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ARTICLE

Resistance to bacterial spot (*Xanthomonas gardneri*) on foliage and fruit of commercial processing tomato cultivars

Tina E. Simonton, Darren Robinson, Chris Gillard, Katerina Jordan, and Cheryl L. Trueman

Abstract: Bacterial spot of tomato (*Xanthomonas gardneri* Šutić) is an economically important disease of processing tomatoes in Ontario, Canada, resulting in premature defoliation and fruit damage. Breeding efforts for host resistance focus on assessments of foliar health as opposed to fruit health but anecdotal reports from industry suggest a poor relationship between fruit and foliar resistance. To investigate this, nine commercial cultivars were inoculated at the vegetative (foliar experiment) or reproductive (fruit experiment) stages in replicated field experiments from 2016 to 2018. In the foliar experiment, the standardized area under the disease progress curve (sAUDPC) for defoliation was 51% to 54% higher for 'TSH18' than 'H9706', 'Hypeel 696', and 'H3406', but equivalent to 'CC337'. Fruit disease incidence was 49% and 47% lower for 'CC337' than 'TSH18' and 'H9706', but equivalent to 'H3406' and 'Hypeel 696'. Fruit disease severity was 63% and 60% lower for 'CC337' than 'H9706'and 'H3406', respectively, but equivalent to 'TSH18' and 'Hypeel 696'. However, in the fruit experiment, fruit disease incidence was equivalent among cultivars, while the disease severity index for 'H9706' (3.4) was higher than 'Hypeel 696' (0.7). Furthermore, rank correlation analysis between sAUDPC and fruit disease variables failed to meet the criteria for a significant and strong relationship ($r \geq 0.8$ or ≤ -0.8 and $P \leq 0.05$). Additional research is needed to better understand the mechanisms of fruit infection by *X. gardneri*. In the meantime, scientists should consider the limitations of assessing only foliar damage as an evaluation method for bacterial spot management tools in tomato.

Key words: Solanum lycopersicum, *Xanthomonas hortorum* pv. *Gardneri*.

Résumé : La tache bactérienne de la tomate (*Xanthomonas gardneri* Šutić) est une maladie d'importance économique pour les tomates de transformation cultivées en Ontario, Canada, car elle entraîne une défoliation prématurée du plant et abîme le fruit. Les programmes d'hybridation visant à rendre l'hôte résistant à la maladie gravitent autour d'une évaluation de la vitalité du feuillage plutôt que du fruit. Pourtant, des rapports anecdotiques de l'industrie laissent croire qu'il existe une faible relation entre la résistance du fruit et celle des feuilles. Pour le vérifier, les auteurs ont inoculé la maladie à neuf cultivars commerciaux au stade végétatif (expérience sur les feuilles) ou au stade reproductif (expérience sur le fruit), sur des parcelles identiques, au champ, de 2016 à 2018. Lors de l'expérience sur le feuillage, la surface normale sous la courbe traçant l'évolution de la maladie (sAUDPC) indiquait une défoliation de 51 à 54 % plus importante chez le cultivar TSH18 que chez les variétés 'H9706', 'Hypeel 696' et 'H3406', mais équivalente à celle du cultivar 'CC337'. L'incidence de la maladie sur le fruit était respectivement 49 % et 47 % plus faible chez 'CC337' que chez 'TSH18' et 'H9706', cependant elle était équivalente à celle observée chez les variétés 'H3406' et 'Hypeel 696'. Le fruit de 'CC337' a été moins atteint par la maladie que celui des cultivars 'H9706' et 'H3406' (de 63 % et de 60 %, respectivement), mais le fruit de 'TSH18' et de 'Hypeel 696' l'a été tout autant. Dans l'expérience sur les fruits, l'incidence de la maladie s'équivalait chez les différents cultivars, même si l'indice de la gravité de la maladie était plus élevé chez 'H9706' (3,4) et plus faible chez 'Hypeel 696' (0,7). Par ailleurs, l'analyse, après classement, des corrélations entre sAUDPC et les variables de la maladie chez le fruit ne révèle aucune relation significative prononcée ($r \geq 0,8$ ou $\leq -0,8$ et $P \leq 0,05$). Il faudrait entreprendre d'autres recherches pour mieux comprendre comment *X. gardneri* contamine le fruit. Dans l'intervalle, les scientifiques devraient tenir compte des limites de la méthode qui consiste à n'évaluer que les dommages subis par le feuillage pour gérer la tache bactérienne de la tomate. [Traduit par la Rédaction]

Mots-clés : Solanum lycopersicum, *Xanthomonas hortorum* pv. *gardneri*.

