with standard reference lines from representative types. Resistance potentially useful in commercial production was not accurately measured when transplanting was delayed until midsummer, when vector populations were very large.

Additional key words: integrated pest management

Tomato breeders have tried for 45 yr to combine genes for resistance to beet curly top virus (BCTV) from wild species of *Lycopersicon* with horticulturally acceptable characteristics in tomato (*L. esculentum* Mill.) (1–3,8,10,18). Breeding lines have been developed with a wide range of resistance to curly top (3,5,8–13,19,22). This type of resistance is disease-escaping or passive as described by Cooper and Jones (4) and involves leafhopper preference and resistance to establishment of infection (17,19–22). Two breeding lines (C5 and CVF4 [5,13]) that have been released have moderate to high levels of resistance. This ability to escape infection is multigenically inherited and is closely linked with undesirable characters (3,6–8,10,12).

Expression of curly top resistance is influenced by many interrelated factors associated with the environment, the virus, and the age, population, and physiology of both the leafhopper (*Circulifer tenellus* Baker) vector and the tomato plants (3,8,10). An important factor in expression of resistance is plant age when exposed to leafhopper feeding. Young plants are generally much more susceptible to BCTV infection (3,8). Standard procedures to screen and evaluate tomato lines for curly top resistance have been described (8,10).

Although curly top-resistant germ plasm and methods for its use are available, effective use requires an understanding of the degree and dependability of resistance expression, age-of-plant effects during inoculation, and accurate methodology to measure resistance.

Reported herein are the development of curly top-resistant tomato germ plasm lines with various levels of resistance to infection, studies of the dependability of the resistance, and the use of these lines in a breeding program as parents and as standard reference lines to judge levels of resistance.

MATERIALS AND METHODS

All trials were conducted at the Washington State University Irrigated Agriculture Research and Extension Center near Prosser, where high exposures to BCTV occurred annually during the experiments. Transplants are more susceptible to curly top than direct-seeded tomatoes (8), so transplants were used in all trials. Plants were grown in flats of soil-peat mix and transplanted to the field when about 6 wk old, spaced 40 or 60 cm apart in rows 1 m apart. An ample supply of viruliferous leafhoppers was ensured by growing three rows of tomatoes between two single rows of previously established sugar beets (*Beta vulgaris* L.). Sugar beet, an excellent host of both BCTV and its vector, *C. tenellus*, served as a virus reservoir and summer propagation host for this migrating leafhopper (8,10). Thus, adjacent plants of tomato, a nonpreferred host upon which the vector feeds for only short periods (16), were subjected to an increasingly severe exposure to BCTV as the growing season progressed.

Field transplanting was done in May,

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when it would normally be done commercially. Plants were well established and growing vigorously before exposure to migrations of sugar beet leafhoppers from surrounding deserts and from the first generation propagated on interplanted sugar beets. To determine the effect of plant age at time of exposure on curly top response, two additional trials were transplanted on 7 June and 9 July. Because some plants in the May and June transplantings were showing symptoms on 9 July, only disease that developed after that date was used to compare the effects of transplant dates (plant age) on disease incidence.

To obtain data that could be easily used in statistical analysis and to draw seasonal disease progress curves, each plant was given a disease rating several times during the summer on a scale of 0 (symptomless) to 5 (death from BCTV). Ratings of 1–4 were used for progressively more severe symptoms ranging from slight discoloration and leaflet twisting to very severe purpling, yellowing, twisting, and stunting. Individual plant ratings were totaled for each replicate and divided by the number of plants to obtain a disease index. Average disease indices for each replicate were used in statistical comparisons and were compared with disease incidence to determine the best measure of the escaping-type resistance.

In five field trials conducted over a 3-yr period, seven tomato breeding lines were compared with cultivars VR Moscow and Owyhee (15) and the VF145 series of cultivars for reactions to severe BCTV incidence. Each trial included eight replicates of 14 plants from each line. The averages of the eight replicates on each reading date were graphed to define seasonal trends in disease indices for each test line and to show the relative responses of these 10 selected lines as exposure became more severe during the season.

