Differential Susceptibility of 39 Tomato Varieties to *Phytophthora infestans* Clonal Lineage US-23

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Abstract

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During the summers of 2012 and 2013, 39 tomato (*Solanum lycopersicum*) lines or varieties were evaluated for resistance to late blight in three separate field trials. In each trial, late blight was caused by field isolates of *Phytophthora infestans* clonal lineage US-23. Varieties with the late blight resistance genes *Ph-1*, *Ph-2*, *Ph-3*, and *Ph-2* + *Ph-3* were included, along with several heirloom varieties with grower-reported resistance and varieties with no known resistance. All six varieties with *Ph-2* + *Ph-3*, along with NC25P, which is homozygous for *Ph-3* only, showed a high level of resistance. Plum Regal F1, which is heterozygous for *Ph-3* only, showed moderate resistance. Legend, the only variety with *Ph-2* alone, also showed moderate resistance. Three heirloom varieties, Matt's Wild Cherry, Lemon Drop, and Mr. Stripey, showed a high level of resistance comparable with that of varieties with *Ph-2* + *Ph-3*. New Yorker, possessing *Ph-1* only, showed no resistance. Indeterminate varieties had significantly less disease than determinate varieties in two of the three trials. Overall, this study suggests that tomato varieties with both *Ph-2* and *Ph-3* can be used to effectively manage late blight caused by *P. infestans* clonal lineage US-23. Varieties possessing only *Ph-2*, or heterozygous for *Ph-3*, were better protected than those without any late blight resistance but might still require supplemental fungicide applications, while the variety that was homozygous for *Ph-3* was highly resistant. Several heirloom varieties were also highly resistant, and the unknown mechanism of their resistance warrants further research. Finally, the plasticity observed in United States *P. infestans* populations over the past several decades necessitates continued monitoring for genetic changes within *P. infestans* that could lead to the breakdown of resistance reported here.

Late blight, caused by the oomycete *Phytophthora infestans* (Mont.) de Bary, is a rapidly progressing and sometimes devastating disease of tomato (*Solanum lycopersicum* L.). Late blight epidemics were first associated with the Irish potato famine of the mid-19th century, and have continued to cause significant economic losses to both potato and tomato. In addition to causing direct losses to tomato growers, late-blight-infected tomato can serve as a source of inoculum and contribute to the estimated $6.7 billion in annual potato yield losses and costs of late blight control measures (14). Economic losses are attributed to direct crop loss as well as costs associated with fungicide applications. The 2009 late blight pandemic in the eastern United States illustrates not only the importance of tomato as a source of inoculum but also the vulnerability of tomato and potato crops when conditions are favorable for the disease (8).

In 2012, U.S. tomato production was valued at over $1.8 billion (6). Recently, organic tomato production has accounted for 2 to 3% of total U.S. tomato acreage. Late blight is especially problematic in organic cropping systems where the use of synthetic fungicide, typically relied upon to manage the disease, are not permitted. Organic tomato production has increased from 3,063 acres in 2000 to 9,271 in 2011 (23). With increased organic tomato production comes an increased need for effective nonchemical control strategies to manage late blight. This benefits the tomato industry at large, because an ineffectively managed field serves as a potential inoculum source for susceptible crops nearby.

Breeding for resistance to tomato late blight began in the 1940s (27,33). The dominant resistance (*R*) gene *Ph-1* was the first to be introgressed into domesticated tomato from a wild relative (*S. pimpinellifolium*). This gene conferred qualitative resistance to *P. infestans* race 0 but was rapidly overcome by novel pathogen genotypes (4,10,11). The single incompletely dominant gene *Ph-2* confers partial resistance to some *P. infestans* genotypes, which resembles quantitative resistance (21,32). *Ph-2* also originated in *S. pimpinellifolium* and was introduced in the 1960s (9). *Ph-3*, an incompletely dominant gene conferring strong resistance, was identified in the 1990s by researchers at the Asian Vegetable Research and Development Center in Taiwan (1). This gene was subsequently bred into fresh-market (12,24), plum (13), and processing tomato lines (19,20).