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Introduction

Xanthomonas gardneri Šutić is the dominant causal agent of bacterial spot of tomatoes (*Solanum lycopersicum* L.) affecting growers in southwestern Ontario (Canada) (Abbasi et al. 2015). There are four species of *Xanthomonas* which cause tomato bacterial spot: *X. euvesicatoria* (Jones, Lacy, Bouzar, Stall & Schaad), *X. vesicatoria* (Doidge) Vauterin, Hoste, Kersters & Swings), *X. perforans* (Jones, Lacy, Bouzar, Stall & Schaad), and *X. gardneri* which are known collectively as the bacterial spot causing Xanthomonads (BSX) (Jones et al. 2004). Recent genome analysis has proposed the name *X. hortorum* pv. *gardneri* for *X. gardneri* (Morinière et al. 2020). An environmentally conducive season for bacterial spot can result in up to 60% yield loss (LeBoeuf et al. 2009; OPVG 2018) in tomato production and this can be quite significant as Ontario field tomatoes had a farm gate value of $52 million in 2017 from over 470 000 harvested tons of tomatoes. Yield reductions occur when the foliar lesions of bacterial spot cause defoliation, reducing productivity, while lesions that develop on the fruit reduce their quality and value (LeBoeuf et al. 2009). From the 1980s to the mid-2010s copper-based sprays were the standard management practice for controlling bacterial spot but sprays needed to be applied often, allowing the pathogen to develop copper resistance (Zevenhuizen et al. 1979; Conover and Gerhold 1982; Abbasi et al. 2015).

Xanthomonad infection of foliage is well documented, and mechanisms include effectors capable of triggering stomata to open to initiate infection (Melotto et al. 2008; Schornack et al. 2008; Gudesblat et al. 2009) and possibly hydathodes (Bernal et al. 2021). Infection processes of fruit remain less clear, with fruit trichomes and flowers identified as entry points (Getz 1983; Bashan and Okon 1985). Reporting foliar disease severity for bacterial spot in tomato breeding research is common and usually involves a rating of defoliation (Scott et al. 1995; Yang et al. 2005; Bernal et al. 2021), but reporting on fruit severity is rare and does not always include specific reports of fruit incidence or severity (Horvath et al. 2012; Bhattarai et al. 2017). Foliar disease evaluations of tomato are less labour intensive than fruit evaluations, but could be selecting only for foliar resistance if the relationship between foliar and fruit resistance is poor.

Examples of variable resistance among plant organs in pathosystems are uncommon but not undocumented. For potato (*Solanum tuberosum* L.), a disassociation between foliar and tuber health exists in cultivars carrying major resistance genes against *Phytophthora infestans* (Mont.) de Bary (Roer and Toxopeus 1961). Major resistance genes in potato cultivars 'Kennebec' and 'Island Sunshine' confer a high level of foliar resistance to late blight, but low resistance to tuber infection. For example, 'Kennebec' had increased surface necrosis and lesion depth on tubers relative to 'Russet', a cultivar with low foliar resistance (Peters et al. 1999). In contrast, late blight tuber severity scores for surface necrosis and lesion depth for 'Island Sunshine,' were less than 'Kennebec'. Conversely, potato cultivar 'Russet Burbank', which is susceptible to *P. infestans* on foliage, had tuber surface necrosis scores equivalent to 'Kennebec' and tuber lesion depth that was shallower than 'Kennebec' (Peters et al. 1999). Thus, foliar resistance to late blight does not predict tuber resistance to *P. infestans* in potato. Roer and Toxopeus (1961) recommended that tubers at various growth stages be directly assessed after inoculation with *P. infestans* as part of cultivar selections, instead of focusing strictly on foliar health. In pepper, root and fruit rot resistance to *Phytophthora capsici* Leonian were found to be moderately correlated, but resistance to root rot was not a strong predictor of fruit rot, or vice versa (Naegele and Hausbeck 2020). The relationship between foliar and fruit resistance against BSX in tomato has not been previously investigated.