These same 10 lines were used as parents and standards for reference, and a large number of early-generation and advanced selections derived from intercrosses were transplanted during May into curly top disease nurseries interplanted with sugar beets. Many hundreds of progenies were intensively tested and retested over a 10-yr period, reselecting among sister lines in each filial generation for ever-higher levels of escaping ability, to determine whether high levels of this type of resistance could be combined with commercially acceptable horticultural attributes.

RESULTS

Levels of curly top resistance. A continuum of resistance was observed in each of three growing seasons, representing three levels of disease exposure (Figs. 1–3). The rankings of the 10 lines tested were consistent, and when the combined data from the three trials were analyzed, there appeared to be six significantly different levels of resistance (Table 1). Within individual tests, there were overlapping levels of significance because of the high experimental error inherent in tomato curly top studies. The order of resistance was detectable whether measured as a disease severity index or as disease incidence (Figs. 3 and 4).

Table 1. Average disease indices for 10 tomato germ plasm sources grown during 3 yr of curly top disease trials at Prosser, WA[x]

Line	Disease indices[y]			
	Test 1	Test 2	Test 3	Combined[z]
VR Moscow	1.72 a	2.50 a	2.55 a	2.26 a
VF145	0.94 b	2.19 a	1.90 b	1.68 b
Owyhee	0.63 bc	1.47 b	1.27 c	1.12 c
C22	0.76 bc	1.32 b	1.24 c	1.11 c
(C5 × VF145)F_1	0.50 cd	1.06 bc	0.90 bc	0.82 d
CVF4	0.51 cd	0.86 cd	0.83 cde	0.73 d
C193	0.21 de	0.61 de	0.45 ef	0.42 e
C27	0.20 de	0.35 ef	0.30 f	0.28 ef
C5	0.07 e	0.17 f	0.15 f	0.13 f
Lycopersicon peruvianum var. *dentatum*	0.02 e	0.13 f	0.07 f	0.07 f
HSD	0.39	0.47	0.50	0.26

[x] Horizontal spaces divide these tomato lines into the six levels of resistance defined by analysis of combined data. Indices in columns followed by the same letter are not significantly different at $P = 0.05$ according to Duncan's multiple range test. When an analysis of variance was used on pairs, C5 was significantly different from C27 even though there was an overlap of significance in the overall analysis. There was no significant interaction between lines and years.

[y] Indices obtained by rating each plant several times during the growing season, between mid-June and mid-September, on a scale of 0 (symptomless) to 5 (death from curly top). Ratings of 1–4 designated increasing severity of foliage curling, purpling, and yellowing.

[z] The combined results of the 3 yr were analyzed as a split-plot design with tests as whole plots and lines as split plots.

Age-of-plant effect. Most of these lines, when transplanted to the field later in the season after large populations of viruliferous leafhoppers were present, had a higher incidence of disease by the end of the season than those transplanted earlier, even though plants from earlier transplanting dates had longer exposure to populations of viruliferous leafhoppers (Table 2).

Some plants in the May and June transplantings were infected and starting to show symptoms when the recording period started on 9 July (Fig. 5). This caused the May and June plantings to have more disease symptoms during July than the July transplanting. The angle of the curve for the July transplanting was extending upward at a steeper angle than those of the other two plantings when frost ended the season. If ample time was given for disease expression, incidence became higher in later plantings (Fig. 5).

In some lines, notably C5, C193, and *L. peruvianum* var. *dentatum* Dun. (PI 128660), plant age at time of exposure was much less important, so disease increase was about equal for early and late transplantings (Figs. 6 and 7). Young plants in these lines were almost as resistant as older plants. In lines like CVF4 and C22, plant age at time of exposure had an important influence on disease response.

Table 2. Effect of transplanting date on incidence of curly top disease that developed after 9 July in 10 tomato lines[a]

Lines	Transplanting date		
	19 May	7 June	9 July
VR Moscow	83	94	96
VF145	70	81	91
C22	43	74	76
Owyhee	33	47	61
(C5 × VF145)F_1	40	45	55
CVF4	30	58	49
C193	19	27	13
C27	13	33	25
C5	14	9	14
Lycopersicon peruvianum var. *dentatum*	9	7	3
Av.	35	48	48

[a] Percentage of plants that developed curly top disease symptoms between 9 July and 11 September.

