Sugar Beet Performance with Curly Top Is Related to Virus Accumulation and Age at Infection

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ABSTRACT

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Resistance to curly top disease caused by *Beet curly top virus* (BCTV) and related curtoviruses has been important to sustainable sugar beet (*Beta vulgaris*) production in the western United States for most of the last century. Recent advances in sugar beet genetics have led to the development of high-yielding cultivars, but these cultivars have little resistance to curly top disease. These cultivars are highly effective when disease management practices or environmental factors minimize curly top incidence, but can result in significant losses in years with early infection or abundant curly top. A greenhouse assay has been developed to rapidly test cultivars for a broad array of factors affecting performance in the presence of curly top. Previous studies have shown that sugar beet plants were more susceptible and losses more severe when seedlings were infected by BCTV, but less severe when plants were larger at the time of infection. To evaluate more precisely the relationship between age at infection, disease severity, virus accumulation, and yield loss in modern cultivars that were not bred for curly top resistance, individual sugar beet plants varying in degree of resistance and susceptibility to curly top were inoculated by viruliferous beet leafhoppers (*Circulifer tenellus*) when plants had two, four, or six true leaves, and maintained in a greenhouse for 6 weeks. When plants were inoculated at the two-leaf stage, all cultivars became severely stunted, with high disease ratings and similar rates of symptom development, regardless of resistance or susceptibility of the cultivar. Plants inoculated at four- and six-leaf stages exhibited increasing separation between resistant and susceptible phenotypes, with highly resistant cultivars performing well with low disease ratings and increased plant weights relative to susceptible cultivars. High-yielding cultivars performed only slightly better than the susceptible control cultivar. Results from greenhouse trials matched those from field trials conducted under heavy curly top pressure. Importantly, low virus concentration was directly correlated with lower disease ratings and higher plant weight, while elevated virus concentrations corresponded to higher disease ratings and lower weights. This demonstrates that a rapid greenhouse assay involving multiple traits can provide a rapid and effective means of selecting cultivars with improved curly top control, and could lead to more rapid incorporation of resistance into high-yielding sugar beet.

Beet curly top virus (BCTV), genus *Curtovirus*, and other closely related curtoviruses transmitted by the beet leafhopper *Circulifer tenellus* (Baker) have caused significant problems to irrigated agriculture in the western United States for over a century (4). BCTV is known to infect a broad range of crop and weed hosts in many plant families (1). The leafhopper vector also feeds and breeds on an extensive range of plants from different families (6), although sugar beet (*Beta vulgaris*) is clearly its favorite crop host. *C. tenellus* transmits curtoviruses most efficiently after a 48-h acquisition-access feed on an infected source plant, but shorter feeding times (2 to 20 min) also result in a low frequency of transmission. Curtovirus

transmission by the vector requires a 4-h latent period following ingestion, and leafhoppers can inoculate healthy plants by feeding for as little as a 1-min inoculation access period. Symptoms develop in plants in a minimum of 5 days. Leafhopper vectors retain the ability to transmit BCTV for days to weeks and often for their lifetime (1).

Many strains (up to 14) of BCTV were initially distinguished on the basis of differential symptomatology in sugar beet (10). Molecular characterization of BCTV in beet demonstrated that the virus primarily existed as three strains, CFH, Worland, or California/Logan, and genotypic variants of these strains (18). Based on sequence similarity and severity on sugar beet, the three strains are currently designated as separate species with the names *Beet severe curly top virus* (BSCTV, formerly CFH), *Beet mild curly top virus* (BMCTV, formerly Worland), and *Beet curly top virus* (BCTV, formerly California/Logan) (17). Studies conducted over the past 2 years have examined epidemiology of curtoviruses to determine if indi-

vidual curtovirus species are specifically associated with certain weed hosts, as well as whether localized areas may serve as reservoirs for the more severe curtovirus species. These studies have suggested some clustering of infection centers in California, but it is not yet clear whether such pockets contribute to prevalence of specific virus species (20).