There are several examples of single *R* genes being overcome by new pathogen genotypes. This occurs because a single *R* gene imposes a strong selection pressure on the pathogen population, in much the same way that fungicides with a single mode of action encourage pathogen evolution toward fungicide resistance (17,29). Some examples include the aforementioned *Ph*-1 gene in tomato, *R* genes for late blight resistance in potato, genes for rust resistance in wheat, and Fusarium wilt resistance in banana and watermelon (2,16,25,27,35). This issue has been addressed through the implementation of gene pyramiding, or the introduction of multiple *R* genes into individual varieties. In order for a pathogen to evade a plant's effector-triggered immune response and cause disease on a variety with multiple *R* genes, it must avoid production of an effector recognized by the product of each specific *R* gene (17,18). This decreases the probability that a novel pathogen genotype, introduced by mutation or migration, will be able to overcome the resistance of the host with multiple *R* genes, thereby increasing the durability of that resistance (31).

With late blight continuing to cause significant economic losses to tomato production annually, especially in the eastern United States, there is a need to determine which tomato varieties are resistant to the current strain of *P. infestans*. In order to simplify terminology, "variety" is used to refer to all experimental entries, including commercial and heirloom tomato varieties as well as

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breeding lines. The heirloom tomato varieties Lemon Drop and Mr. Stripey have grower-reported late blight resistance that had yet to be confirmed or characterized. Grower-reported resistance in Matt's Wild Cherry, another heirloom variety, was recently confirmed (28). The goal of our research was to screen 39 tomato varieties for resistance to the current predominant U.S. clonal lineage of *P. infestans* (US-23). Varieties with the late blight resistance genes *Ph-2* and *Ph-3*, both alone and in combination, were evaluated along with heirloom varieties with grower-reported resistance and varieties without any known resistance.

Materials and Methods

Experimental design and transplant production. The experiment was done three times: twice in Freeville, NY (2012 and 2013) and once in Geneva, NY (2013). The experimental design was a randomized complete block with four replications. Thirty-seven tomato varieties were selected for the experiment in 2012. Two additional varieties were included in 2013 (Table 1). Varieties were chosen based on their late blight resistance genes (*Ph*-1, *Ph*-2, or *Ph*-3) or grower-reported resistance. Several susceptible control varieties were also included. Tomato plants for the Freeville experiments were seeded in 72-cell flats and placed in the greenhouse on 19 June 2012 and 2013. Tomato plants for the Geneva experiment were seeded in 72-cell flats and placed in the greenhouse on 14 May 2013.

Freeville field plot establishment. The 2012 experiment was conducted at the Cornell University Homer C. Thompson Vegetable Research Farm in Freeville, NY. The soil type is Howard gravelly loam. Five seedlings per plot were transplanted directly into soil on 30 July using a waterwheel planter which delivered 21-5-20 fertilizer (Jr Peters Inc.) at a rate of 1 kg 208 liter^{-1}. Plants were spaced 0.46 m apart with 1.37 m between plots, and irrigated with overhead irrigation when necessary. Rows were spaced 1.8 m apart. The preplant herbicides metolachlor (1,169 ml ha^{-1}) and metribuzin (387 ml ha^{-1}) were applied on 20 July 2012 to manage weeds. Monthly rainfall totals in August and September were 9.7 and 8.1 cm, respectively.

The 2013 experiment was conducted in a field adjacent to the site of the 2012 experiment. Five seedlings per plot were transplanted directly into soil on 29 July as described above, except rows were spaced 1.4 m apart. Plants were irrigated with overhead irrigation when necessary. The preplant herbicides metolachlor (1,169 ml ha^{-1}), metribuzin (387 ml ha^{-1}), and halosulfuron (36.5 ml ha^{-1}) were applied on 26 July 2013 to manage weeds. Monthly rainfall totals in August and September were 19.8 and 7.5 cm, respectively.