As the relationship between bacterial spot intensity on tomato fruit and foliage is sparsely documented, the objective of this research was to establish if foliar bacterial spot measurements, specifically those derived from defoliation assessments, are related to bacterial spot incidence and severity on fruit. Parallel field trials were completed from 2016 to 2018 using nine commercial processing tomato cultivars, with tomatoes inoculated either at the vegetative or reproductive stage and the relationship between foliar disease severity and fruit severity was compared.

Materials and Methods

Each year two parallel field trials were conducted at the University of Guelph, Ridgetown Campus, Ridgetown, ON, Canada (42°26′55.9″ N 81°53′05.3″ W). One trial had the foliage inoculated with *X. gardneri,* while the other had both fruit and flowers inoculated to investigate potential differences in foliar and fruit resistance within commonly grown commercial processing tomato cultivars. These trials were repeated over 3 yr (2016 to 2018) using cultivars 'CC337' and 'N3306' (Conagra Brands, Dresden, ON), 'H5108', 'H9706', 'H1178', and 'H3406' (HeinzSeed, Leamington, ON), 'Hypeel 696' (Seminis Vegetable Seeds Inc. Santiago Chile), and 'TSH28' and 'TSH18' (Tomato Solutions, Chatham, ON). Of the cultivars tested, 'H5108', 'H9706', 'H3406', and 'TSH18' have no reported resistance or tolerance to *Xanthomonas* spp. (Dick and Dick 2021), while no information is available for 'CC337', 'N3306', 'Hypeel 696', and 'TSH28'. Heinz Seed (2021) report tolerance of 'H1178' to *Xanthomonas* spp.; however, the mechanism of this tolerance is not reported.

All trials were arranged in a randomized complete block design with four replications. Cultivars were seeded in 288-cell trays and grown in a local commercial greenhouse using standard production practices. Transplants were transported to the University of

Guelph, Ridgetown Campus, and kept outdoors before planting for up to one week. Trials were transplanted on 24 May 2016, 24 May 2017 and 24 May 2018 using a custom carousel transplanter (RJ Equipment, Blenheim, ON). Each plot consisted of a 7-m long twin row planted on 2-m centers, with an in-row spacing of three plants per meter. Each plot was separated by one guard row, consisting of 'Hypeel 696', because of anecdotal industry reports of tolerance to BSX and the unavailability of a cultivar with qualitative resistance. Minimum and maximum daily temperature and rainfall data were obtained from the weather station located at Ridgetown Campus through Environment Canada and summarized in Simonton et al. (2021).

Foliar inoculation and assessments

Foliar trials were inoculated with a solution of *X. gardneri* DC00T7A (Cuppels et al. 2006), which was originally isolated in southwestern Ontario in 2000, at a concentration of 1×10^6 CFU/mL using ULD 120-02 nozzles and a water volume of 200 L/ha. Inoculation occurred 10 d after planting in 2016 and 8 d after planting in 2017. In 2018, inoculation initially occurred 8 d after transplanting but plots were re-inoculated 22 d after transplanting due to dry conditions, and no symptoms developed from the initial inoculation. Inoculum was applied in the evening, with air temperatures and relative humidity ranging from 18 to 24 °C and 36% to 71%, respectively, and no precipitation recorded on the day of inoculation.