The wide host range of curly top and abundance of the leafhopper vector has made managing the virus difficult. The present management strategy focuses on the use of curly top-resistant cultivars when available for a specific crop and large-scale spraying of insecticides to control the leafhopper vector in its overwintering grounds (1,5). The spraying of overwintering ground is believed to be effective in some years, but effectiveness varies considerably from year to year (13). Losses to curly top are most severe when sugar beet plants are infected as seedlings, and losses decrease with increasing plant age and size at the time of infection (7). Consequently, early planting is recommended to allow significant growth prior to infection, and seed- or crop-applied insecticides are recommended to delay infection (9). Curly top-resistant sugar beet cultivars have been grown successfully in California, but currently available curly top-resistant cultivars do not yield as well as susceptible cultivars in the absence of curly top (9). The resistance is a multi-genic trait with low heritability that has been difficult to move between breeding and parental lines (15). Field applied insecticides can delay infection and reduce the rate of secondary transmission when applied appropriately (9); however, since the vector needs only a brief feeding interval in which to introduce the virus into a healthy plant, insecticides will not block virus transmission.

The current system for evaluation of curly top resistance is based entirely on field evaluation of varieties in industry-maintained disease nurseries. Although these nurseries are effective for curly top resistance testing, the process requires several seasons for evaluation, and effectiveness can vary from year to year depending on environmental influences. Furthermore, field-testing does not account for plants that are not infected; rather, all plants are considered in an evaluation, a fact that has on occasion compromised the quality of variety selection in the field. In an effort to develop a more rapid and con-

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sistent preliminary test of cultivar performance under heavy disease pressure, a greenhouse testing system was developed that allows for strict control over the amount of inoculum and other variables including plant size at infection, fertilizer regime, and environment. The study described herein compares performance of modern sugar beet cultivars using this greenhouse germplasm evaluation method, which can be completed within a 2-month period with results comparable to those obtained through field trials.

High-yielding, curly top-susceptible cultivars were compared with some of the most resistant cultivars available. Some of the resistant cultivars used in this study are not adapted for growth under California field conditions, but they provide a direct comparison as to how performance might be influenced by the availability of resistance, whether traditional or through genetic engineering. Virus concentration also was analyzed in resistant and susceptible cultivars to determine whether virus concentration can be a useful tool in cultivar testing.

MATERIALS AND METHODS

Nine sugar beet cultivars were compared for curly top severity, virus concentration, and effect of disease on plant weight in greenhouse experiments. Seedex Monohikari (Seedex, Inc., Longmont, CO) was used as the susceptible control, since this cultivar is one of the most susceptible known. Resistant controls consisted of the California-adapted resistant hybrid USH11, as well as three cultivars adapted for the Inter-mountain West production area considered to be curly top resistant, including HM Owyhee, HM PM21 (Hille-shog Mono-Hy, Longmont, CO), and Beta 8118 (Betaseed Inc., Shakopee, MN). These cultivars do accumulate BCTV, but they produce higher yields in the presence of curly top than susceptible cultivars. HM PM21 has consistently performed better under curly top disease pressure than HM Owyhee or Beta 8118 (2), and was clearly the most resistant cultivar in the experiments. The resistant cultivars were compared with the current cultivars grown in

California, Beta 4430 (Betaseed), HH Phoenix, HH 142, and HH Alpine (Holly Hybrids, Sheridan, WY). Beet leafhopper (*C. tenellus*) was reared on sugar beet plants infected with *Beet curly top virus* (BCTV; formerly known as the California/Logan strain of BCTV).

Each experiment consisted of 10 plants per cultivar, per age class (two, four, or six true leaves) at inoculation. Half the plants in each age class (five plants) were inoculated by attaching leaf cages containing 20 viruliferous leafhoppers each, when plants had either two, four, or six true leaves. Leafhoppers were allowed to feed on plants for 48 h, after which cages were removed. Uninoculated control plants were not exposed to leafhoppers because previous studies have shown that nonviruliferous leafhopper feeding did not affect plant size (W. M. Wintermantel, *unpublished*). Plants were placed in a greenhouse under standard summer conditions and maintained insect and disease free for the remainder of the experiment. Disease severity was rated weekly for 6 weeks after inoculation, using the industry standard curly top disease severity scale (Table 1) developed by the Beet Sugar Development Foundation (Denver, CO). Seven weeks after inoculation, plants were harvested, soil was washed from roots, and total plant biomass was determined. Mean plant weight was determined for each cultivar at each inoculation stage and compared by ANOVA using JMP 4.0 (SAS Institute, Cary, NC).