Geneva 2013 field plot establishment. The experiment was conducted at the New York State Agricultural Experiment Station in Geneva, NY. The soil type is Lima loam. Prior to transplanting in Geneva, raised beds were formed, 0.9 m wide and 1.8 m between centers, and covered with black high-density polyethylene mulch. Drip irrigation tape was laid beneath the plastic. Five seedlings per plot were transplanted on 26 June, spaced 0.5 m apart with 1.8 m between plots, using the waterwheel transplanter as

Table 1. Tomato varieties used in the experiments and their late blight resistance genes, growth habits, classes, and seed sources

Variety	Resistance	Growth habit	Tomato class	Seed source
New Yorker OP	Homozygous *Ph-1*	Indeterminate	Fresh market	Totally Tomatoes
Legend OP	Homozygous *Ph-2*	Determinate	Fresh market	Tomato Growers Supply Company
NC25P[x]	Homozygous *Ph-3*	Determinate	Plum	Dilip Panthee, North Carolina State
Plum Regal F1[x]	Heterozygous *Ph-3*	Determinate	Plum	Bejo Seeds
NC1CELBR[y,z]	Homozygous *Ph-2*+ homozygous *Ph-3*	Determinate	Fresh market	Dilip Panthee, North Carolina State
NC2CELBR[y]	Homozygous *Ph-2*+ homozygous *Ph-3*	Determinate	Fresh market	Dilip Panthee, North Carolina State
Legend × NC1CELBR[z]	Homozygous *Ph-2* + heterozygous *Ph-3*	Determinate	Fresh market	Martha Mutschler-Chu, Cornell University
Defiant PHR F1	Heterozygous *Ph-2*+ heterozygous *Ph-3*	Determinate	Fresh market	Johnny's Selected Seeds
Mountain Magic F1[z]	Heterozygous *Ph-2*+ heterozygous *Ph-3*	Indeterminate	Cherry	Bejo Seeds
Mountain Merit[z]	Heterozygous *Ph-2*+ heterozygous *Ph-3*	Determinate	Fresh market	Bejo Seeds
Amish Paste	Unknown	Indeterminate	Plum	Totally Tomatoes
Aunt Ginny's Purple	Unknown	Indeterminate	Fresh market	Tomato Growers Supply Company
BHN1009	Unknown	Determinate	Fresh market	Siegers Seed Company
Brandywine	Unknown	Indeterminate	Fresh market	Harris Seeds
Charger	Unknown	Determinate	Fresh market	Siegers Seed Company
FL 8059	Unknown	Determinate	Fresh market	Jay Scott, University of Florida
FL 8111	Unknown	Determinate	Fresh market	Jay Scott, University of Florida
Florida 47	Unknown	Determinate	Fresh market	Harris Seeds
Golden Sweet F1	Unknown	Indeterminate	Cherry	Tomato Growers Supply Company
H3402	Unknown	Determinate	Plum	Beth Gugino, The Pennsylvania State University
H9704	Unknown	Determinate	Plum	Beth Gugino, The Pennsylvania State University
Heinz 1439	Unknown	Determinate	Plum	Tomato Growers Supply Company
Heinz H9780	Unknown	Determinate	Plum	Eugene Miyao, University of California
Juliet	Unknown	Indeterminate	Plum	Tomato Growers Supply Company
Lemon drop	Unknown	Indeterminate	Cherry	Totally Tomatoes
Matt's Wild Cherry	Unknown	Indeterminate	Cherry	Johnny's Selected Seeds
Monsanto AB2	Unknown	Determinate	Plum	Eugene Miyao, University of California
Mountain Fresh Plus	Unknown	Determinate	Fresh market	Harris Seeds
Mr. Stripey	Unknown	Indeterminate	Fresh market	Harris Seeds
NC 84-173	Unknown	Determinate	Plum	Martha Mutschler-Chu, Cornell University
Primo Red	Unknown	Determinate	Fresh market	Harris Seeds
Red Bounty	Unknown	Determinate	Fresh market	Harris Seeds
Red Deuce	Unknown	Determinate	Fresh market	Harris Seeds
Red Pearl	Unknown	indeterminate	Cherry	Johnny's Selected Seeds
Rockytop	Unknown	Determinate	Fresh market	Siegers Seed Company
Scarlet Red	Unknown	Determinate	Fresh market	Harris Seeds
Sungold	Unknown	Indeterminate	Cherry	Johnny's Selected Seeds
Tasti Lee	Unknown	Determinate	Fresh market	Bejo Seeds
West Virginia 63 OP	Unknown	Indeterminate	Fresh market	Karen Hyde, West Virginia

[x] NC25P is a parent of Plum Regal F1.
[y] NC1CELBR and NC2CELBR are sister lines developed from the same pedigree.
[z] NC1CELBR is a parent of Mountain Magic, Mountain Merit, as well as the Legend × NC1CELBR hybrid.

described above. Monthly rainfall totals in August and September were 10.8 and 4.1 cm, respectively.