Plots in the foliar field trial were visually assessed for bacterial spot symptoms daily beginning 7 d after inoculation to determine the number of days to symptom (DTS) appearance. Five plants from each plot were randomly selected, and every leaflet was visually inspected until symptoms were observed in that plot. To confirm diagnosis, leaf samples were collected, sampled, and plated on tryptic soy agar (Fisher Scientific, Canada) and Chang Kama Tween Medium, which is semi-selective for *Xanthomonas*, to confirm that colonies phenotypically resembled *X. gardneri* according to the methods of Sijam et al. (1991), Cuppels et al. (2006), and Simonton et al. (2021). Representative samples were sent to the Pest Diagnostic Clinic at the University of Guelph, Laboratory Services (Guelph, ON) to confirm colony identification using amplified fragment length polymorphism primers to differentiate BSX species (Koenraadt et al. 2009).

Plots were monitored for defoliation weekly using a 5% incremental scale. Due to the assortment of early, mid, and late maturing cultivars, defoliation values were considered based on days before harvest (DBH) classification rather than the calendar date. The DBH classification categories were 43 to 47 DBH, 32 to 36 DBH, 20 to 26 DBH, and 11 to 17 DBH. These categories were used to calculate the area under the disease progress curve (AUDPC) using the following equation:

$$\text{AUDPC} = \sum\{[(Y_i + Y_{i-1})(X_i - X_{i-1})]/2\},$$

where Y_i is percent defoliation at DBH category X_i, and Y_{i-1} is percent defoliation at DBH category X_{i-1} (van der Plank 1963).

These values were standardized for the length of assessment period with (Duveiller et al. 2005):

$$\text{sAUDPC} = \text{AUDPC}/\text{number of days},$$

where sAUDPC is the standardized area under the disease progress curve and number of days is the midpoint for each DBH category.

Individual plots were harvested by hand when fruit colour reached approximately 90% red. A 2-m section of the plot was randomly selected for harvest. Red fruit, green fruit, and rots were separated and weighed, and then a random 100-fruit subsample of red fruits was collected. Fruits were assessed for incidence of bacterial spot by separating them into the following categories: 0 = no bacterial spot, 1 = 1 spot, 2 = 2 spots, 3 = 3 spots, 4 = 4 spots, 5 = 5 or more spots. A disease severity index (DSI) was calculated using the following equation (Kobriger and Hagedorn 1983):

$$\text{DSI} = \sum[(\text{class no.})(\text{no. of fruit in each class})]/$$
$$[(\text{total no. fruit per sample})(\text{no. classes} - 1)] \times 100$$

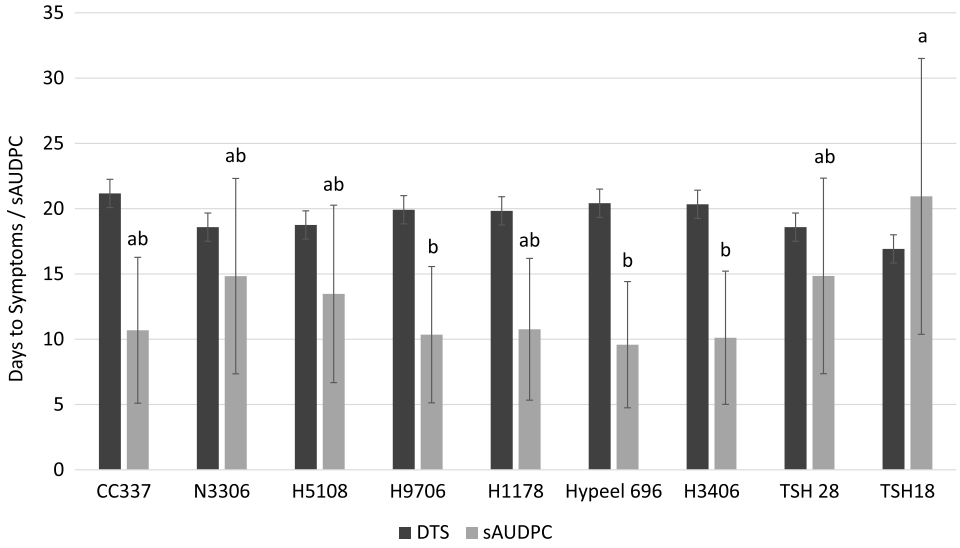
The fruit was then re-sorted into additional categories which included "small" lesions <5 mm diameter, "split" lesions with skin broken open within the spot, "large" lesions >5 mm diameter, and "not split" lesions where the skin was intact. Incidence was calculated for each category.