At harvest, 0.5 g of partially expanded beet leaf tissue was collected from each plant, ground in 2.5 ml of enzyme-linked immunosorbent assay (ELISA) grinding buffer, and tested by double antibody sandwich ELISA, using antiserum against BCTV (11). Absorbance readings (405 nm) were taken at 30 min and 1 h, and all samples were run in duplicate. Absorbance values for uninfected plants were determined for each cultivar for each age class at infection by determining the mean absorbance value (405 nm) for each group of healthy beets per cultivar. The mean uninfected value per each cultivar was then

subtracted from the mean absorbance reading for each individual inoculated beet of that cultivar to determine the relative virus concentration in infected plants. Each experiment was repeated twice. An ANOVA was performed on the corrected A_{405nm} readings using JMP v4.0 followed by a Tukey-Kramer HSD test.

A large-scale resistance trial testing sugar beet varietal performance in California was conducted during a severe curly top outbreak at the University of California West Side Research and Education Center (WSREC) near Five Points in Fresno County, CA, in 2001. This experiment also used Seedex Monohikari as the susceptible and USH11 and HM Owyhee as resistant controls. Twenty-seven individual cultivars were included in the trial. Plots were planted as single rows, 8 m in length, with at least 6.6 plants per meter and three replications per entry, resulting in at least 160 plants per variety. Plants were scored for disease severity four times over the summer using the standard curly top disease severity scale (Table 1). Each plot was scored as a single value representative of the average rating of all plants in the plot (9). Results of the trial were compared with greenhouse data in order to determine if greenhouse evaluations were consistent with field results.

RESULTS

Disease severity. At 6 weeks postinoculation (wpi), resistant cultivars had much lower disease severity scores than the susceptible control, Seedex Monohikari, and modern cultivars Beta 4430 and HH Phoenix (Table 2). HM Owyhee received the lowest score, with a mean score of 3.6 when infected at the two-leaf stage, when all plants in the experiment were demonstrated to be most susceptible. USH11, Beta 8118, and HM PM21, all resistant cultivars, had slightly higher severity scores than HM Owyhee, but did not differ significantly from HM Owyhee. When plants were inoculated at four- and six-leaf stages, these same four cultivars continued to have comparatively low disease severity scores (Table 2). In contrast, current high-yielding cultivars used in California (Beta 4430, HH Phoenix, HH142, and HH Alpine) were all highly susceptible when inoculated at the two-leaf stage. With later inoculation, however, two of the newer cultivars, HH 142 and HH Alpine, performed slightly better with regard to disease severity scores than the standard California cultivars (Table 2). Severity results in the greenhouse trials closely resembled those of a field trial conducted in 2001, when curly top incidence was at its highest level in more than a decade (Fig. 1). In the field study, disease severity ratings of all California cultivars tested were higher than the average of 27 test cultivars, and some were almost identical in severity to the susceptible control.

Table 1. Curly top disease severity rating scale for sugar beet²

Scale	Symptoms
1	Vein clearing of core leaves, slight enations on veins on the underside of leaves
2	Slight leaf curling of the edges of new leaves; enations on the veins of the underside of leaves
3	Center few whorls of leaves with curling edges
4	Most leaves moderately curling; more than half of the upper surface of the leaf remains visible
5	Slight stunting, severe leaf curling; less than half of the upper leaf surface is visible due to curling; most larger leaves remain erect
6	Stunting, slight yellowing, most larger leaves becoming prostrate
7	Severe stunting, yellowing, leaves prostrate and some leaves dead
8	Only the center few whorls of leaves remain green and alive
9	Plant dead

² The curly top disease severity scale as listed above was developed by the Beet Sugar Development Foundation (Denver, CO).