The pattern of disease response in an F_1 of a cross between C5 and VF145 was similar to that of the VF145 parent (Fig. 8). The age-related susceptibility factor is probably additive or incompletely dominant in inheritance in VF145.

Usefulness of curly top resistance. We have not been successful in combining high levels of escaping-type resistance, represented by C5 and C27, with all horticultural characteristics required by the tomato industry. However, several selections have been identified that have commercially acceptable and even superior horticultural characteristics combined with intermediate levels of resistance that would be very beneficial in areas where curly top disease is a production hazard (Tables 3 and 4).

During 1974–1978 (Table 3), 100% of

the plants of most commercial cultivars were killed before flowering because of very severe disease exposure in our disease nurseries. Many plants of resistant cultivars (Roza, Columbian, Rowpac, and occasionally, Saladmaster) also had curly top disease, but usually 50% or more of the plants remained healthy enough to produce a crop. In years with less severe exposures, when 10–30% of the plants of commercial cultivars survived, resistant cultivars and breeding lines had only minimal to moderate levels of curly top disease (Tables 3 and 4). These trials involved widely spaced transplants grown next to leafhopper-infested sugar beets, providing exposures of a severity seldom encountered in commercial fields.

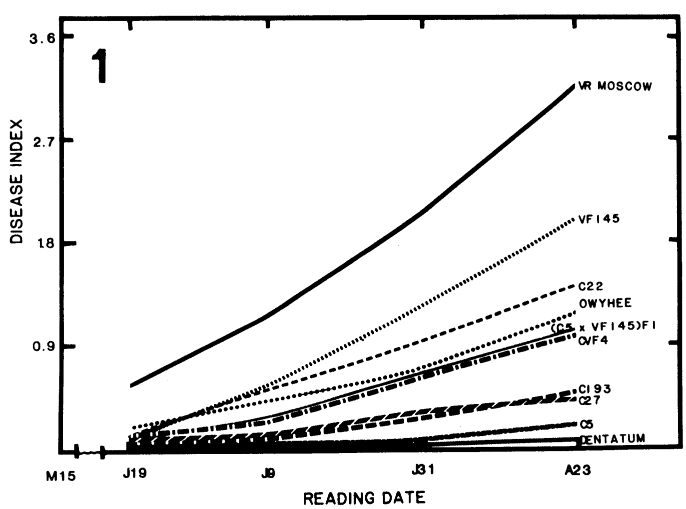
DISCUSSION

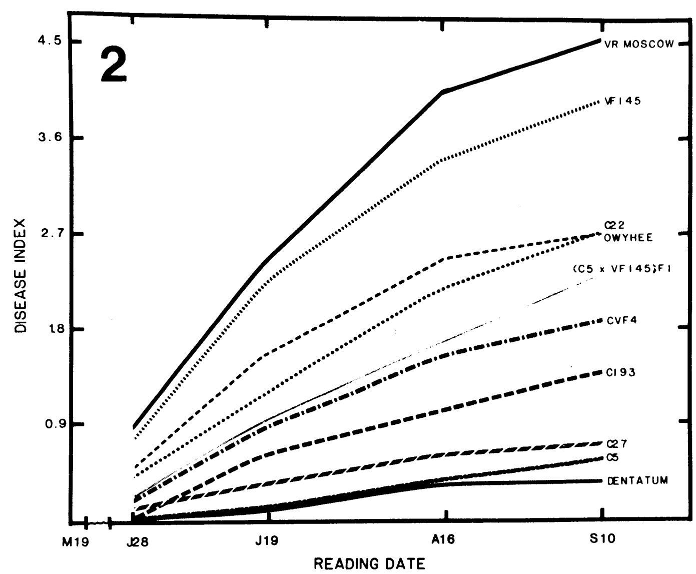
If tomato lines had been put in the field during the normal transplanting season, relative resistance of these 10 germ plasm lines would have been ranked in essentially the same order no matter when during the growing season disease evaluations were made or what level of curly top disease exposure occurred during the year they were grown. Erratic results are the rule with this leafhopper-transmitted disease, especially in studies involving natural field epiphytotics (8), so such consistent results were not expected.