Fruit inoculation and assessments

On the day of inoculation, two reproductive clusters with green fruit and two clusters with open flowers but no set fruit were marked in each plot. The numbers of set fruits and spent, aborted, open, or closed flowers were recorded. In the evening, the marked clusters were inoculated with a solution of *X. gardneri* DC00T7A (1×10^6 CFU/mL) and distilled water using a small hand pump sprayer (Carter's Home Hardware, Ridgetown, ON). Inoculation occurred twice, once in early July and again in mid-July (7 and 19 July 2016, 4 and 11 July 2017, 4 and 11 July 2018) so that a total of eight reproductive clusters were marked and sprayed per plot. In addition, during each inoculation event, 10 clusters of fruit and flowers were marked and inoculated with distilled water within the trial as controls.

Beginning in mid-August fruit were assessed weekly for ripeness. Marked clusters were harvested and bagged when all fruit in the cluster reached at minimum the breaker stage. As it became apparent in 2016 that the abortion rate in inoculated clusters was high, 100 fruit per plot were randomly harvested when fruit in the plot

Fig. 1. Days to first bacterial spot symptoms (DTS) on leaves and standardized area under the disease progress curve (sAUDPC) for defoliation of tomato cultivars inoculated with *Xanthomonas gardneri* seven to ten days after transplanting. Error bars represent standard error of the mean. Bars without letters are not significantly different at $P \leq 0.05$, Tukey's Honestly Significant Difference.



were 90% ripe. This was done by randomly throwing a 2 m long stick in the middle of the plot and harvesting all fruit touching the stick. From each tagged cluster and sample of 100 randomly collected fruit, the total number of fruit and number of fruits with bacterial spot symptoms were categorized and recorded, and the DSI calculated as described previously.

Statistical analysis

The data were analyzed using SAS version 9.4 (SAS Institute Inc., Cary, NC). The analysis of variance was performed with PROC GLIMMIX ($P \leq 0.05$). Tukey's Honestly Significant Difference ($P \leq 0.05$) was used to separate the means for every trial. Location, year, and replicate were treated as random effects. Shapiro-Wilk and AIC values were used to test the normality of residuals, and the distribution of errors was assessed using residual plots. Covtest-WALD (Z test) was used to validate combining data for the trials.

For the field foliar resistance data, only the DTS and spot incidence data for "any" spots on fruit in the 100-fruit random sample, the percent of fruit with large lesions, and percent of fruit with not split lesions were run on the normal scale. All other data categories from the field foliar trials were processed on the log scale and back transformed using the ILINK statement. Of the variables collected in the fruit inoculated trails, fruit recovery data were run on the normal scale, all other data were run on the log scale and back transformed using the ILINK statement; this included 'H1178' in 2018, which was only replicated three times due to a shortage of transplants.

Ranked correlation tests were done using Spearman's Rho for sAUDPC and incidence and severity of bacterial spot on fruit variable pairings using PROC COR. Foliar variables from the foliage inoculation trials were compared with lesion variables from both the foliage and fruit trials to account for differences in inoculation techniques between the trials, including foliar sAUDPC to fruit variables obtained from plants in the same trials and to fruit variables obtained from fruit bulk harvested in the fruit trials. Data were sorted by treatment order in the foliar trial. Only strong relationships, defined as $r \geq 0.8$ for positive relationships or $r \leq -0.8$ for negative relationships, that demonstrated significance at $P \leq 0.05$, were considered (Xu et al. 2013).

Results

Foliar resistance

There were no differences ($P > 0.05$) among cultivars in the DTS on the foliage (Fig. 1). When percent defoliation was analyzed using DBH categories, it differed between three cultivars at only two points in time (Supplementary Table S1[1]). For sAUDPC, values of 'H9706', 'Hypeel 696', and 'H3406' were approximately half that of 'TSH18', but all other cultivars had similar sAUDPC values, rendering them indistinguishable from the low or high sAUDPC groups (Fig. 1). Thus, while bacterial spot symptom appearance did not differ among cultivars, disease development over the growing season was greater for 'TSH18' than 'H9706', 'Hypeel 696', and 'H3406'.