Estimated yield potential by age at infection. At the conclusion of experiments (6 weeks after inoculation), soil was carefully removed from roots by washing, and total plant fresh weight was determined. Total weight is a better estimation of yield potential under greenhouse conditions than root weight, since it is more difficult in the greenhouse to establish fertilizer regimes that enhance root rather than top growth, as would be done in the field. Figure 2A lists a comparison of total weights among cultivars for plants inoculated at the two-leaf growth stage. Clearly the greatest impact of curly top on sugar beet occurs when plants are very young at the time of inoculation. At this stage, the effect of BCTV infection on sugar beet plants is so severe that even growth of cultivars considered to be resistant is severely reduced by BCTV infection, as determined by plant weight (Fig. 2A). Most cultivars inoculated at the two-leaf stage were uniformly stunted as a result of curly top infection (Fig. 2A). As plants achieved larger size prior to infection, the effect of curly top on plant weight in greenhouse tests was diminished (Fig. 2B and C), particularly in cultivars considered to be resistant.

In addition, the differential in total plant weight between healthy and infected plants at 7 wpi gradually decreased with increasing plant age at inoculation. When plants were inoculated at the two-leaf stage, the effect of infection on plant weight was dramatic, with an average of a threefold reduction in plant weight compared with healthy controls (Fig. 2A). In contrast, when inoculation occurred at the six-leaf stage, only the most susceptible cultivars exhibited significant weight differences between healthy and diseased plants by 7 wpi (Fig. 2C).

Virus concentration versus disease severity and resistance. Although previous studies have examined the effects of plant age at inoculation on disease severity (7), none have examined the relationship between virus concentration in infected plants and disease severity or cultivar performance. Cumulative data examining all plants from all cultivars indicate significantly higher virus concentrations were found in plants with higher disease severity scores, and lower virus concentrations were found in plants with lower disease severity scores ($P < 0.0001$) (Fig. 3). The trend was most apparent when data from all experiments were pooled, suggesting that larger sample sizes than were used in the studies presented herein may result in stronger relationships between virus concentration and disease severity.

Similar results were observed when virus concentration was compared by cultivar ($P < 0.0001$). Cultivars considered highly resistant or resistant had the lowest levels of virus at the conclusion of the experiment, while the most susceptible cultivars had the highest levels of virus

(Fig. 4). As with comparisons of virus titer and disease severity score, there was a trend indicating that virus concentration is lowest in cultivars that perform well when infected with curly top and higher in those

that do not perform as well. The highly susceptible control cultivar SX Monohikari and test cultivar HH Phoenix exhibited the highest virus concentrations. In contrast, the most resistant cultivars tested, HM

Table 2. Median curly top severity scores by cultivar in sugar beet plants inoculated when plants had two, four, and six true leaves^x

Cultivar	Res./Susc. ^y	2 Leaf	4 Leaf	6 Leaf
SX Monohikari	VS	7.1 ^z a	6.8 a	7.0 a
USH11	R	5.0 bcd	4.7 cd	4.1 cd
HM Owyhee	VR	3.6 d	3.7 d	2.9 e
HM PM21	VR	4.5 cd	3.0 d	2.2 e
B 8118	R	4.2 d	4.4 cd	3.2 de
B 4430	Test	6.3 ab	6.1 ab	6.1 b
HH Phoenix	Test	6.2 ab	6.1 ab	5.8 b
HH 142	Test	5.7 abc	5.6 bc	4.7 c
HH Alpine	Test	5.8 ab	5.0 bcd	4.4 cd

^x Plants were inoculated using 20 virus-containing leafhoppers per leaf cage and one leaf cage per plant.

^y Level of resistance/susceptibility of each cultivar. R, resistant; S, susceptible; VR, very resistant; VS, very susceptible. Test cultivars are those being tested to determine level of resistance or susceptibility. Resistance of control cultivars is based on performance against curly top in Amalgamated Sugar/University of Idaho comparative variety trials (published online). Seedex Monohikari has long been the industry standard for susceptibility to curly top. USH11 has been used for many years as a curly top severity indexing variety.