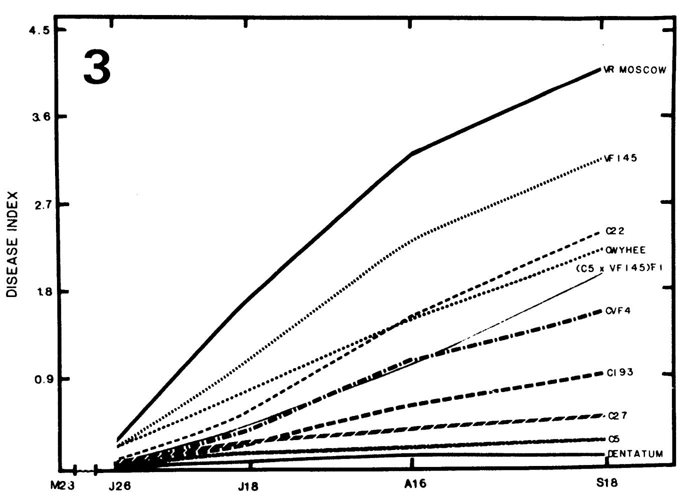
As levels of resistance were being defined, it did not matter whether diseased plants were simply counted or each plant was periodically rated for disease severity using a scale of 1–5. This provides evidence that supports results of earlier studies (19,21,22) showing that the resistance expressed by these lines is not tolerance but is a tendency to escape BCTV disease. Once a plant of any of these lines starts showing curly top symptoms, it soon dies.

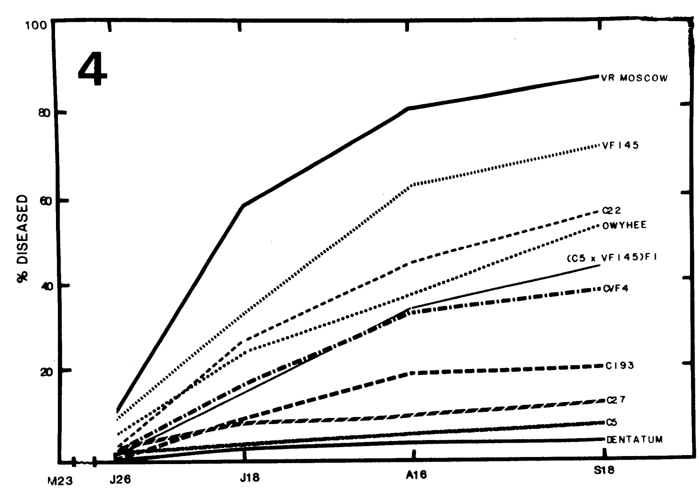
We concluded that only two disease readings were necessary to rate resistance, one late in June to record young diseased plants that might be subsequently overgrown and one late in July or early in August, when disease was near its maximum incidence and severity. Some plants subsequently expressed disease, but selection accuracy was improved very little by recording them in September and October.

Date of transplanting was the only factor that caused serious alterations in relative disease response. Younger plants are more susceptible (3,8), so amount of curly top disease and rate of disease increase were generally higher when plants were transplanted to the field later in the season, when exposure was unusually severe. However, because large differences in this age-of-plant effect exist among genotypes, caution had to be used in manipulating disease severity by transplanting later. Results could be more strongly influenced by age of plants being exposed than by inherent levels of resistance, which would be expressed with normal commercial planting dates and cultural practices. Lines such as C22, Owyhee, CVF4, and C27 showed moderate to high levels of resistance when transplanted in May but relatively less resistance when transplanted in June and July. These valuable lines would