[1]Supplementary data are available with the article at https://doi.org/10.1139/cjps-2021-0231.

Table 1. Incidence of bacterial spot lesions on fruit, and associated disease severity index (DSI) from different tomato cultivars inoculated with *Xanthomonas gardneri* 7 to 10 d after transplanting at the University of Guelph, Ridgetown, ON, 2016–2018.

		Incidence (%) ± SE				
Cultivar	DSI ± SE	Any	< 5 mm	≥ 5 mm	Not Split	Split
CC337	4.0 ± 1.08c	15.6 ± 8.47b	4.5 ± 1.08a	6.3 ± 4.67b	5.0 ± 1.71b	7.1 ± 5.00a
N3306	4.8 ± 1.08bc	20.7 ± 8.47ab	4.5 ± 1.08a	8.9 ± 6.67ab	3.9 ± 1.32b	8.1 ± 5.71a
H5108	5.5 ± 1.08abc	22.6 ± 8.47ab	4.4 ± 1.00a	10.8 ± 8.04ab	6.9 ± 2.34ab	7.7 ± 5.44a
H9706	10.8 ± 1.08a	29.6 ± 8.47a	7.1 ± 1.54a	15.9 ± 11.78a	13.4 ± 4.59a	8.6 ± 6.09a
H1178	7.6 ± 1.08abc	23.3 ± 8.47ab	3.8 ± 0.83a	14.4 ± 10.72a	8.0 ± 2.74ab	8.0 ± 5.65a
Hypeel 696	4.9 ± 1.08abc	18.3 ± 8.47ab	3.4 ± 0.75a	7.9 ± 5.88ab	6.3 ± 2.14ab	6.2 ± 4.36a
H3406	10.1 ± 1.08ab	26.6 ± 8.47ab	6.2 ± 1.36a	12.4 ± 9.22ab	12.8 ± 4.36a	7.6 ± 5.42a
TSH28	7.3 ± 1.08abc	27.5 ± 8.47ab	5.8 ± 1.33a	10.8 ± 8.05ab	7.5 ± 2.59ab	11.9 ± 8.44a
TSH18	7.5 ± 1.08abc	30.5 ± 8.47a	6.5 ± 1.66a	16.7 ± 12.48a	7.4 ± 2.56ab	15.8 ± 11.32a
P	0.0013	0.0019	0.2580	0.0003	0.0003	0.0571

Note: A random sample of 100 fruit was assessed. Numbers in a column followed by the same lowercase letter are not significantly different at $P \leq 0.05$; Tukey's Honestly Significant Difference, data, and standard error were processed on the lognormal scale and returned to the normal scale using ILINK. SE, standard error of the mean.

Fruit resistance

Fruit resistance: inoculation at vegetative stage

For the fruit symptom assessments for the trial with foliage inoculated, the DSI for cultivars 'H3406' and 'H9706' were 6 and 7 points higher than 'CC337', respectively (Table 1). Additionally, 'N3306' had a DSI 56% lower than that of 'H9706'. Cultivar 'CC337' also had fewer than half as many fruit with lesions of "any" size or type than either 'H9706' or 'TSH18'. There was no variation between cultivars in the incidence of fruit with "small" lesions (<5 mm) or those with "split" lesions. In contrast, the incidence of "large" lesions (>5 mm) for 'CC337' cultivar was 56%, 60%, and 62% lower than for 'H1178', 'H9706', and 'TSH18', respectively. Incidence of fruit with lesions that were "not split" were 65% to 76% greater in 'H9706 and 'H3406' cultivars than in 'CC337' and 'N3306' (Table 1).