Late blight inoculations. Plants in the Geneva experiment were infected via natural inoculum. Plants in the Freeville experiments were artificially inoculated with *P. infestans* US-23 in 2012 and 2013. In each of the three experiments, late blight was caused by *P. infestans* clonal lineage US-23, based on restriction fragment length polymorphism and simple sequence repeat analyses (7). Inoculum was generated with infected tomato leaves from naturally occurring late blight outbreaks in Dryden, NY and Geneva, NY. Infected tomato leaves were incubated overnight at room temperature in plastic bags containing wet paper towels to encourage pathogen sporulation. Sporulating tomato leaves were then rinsed in a beaker containing 500 to 1,000 ml of distilled water. *P. infestans* sporangia were counted using a microscope and hemacytometer, and the suspension was diluted to a concentration of 4,000 sporangia ml^{-1}. The spore suspension was stored at 4°C for approximately 2 h prior to inoculation to encourage the release of zoospores. On the evenings of 22 August 2012, and 4 September 2013, whole plots were inoculated with 20 ml of zoospore suspension at 4,000 sporangia ml^{-1} with a handheld pump sprayer. Prior to inoculation, overhead irrigation was run for approximately 30 min to ensure adequate moisture for infection.

Table 2. Area under the disease progress curve (AUDPC) values for each of the three experiments

Variety	AUDPC[z]		
	Freeville 2012	Freeville 2013	Geneva 2013
NC2CELBR	0 A	0 A	4 A
Mountain Merit	0 A	20 A	109 A
Matt's Wild Cherry	0 A	9 A	2 A
NC25P	0 A	12 A	52 A
NC1CELBR	0 A	0 A	2 A
Legend × NC1CELBR	NI	0 A	98 A
Mountain Magic F1	0 A	1 A	6 A
Lemon drop	3 A	3 A	6 A
Defiant PHR F1	20 A	3 A	30 A
Plum Regal F1	123 A	279 AB	492 BC
Mr. Stripey	127 A	35 A	50 A
Legend OP	796 B	590 BC	435 B
Heinz 1439	1,220 C	849 CDE	1,011 FGH
Brandywine	1,393 CD	967 DEF	901 EFG
Juliet	1,506 CDE	1,041 DEF	775 DE
Mountain Fresh Plus	1,511 CDE	900 CDEF	1,006 FGH
Red Pearl	1,572 CDE	1,056 DEF	662 CD
Tasti Lee	1,594 CDE	964 DEF	981 FGH
Florida 47	1,611 CDE	1,038 DEF	1,042 FGH
Charger	1,614 CDE	1,006 DEF	1,052 FGH
Aunt Ginny's Purple	1,649 DE	814 CD	1,008 FGH
FL 8059	1,658 DE	1,029 DEF	1,001 FGH
Amish Paste	1,671 DE	1,069 DEF	970 FGH
Monsanto AB2	1,683 DE	1,132 DEF	1,084 GH
New Yorker OP	1,715 DEF	1,167 EF	1,051 FGH
Sungold	1,730 DEF	1,010 DEF	884 EF
Red Bounty	1,752 DEF	1,083 DEF	1,002 FGH
Rockytop	1,803 EFG	1,069 DEF	1,004 FGH
Scarlet Red	1,824 EFGH	1,065 DEF	1,036 FGH
West Virginia 63 OP	1,825 EFGH	1,181 F	1,030 FGH
H9704	1,842 EFGHI	1,077 DEF	1,125 H
Red Deuce	1,844 EFGHI	1,067 DEF	1,080 GH
H3402	1,853 EFGHI	1,108 DEF	1,062 FGH
Primo Red	1,876 EFGHI	1,150 EF	1,068 FGH
Heinz H9780	2,096 FGHI	1,017 DEF	1,063 FGH
BHN1009	2,184 GHI	1,029 DEF	990 FGH
NC 84-173	NI	941 DEF	1,053 FGH
FL 8111	2,229 HI	1,176 F	1,110 H
Golden Sweet F1	2,250 I	1,058 DEF	754 DE

[z] All values are the mean of four replicates. Means followed by the same letter within each experiment are not significantly different, Tukey-Kramer honestly significant difference ($P < 0.05$). NI indicates Legend × NC1CELBR and NC 84-173 were not included in the Freeville 2012 experiment.