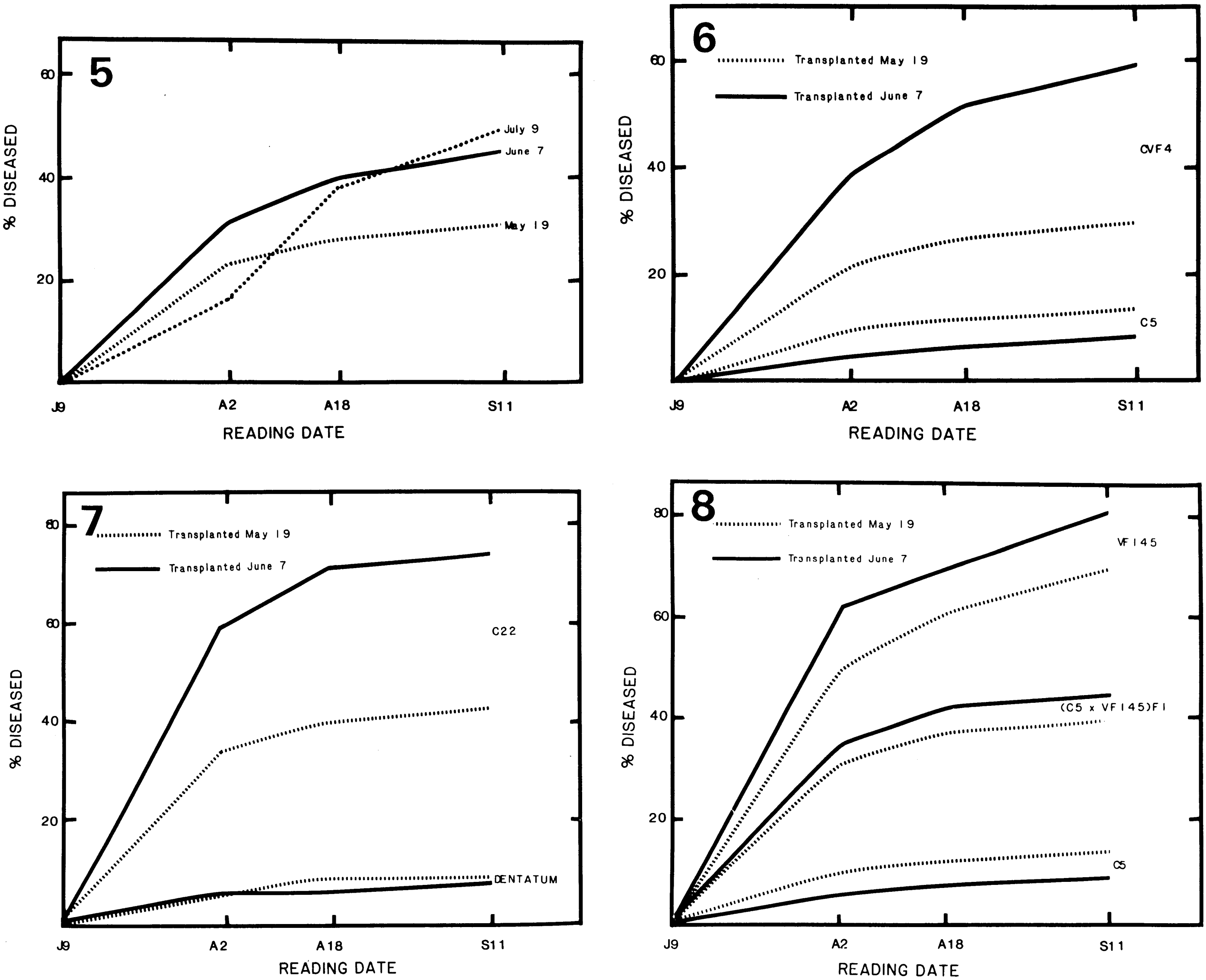








Figs. 1–4. (1–3) Progress of curly top based on disease indices in 10 tomato lines grown under continuous disease exposure in transplanted fields at Prosser, WA, during three growing seasons of differing disease exposure. Disease indices obtained by rating each plant several times during the season on a scale of 0 (symptomless) to 5 (death from curly top). **(4)** Incidence of curly top in the 10 tomato lines during the growing season corresponding to Figure 3.



Figs. 5–8. **(5)** Effect of plant age on incidence of curly top (combined averages of 10 lines varying widely in resistance). Curves show the percentage of plants in each age group that began to express disease symptoms after 9 July. **(6)** Effect of plant age on incidence of curly top, showing contrasting results in two curly top-resistant lines, C5 and CVF4. For simplicity, only the first two dates of transplanting are shown, the first made before leafhopper buildup in the field and the other, after. **(7)** Effect of plant age on incidence of curly top, showing contrasting results in C22 and its resistant parent, *Lycopersicon peruvianum* var. *dentatum*. **(8)** Effect of plant age on incidence of curly top in three tomato lines, C5, VF145, and the F_1 hybrid of a cross between them.