^z Score shown is the mean disease severity score (see Table 1) from two replications of the experiment of all infected plants for each variety at 7 weeks postinoculation, analyzed by ANOVA, followed by Tukey-Kramer HSD (letters).

Fig. 1. Comparison of disease severity scores (Table 1) among four sugar beet cultivars currently available in California, Beta 4430, Beta 4776, Beta 4300, and Phoenix, with the moderately resistant cultivar USH11 and the average of 27 cultivars and experimental lines. Twenty-seven individual cultivars were included in the trial. Plots were planted as single rows, 8 m long, with at least 6.6 plants per meter and three replications per entry, resulting in at least 160 plants per variety. Scores were recorded monthly for 3 months and just prior to harvest (30 August). Each plot was scored as a single value representative of the average rating of all plants in the plot. The trial was conducted at the University of California Westside Research and Extension Center near Five Points, CA, in summer 2001, a year with severe curly top infection in the region.

Owyhee and HM PM21, had the lowest virus concentrations (Fig. 4).

DISCUSSION

Traditional breeding for curly top resistance has focused on identifying breeding lines with reduced disease severity and sufficient yield. The first curly top resistant cultivars were introduced in 1926, based on a breeding project that began in 1918 (1,3). This was the beginning of a long and ongoing breeding effort toward the development of curly top-resistant sugar beet cultivars. This breeding effort has not iden-

tified complete resistance, but rather partial resistance to curly top. BCTV and related curtoviruses can accumulate even in cultivars considered resistant by the industry; however, yield is dramatically improved in these cultivars compared with those susceptible to curly top. The current source of resistance, which is believed to have originated from wild beet (*Beta vulgaris* subsp. *maritima*) (14), is difficult to transfer between cultivars. Early studies estimated the resistance involved more than two genes (16), and although there are no definitive estimates of heritability or the

number of loci controlling resistance, most geneticists currently believe the resistance to be polygenic (15).

Curly top-resistant cultivars are still routinely used in many areas of the western United States, and are mandatory in some. Curly top-resistant cultivars adapted for California growing conditions also were used successfully in California, but these were abandoned in the mid-1990s in favor of high-yielding but susceptible cultivars in an effort to increase yield and profits as sugar prices declined (9). The high-yielding susceptible cultivars produce dramatically larger yields than were possible with the traditional curly top-resistant cultivars, and have resulted in California growers obtaining world record yields in areas of California where curly top is not problematic (9). Following widespread adoption of these high-yielding susceptible cultivars, low curly top incidence limited disease problems for a few years, but curly top re-emerged severely in 2001, and again in 2003, resulting in early infection and in some cases substantial yield losses (9,19,21). These recent outbreaks demonstrated that although effective management methods can minimize losses, in some years even the best management strategies fail to prevent infection and loss. Control of curly top in the San Joaquin Valley of central California has traditionally involved a combination of insecticide application to fields, insecticide application to areas where the vector over winters in the western foothills along the San Joaquin Valley, coordinated planting and harvest times, and resistant cultivars (9,19). Management practices involving field application of insecticides and government sponsored spray programs are only partial solutions, and rely heavily on federal funds and environmental waivers for spraying of rangeland, as well as the availability of approved and effective field-applied insecticides. In recent years, there also has been an increase in fallow land, bordering cultivated land, that has been taken out of production due to a combination of economics and stricter environmental regulations. Consequently, the best solution to obtain high yields with minimal threat from curly top will rely on incorporation of curly top resistance into modern high-yielding sugar beet cultivars either through traditional breeding or genetic engineering.