Disease ratings and statistical analysis. Late blight disease severity ratings were taken as percentage of diseased tissue of entire plots with the aid of the assessment key described by James (15). Severity was rated one to two times a week throughout each experiment until the majority of susceptible plants had died from late blight. In Freeville in 2012, 11 disease severity ratings were taken between 21 August and 3 October. In Freeville in 2013, seven disease severity ratings were taken between 6 and 29 September. In Geneva in 2013, 10 disease severity ratings were taken between 16 August and 12 September.

After disease severity data were collected, the mean area under the disease progress curve (AUDPC) was calculated for each tomato variety in each experiment (5). AUDPC values were calculated using Microsoft Excel and analyzed using PROC GLIMMIX in SAS (SAS Inc.). Data for each experiment were analyzed separately using the Tukey-Kramer honestly significant difference (HSD) test to determine mean separations. Replications were considered random effects and tomato varieties were considered fixed effects.

An additional analysis was done in which tomato varieties were divided into two groups—growth habit and fruit type—to determine differences between groups. Groups were divided into subcategories and each group was analyzed separately. Growth habit was divided into two subcategories: determinate and indeterminate. Fruit type was divided into three subcategories: fresh market, plum, and cherry. Data were analyzed using PROC GLIMMIX in SAS (SAS Inc.). Mean separations were determined using the Tukey-Kramer HSD test. Replications were considered random effects and growth habit and fruit type were considered fixed effects.

Results

Disease development. In the Freeville experiments, late blight symptoms were first observed on 26 August 2012 and 4 September 2013. In Geneva, late blight symptoms were first observed on 19 August 2013. Disease progress was relatively consistent among late-blight-resistant tomato varieties across the three experiments (Table 2). In the 2012 Freeville experiment, six varieties remained late-blight free: NC2CELBR, NC1CELBR, Mountain Merit, Matt's Wild Cherry, NC25P, and Mountain Magic F1. Four varieties—Lemon Drop, Defiant PHR F1, Plum Regal F1, and Mr. Stripey—had a very small amount of disease. These varieties were still highly resistant to late blight and were statistically grouped with the late-blight free varieties. Legend OP was moderately resistant and the remaining varieties were susceptible to late blight caused by *P. infestans* US-23 (Table 2).

In the 2013 Freeville experiment, three varieties remained disease free: NC2CELBR, NC1CELBR, and the newly added Legend × NC1CELBR hybrid. The disease-free varieties were statistically grouped together with the same highly resistant varieties as in 2012. Plum Regal F1 was also statistically grouped with Legend OP. The remaining varieties were susceptible to varying degrees (Table 2).

In the 2013 Geneva experiment, none of the varieties remained disease-free (Table 2). However, the same varieties that showed a high degree of resistance in the first two experiments displayed similar results in Geneva in 2013. One exception was Plum Regal F1, which had significantly more disease than the highly resistant varieties in the 2013 Geneva experiment only.