Table 3. Curly top incidence in tomato cultivars resistant to beet curly top virus compared with that of their parents and susceptible cultivars

Cultivar or line	Percent diseased[w] 1974	1975	1976	1978	1979	1980	1981	1982	Av.[x]
Parent lines									
VF145-21-4	87 a	42 a	89 a	84 ab	29 a	28 a	12	13 a	48 a
C5	16 c	7 b	9 c	25 c	(10)[y]	11 b	3	0 c	10 c
Resistant cultivars									
Roza	53 b	19 ab	37 b	74 ab	13 ab	29 a	5	6 b	30 b
Columbian	54 b	23 ab	40 b	89 a	9 b	17 ab	6	3 b	30 b
Rowpac	61 b	33 ab	46 b	81 ab	13 ab	27 a	3	5 b	34 b
Saladmaster	14 c	41 a	13 c	50 bc	(10)	9 b	(2)NS	(2)	18 c
Susceptible cultivars[z]									
	90–100	80–100	90–100	100	60–90	60–85	50–85	35–80	70–100

[w] Total percentage of diseased plants based on three counts made at approximately monthly intervals during each of eight summers in transplanted fields interplanted with sugar beets to provide severe disease exposure. Average of three or four replicates of 18 or 36 plants each year. Numbers in columns followed by the same letter are not significantly different at $P = 0.10$ according to Duncan's multiple range test. Arc sine $(SQR(X))$ transformation of data before analysis.

[x] The combined results of 8 yr were analyzed as a split-plot design with tests as whole plots and lines as split plots.

[y] Numbers in parentheses are computed missing plots.

[z] Range of percentage of curly top-diseased plants in susceptible commercial cultivars in these trials. These were not included in statistical analysis.

probably be discarded in late-planted trials.

The same caution applies to the severe greenhouse seedling tests used earlier in our breeding program (3,8,10) and by other breeders. Such seedling tests made it possible to screen large populations rapidly and to identify very resistant progenies, but so far, this level of resistance has not been combined with all the horticultural characteristics needed for commercial production. Moderate levels of resistance that are valuable in commercial production and can be combined with good horticultural characteristics seldom survive such seedling tests. In greenhouse seedling tests with severe exposures, C5 and CVF4 showed less resistance than that reported here (14). Such severe exposure rarely occurs in the field, and even then, only on transplanted tomatoes.

The resistance of C5, C27, and CVF4, if incorporated into processing or fresh-market cultivars, is adequate to permit profitable commercial production in arid areas of the western United States, including areas where curly top is now a serious limiting factor in tomato production. These moderate levels of disease-escaping ability would be an important component of the integrated pest management (IPM) approach to curly top control, which has gradually evolved in the western states. This IPM approach involves partial control of the leafhopper vector and its weed hosts in desert, ditchbank, and waste areas, direct-seeding to thick stands, and use of cultivars with some disease-escaping abilities, such as VF145 (Tables 1–3 and Figs. 1–4). Higher levels of resistance provide an important enhancing effect in this IPM approach and greatly reduce the risk of serious losses to curly top.

In many trials during the past 10 yr, our resistant cultivars and breeding lines, along with commercial cultivars, were direct-seeded into fields with a precision seeder, which planted a clump of three to five seeds every 23 cm. This normal commercial method of planting processing tomatoes produces a thick stand of clumps of seedlings that are usually left unthinned, because clumps of seedlings tend to function as single plants. Many of these trials received moderate to severe exposures to viruliferous leafhoppers from interplanted sugar beets or surrounding leafhopper-infested desert areas. Occasionally, economically important levels of curly top disease occurred in susceptible cultivars but not complete elimination such as occurred in transplanted disease nurseries. Resistant cultivars and breeding lines, even those with only intermediate levels of resistance, suffered insignificant curly top losses. Some seedlings in resistant lines became diseased but soon died and were overgrown by healthy seedlings in the same or adjoining clumps, so by fruit set, their loss was not detectable.

The levels of resistance identified in this study are only a sampling of those available in USDA breeding stocks. If methods were available to measure resistance accurately, an array of breeding lines could be separated into many BCTV resistance levels.