We have developed a rapid and effective greenhouse method to test sugar beet plants for resistance to curly top disease caused by the curtoviruses BCTV, BMCTV, or BSCTV. These three virus species are very closely related to one another and only recently were given species status (17). The experiments described herein were conducted using BCTV; however, limited studies conducted with BSCTV produced similar results (data not shown), indicating that these methods should be broadly applicable to all curtovi-

Fig. 2. Mean fresh weight (g) of inoculated and uninoculated sugar beet plants 7 weeks after inoculation when inoculated at either **A**, two-true leaf, **B**, four-true leaf or **C**, six-true leaf growth stage. Results are from two replications of the experiment analyzed by ANOVA.

ruces, and their application should facilitate more rapid and improved selection of curly top-resistant germplasm. Unlike field tests, which can require an entire growing season, the greenhouse trial can be completed in 8 weeks with results comparable to those obtained under field conditions. Only one field trial can be conducted per growing season per location, but three greenhouse trials can be run using the greenhouse assay in the 6 months needed to conduct a single field trial, and even more if greenhouse trials are run concurrently. Conducting preliminary resistance testing in the greenhouse can provide a much more rapid preliminary screen of cultivar performance, and can test plants at an earlier stage of development than is usually possible under field conditions. Greenhouse experiments also allow strict

control over the amount of inoculum and other variables including plant size at infection, fertilizer regime, and environment. Furthermore, field-testing does not account for plants that are not infected; rather, all plants are considered in an evaluation. This has on occasion compromised the quality of variety selection in the field. Using the greenhouse testing method described here, only plants actually infected by virus are considered in the evaluation, resulting in more accurate analysis of variety performance than can be obtained in field tests. A previous greenhouse assay for curly top resistance testing was developed in the 1960s, but it focused only on disease severity ratings (12). The assay presented here classifies sugar beet plants by disease severity using the same scale as is used in field trials (Table 1), but also by total plant

fresh weight and virus concentration. Although yield and disease severity ratings are routinely used in evaluation of field experiments, virus concentration has never been thoroughly tested as a means of evaluating sugar beet plants for resistance or tolerance to curly top disease. The greenhouse experiments described here were inoculated using viruliferous beet leafhoppers. It should be possible to obtain equally effective results using *Agrobacterium*-mediated virus inoculation methods; however, this remains to be tested. Evaluation of plants for virus concentration in relation to disease severity adds another level of screening, but may ultimately lead to improved resistance against curly top. By selecting cultivars with lower virus accumulation, overall performance of cultivars in the presence of curly top may be improved.

Most curly top-resistant cultivars still accumulate fairly high levels of virus, including USH11, the traditional California standard for curly top resistance. Only two of the more modern resistant cultivars exhibited significantly reduced levels of BCTV accumulation in the experiments presented here. In addition to having significantly lower virus accumulation than other cultivars (Fig. 4), HM Owyhee and HM PM21 both outperformed all other cultivars with regard to total plant fresh weight (Fig. 2) and low disease severity (Table 2) under the controlled conditions used in these studies. These cultivars are also recognized as some of the best cultivars for field performance in curly top infested areas (2,8). The separation of HM Owyhee and HM PM21 from other cultivars in the analysis by each of the three parameters used in scoring demonstrates the value of combining virus concentration analysis with yield and severity score in resistance tests. By combining the results obtained from analyzing all three parameters, one can select cultivars with reduced virus accumulation, in addition to low disease severity and high yield, which may lead to more rapid development of cultivars with better performance in curly top infested areas.

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Fig. 3. Mean virus concentration measured by absorbance at 405 nm by double-antibody sandwich enzyme-linked immunosorbent assay at 7 weeks postinoculation for all plants from all experiments compared by disease severity index scores. Results are from two replications of the experiment analyzed by ANOVA (error bars), followed by Tukey-Kramer HSD (letters).

Fig. 4. Mean virus concentration at 7 weeks postinoculation for all plants from all experiments compared by cultivar. Virus concentration is measured by absorbance at 405 nm by double-antibody sandwich enzyme-linked immunosorbent assay. Dark bars indicate cultivars considered by the sugar beet industry to be curly top resistant, white bars represent cultivars considered to have intermediate resistance, and medium bars represent cultivars considered highly susceptible to curly top. Statistical analysis was conducted using ANOVA (error bars), followed by Student's *t* test (letters).

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