Efficacy of resistance genes. Varieties heterozygous or homozygous for both the *Ph-2* and *Ph-3* (*Ph-2* + *Ph-3*) resistance genes were highly resistant to *P. infestans* US-23 in all three experiments (Tables 1 and 2). Mean AUDPC values for varieties with *Ph-2* + *Ph-3* were not significantly different from one another (Table 2). The heirloom varieties Matt's Wild Cherry, Lemon Drop, and Mr. Stripey were also highly resistant and grouped with the *Ph-2* + *Ph-3* varieties (Table 2). The plum line NC25P, which is homozygous for *Ph-3* only, was also highly resistant and not significantly different from *Ph-2* + *Ph-3* varieties. Plum Regal F1, which is heterozygous for *Ph-3* only, was moderately resistant. In Freeville in 2012, Plum Regal F1, for which NC25P is one parent, had slightly more disease than *Ph-2* + *Ph-3* varieties but the difference was not statistically significant. In Freeville in 2013, Plum Regal F1 was moderately resistant and grouped with *Ph-2* + *Ph-3* varieties as well as Legend OP, which has *Ph-2* only. In Geneva in 2013, Plum Regal F1 was moderately resistant and grouped with both Legend OP and 'Red Pearl', the latter of which is not known to possess any late blight resistance genes. Legend OP, which is homozygous for *Ph-2* only, was significantly less resistant to *P. infestans* US-23 than *Ph-2* + *Ph-3* varieties in each of the three experiments. Legend OP had AUDPC values which fell between those of *Ph-2* + *Ph-3* varieties and susceptible varieties in each experiment (Table 2). The hybrid of Legend × NC1CELBR was not significantly less resistant than its *Ph-2* + *Ph-3* parent NC1CELBR but was significantly more resistant than its *Ph-2* parent Legend. New Yorker, which is homozygous for *Ph*-1 only, was susceptible to *P. infestans* US-23 in all three experiments and was statistically grouped with the majority of other susceptible varieties. Several significant differences were observed among susceptible varieties in each of the three experiments. However, none of the significant differences remained consistent across all three experiments (Table 2).

Effect of tomato growth habit and class on late blight severity ratings. Resistant varieties were excluded from the analysis because there were not equal numbers of resistant varieties in each category. Resistant varieties included those with the lowest AUDPC values, up to and including Plum Regal F1 and Legend (Tables 1 and 2). Growth habit was a significant factor in Geneva in 2013, where the mean AUDPC was smaller for the indeterminate versus determinate category (Table 3). Fruit type was a significant factor in the analysis of susceptible varieties in Geneva 2013, where the mean AUDPC value for the cherry tomato class was significantly lower than that of the plum and fresh-market classes, which grouped together according to Tukey's HSD (Table 3). Neither growth habit nor class were significant factors in Freeville in 2012 or 2013.

Discussion

Late blight epidemics were successfully established in tomato variety field trials in both 2012 and 2013. The experiments contained susceptible varieties as well as varieties containing both *Ph*-2 and *Ph*-3, which were highly resistant to *P. infestans* US-23. These experiments support previous reports that *Ph*-3 provides qualitative or race-specific resistance (3,22), and that *Ph*-3 is a partially dominant allele which confers stronger resistance to *P. infestans* when it is in the homozygous condition versus the heterozygous condition. This is shown by the differences in disease severity observed in NC25P, homozygous for *Ph*-3, and Plum Regal F1, heterozygous for *Ph*-3. In each experiment, NC25P showed less disease than Plum Regal F1, despite the fact that both varieties contain *Ph*-3 only. A caveat is that the differences observed between NC25P and Plum Regal F1 may be due to other genetic components because the varieties have different parental backgrounds. Plum Regal F1 is the F1 hybrid created by the cross of NC25P and NC30P, a breeding line not included in these experiments. It is possible that, in addition to conferring heterozygosity for the *Ph*-3 allele, the cross resulted in the loss of the action of unknown recessive quantitative resistance genes possessed by NC25P.

Legend OP, homozygous for *Ph*-2, was consistently less resistant than the *Ph-2* + *Ph-3* varieties in all three experiments. Its statistical groupings varied in each experiment but its AUDPC values consistently ranked between the highly resistant varieties and the highly susceptible varieties. Our observations support existing literature indicating that *Ph*-2 is an incompletely dominant gene which confers partial resistance to *P. infestans*, in this case clonal lineage US-23 (21,22).

Tomato growth habit and tomato class were analyzed to determine whether differences among susceptible varieties were associated with these factors. The effect of growth habit was significant in Geneva in 2013 but not in Freeville in 2012 or 2013. The difference in the effect of growth habit observed between experiments is probably due to the speed with which disease progressed. As late blight progresses, indeterminate tomato varieties can continue to add new foliar growth on the tips of infected stems. This can even be observed on severely infected plants that are rated at 90% or greater disease severity. Determinate varieties do not display this characteristic. As a result, a more pronounced effect of growth habit is observed when disease progresses slowly and more disease severity ratings are taken compared with when disease progresses rapidly and fewer disease severity ratings are taken. The Freeville 2013 experiment had the fastest disease progress of the three experiments and the fewest disease severity ratings. In that experiment, there was almost no difference in the mean AUDPC value between determinate and indeterminate susceptible varieties. In Geneva in 2013, the disease progressed more slowly and more disease severity ratings were taken, allowing more time to observe the effect of indeterminate regrowth. This may also account for the numerically higher mean AUDPC for determinate susceptible varieties observed in Freeville in 2012 compared with indeterminate susceptible varieties, although that difference was not significant (Tukey's HSD, $P = 0.17$). Additionally, several studies have indicated that the dominant self-pruning allele, which confers an indeterminate growth habit, is linked to quantitative late blight resistance (26,34). However, it is difficult to determine whether the observed effect is truly due to host resistance or is a result of indeterminate regrowth, as previously discussed (30).