Inclusion of the BCTV-resistant breeding lines C5, C27, C193, CVF4, and C22 and the cultivars VF145 and VR Moscow in curly top tests would provide a complete range of resistance levels that could be used as references in measuring degrees of resistance of previously untested lines. Owyhee seems to have resistance equal to that of C22, so it could be substituted at this level.

The disease response differences between C27 and C193 were not statistically significant, but they derive resistance from different wild *Lycopersicon* species (11) and differ somewhat in expression and level of resistance (19). The same is true for C5 and *L. peruvianum* var. *dentatum*. The latter has much smaller seeds and seedlings and was slower growing than the other nine, which are all *L. esculentum* lines, so direct comparisons with the others was difficult. It is probably not necessary to include this wild species in curly top studies unless very high levels of resistance are being evaluated.

Curly top exposure during the years of this study was not as severe as it had been in earlier years in eastern Washington and Oregon. Occasionally in the past, immense populations of viruliferous leafhoppers survived mild winters and moved into cultivated areas in early summer, causing devastating losses in tomatoes. In such years, serious losses occurred even in our most resistant breeding lines when transplanted in trials and interplanted with sugar beets. Since the sugar beet industry left the Northwest 8 yr ago, there have been progressively lower populations of sugar beet leafhoppers and, consequently, lower incidences of curly top. Lower levels of curly top resistance are now required for commercial production of tomatoes and other susceptible crops.

Large yields of both fresh-market and processing tomatoes, with minimal losses to curly top, have been reported the last 10 yr from hundreds of transplanted and direct-seeded trials, both home garden and commercial plantings, involving these moderately resistant cultivars and germ plasm releases. These trials have been conducted throughout the Intermountain West from the Canadian to the Mexican borders. Occasional moderate to severe losses have been suffered by those who transplanted a few widely spaced plants under intense disease exposure, but in most cases, growers have reported no problems with curly top, though in the past, they consistently suffered complete or serious losses from this devastating disease.

Table 4. Reaction of tomato germ plasm to beet curly top virus compared with that of resistant parents and susceptible cultivars

	Percent diseased[w]					
	1979	1980	1981	1982	1983	Av.[x]
			Fresh-market-type germ plasm			
CF8-2	13 b	31 ab	0 b	7.5	8.0 ab	12 a
CVF11-3	29 ab	33 ab	1.7 b	4.0	8.0 ab	15 a
CVF13-2	35 ab	35 a	2.0 b	3.5	11.6 a	17 a
			Resistant parents			
Rowpac	13 b	27 abc	2.7 b	4.8	(4)[y]	10 a
Roza	13 b	29 ab	3.3 b	5.5	6.8 ab	12 a
			Machine harvest-type germ plasm			
CVF1-3	17 b	34 a	4.3 b	2.0	9.6 a	13 a
CVF3-1	16 b	27 abc	18.0 a	6.3	9.6 a	15 a
CVF6-1	22 b	12 cd	3.0 b	4.0	7.4 ab	10 a
CVF7-1	42 a	23 abcd	0 b	4.5	2.4 b	14 a
CF9-1	55 a	15 bcd	0 b	7.3	4.8 ab	16 a
			Resistant parent			
Saladmaster	10 b	9 d	0	(0)NS	(4)	5 b
			Susceptible cultivars[z]			
	60–90	60–85	50–85	35–80	15–20	50–80

[w]Total percentage of diseased plants based on three counts made at approximately monthly intervals during each of five summers in transplanted fields interplanted with sugar beets to provide severe disease exposure. Average of three or four replicates of 18 or 36 plants each year. Numbers in columns followed by the same letter are not significantly different at $P = 0.10$ according to Duncan's multiple range test. The 1983 data were obtained from trials conducted by Darrel Bienz and the first author for Campbell's Soup Co. Arc sine ($SQR(X)$) transformation of data before analysis.

[x]The combined results of 5 yr were analyzed as a split-plot design with tests as whole plots and lines as split plots.

[y]Numbers in parentheses are computed missing plots.

[z]Range of the percentage of curly top-diseased plants in susceptible commercial cultivars in these trials. These were not included in statistical analysis.

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