Similarly, it was thought that harvest index, or the ratio between fruit weight and total plant biomass at the time of harvest, might affect the disease ratings of late-blight-susceptible tomato varieties. Varieties with a high harvest index put little energy into foliar growth once fruit development is occurring. On the other hand, varieties with a low harvest index will continue to put energy into both foliar and fruit growth simultaneously. Tomato plants of the plum or processing classes tend to be highly branched and strongly determinate, and have a high harvest index whereas most cherry tomato plants tend to be indeterminate and have a low harvest index. Fresh-market tomato plants may either be of indeterminate or determinate growth habits. In general, fresh-market tomato plants are less highly branched than plum or processing tomato plants and have harvest indices that are variable but generally less than plum or processing tomato. Tomato class was a significant factor among susceptible varieties in Geneva in 2013, where the mean AUDPC for susceptible cherry varieties was lower than that of plum and fresh-market varieties. This result was not observed in either of the Freeville experiments. In fact, in Freeville in 2012, the cherry category had the highest mean AUDPC, although it was not significantly different from the fresh-market and plum categories. These inconsistent and somewhat contradictory results do not allow us to draw meaningful conclusions about the effect of tomato class on late blight disease severity ratings.

Table 3. Growth habit and fruit type analyses excluding resistant varieties

Variable[z]	Mean AUDPC[y] Freeville 2012	Mean AUDPC[y] Freeville 2013	Mean AUDPC[y] Geneva 2013
Growth habit			
Indeterminate ($n = 11$)	1,701 A	1,040 A	893 A
Determinate ($n = 18$)	1,776 A	1,039 A	1,043 B
P value	0.168	0.959	<0.0001
Tomato class			
Plum ($n = 8$)	1,696 A	1,029 A	1,018 B
Fresh market ($n = 16$)	1,755 A	1,044 A	1,023 B
Cherry ($n = 5$)	1,851 A	1,041 A	766 A
P value	0.229	0.899	<0.0001

[y] Means in each column followed by the same letter within the growth habit grouping or within the fruit type grouping are not significantly different according to Tukey-Kramer honestly significant difference ($P < 0.05$).

[z] In Freeville in 2012, 17 determinate varieties and 7 plum varieties were planted ('NC 84-173' was not included). *P* value indicates probability that means are not significantly different (*F* test).

Our results show that, over two seasons, varieties with tomato late blight resistance genes *Ph-2* and *Ph-3* had a high level of protection against *P. infestans* US-23, while the majority of varieties (which did not have either *Ph-2* or *Ph-3*) were susceptible. The variety containing the resistance gene *Ph-1* was also susceptible. The *R* gene *Ph-2* alone provides modest resistance, slows late blight epidemics, and may allow growers to reduce the number of fungicide applications depending on the level of disease pressure. Similarly, the *Ph-3* gene, when heterozygous, provided moderate resistance, with a higher level of resistance in the variety that was homozygous for *Ph-3*. This finding supports that *Ph-3* is a partially dominant gene. Varieties with both *Ph-2* and *Ph-3* were consistently highly resistant to *P. infestans* US-23. The heirloom varieties Matt's Wild Cherry, Lemon Drop, and Mr. Stripey were all resistant to late blight in this study, and it would be interesting to identify the mechanisms underlying this resistance. Growers now have several options for tomato varieties that are resistant to the clonal lineage that has been most common over the past several seasons, and the presence of two resistance genes in many of the varieties may delay the occurrence of resistance-breaking strains of the pathogen.

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