Fruit resistance: inoculation at reproductive stage

No differences were found in the DSI when inoculated fruit clusters were evaluated, regardless of growth stage at inoculation (Supplementary Table S2[1]). There was no difference between cultivars for fruit DSI when inoculation occurred at the fruit stage. The incidence of spots in clusters inoculated at the flower stage differed only between cultivars 'TSH18' (0.1%), 'H3406' (40%) and 'H1178' (36%) (Supplementary Table S2[1]). However, tomato fruit abortion rate, based on the number of flowers or fruit present at the time of inoculation versus the number of fruit present at harvest, ranged from 48% to 72% and 20% to 44% for flower and fruit clusters, respectively (data not shown). Abortion rate was not affected by the application of inoculum or sterile distilled water.

Evaluation of 100 random fruit samples revealed cultivars 'TSH28', 'Hypeel 696', and 'N3306' had a DSI 79% to 82% lower than 'H9706' (Table 2). Cultivar 'H9706' also had a higher incidence of "not split" lesions than 'N3306' (81% lower), and 'Hypeel 696' (76% lower), but 'Hypeel 696' did not vary from any other cultivars. When "small" lesions were assessed, the incidence was 60% to 64% higher in cultivar 'H3406' than in 'Hypeel 696', 'CC337', 'TSH18', and 'TSH28'.

Relationship among foliar and fruit disease variables

A range of significant positive and negative correlations were found between measured foliar and fruit disease variables, but all failed to meet the criteria for a significant and strong positive or strong negative relationship ($r \geq 0.8$ or ≤ -0.8 and $P \leq 0.05$), including between foliar sAUDPC and fruit disease variables obtained from plants in the same foliar inoculated trials (Table 3), and foliar sAUDPC values from the foliar inoculated trials and fruit disease variables obtained from trials inoculated at the reproductive stage (Table 4).

Discussion

The objective of this study was to determine the relationship between bacterial spot incidence and severity variables on foliage and fruit in commercial processing tomato cultivars under field conditions in Ontario. Variables that were considered less time consuming to assess, such as the days to foliar symptoms, defoliation, and foliar sAUDPC were assessed in parallel with fruit symptom incidence and severity, which are more laborious to obtain. There were no differences among cultivars for DTS on leaves (Fig. 1), and DTS is not generally reported in the literature, so the sAUDPC was compared with the fruit metrics using Spearman's Rho ranked correlation. None of the correlations between sAUDPC and fruit disease had a strong ($r > 0.8$) and statistically significant ($P \leq 0.05$) relationship for any cultivars.

Table 2. Incidence of bacterial spot lesions on fruit and associated disease severity index (DSI) from different tomato cultivars inoculated with *Xanthomonas gardneri* at the reproductive stage at the University of Guelph, Ridgetown, ON, 2016–2018.

		Incidence (%) ± SE				
Cultivar	DSI ± SE	Any	< 5 mm	≥ 5 mm	Not split	Split
CC337	1.0 ± 0.53ab	3.4 ± 1.70a	1.8 ± 0.74b	2.9 ± 1.42a	2.7 ± 1.22abc	3.4 ± 1.00a
N3306	0.6 ± 0.29b	2.3 ± 1.11a	2.2 ± 0.91ab	1.6 ± 0.70a	1.8 ± 0.77c	2.3 ± 0.46a
H5108	1.8 ± 0.97ab	5.1 ± 2.56a	3.0 ± 1.21ab	3.8 ± 1.77a	4.5 ± 1.96abc	5.1 ± 0.54a
H9706	3.4 ± 1.82a	7.5 ± 3.71a	3.6 ± 1.50ab	5.7 ± 2.60a	9.5 ± 4.67a	7.5 ± 0.96a
H1178	1.6 ± 0.89ab	6.1 ± 3.02a	2.4 ± 0.96ab	3.1 ± 1.33a	4.5 ± 1.96abc	6.1 ± 0.87a
Hypeel 696	0.7 ± 0.35b	2.6 ± 1.24a	1.9 ± 0.73b	2.7 ± 1.24a	2.3 ± 0.96bc	2.6 ± 0.65a
H3406	2.1 ± 1.10ab	6.4 ± 3.12a	4.8 ± 1.92a	4.3 ± 1.77a	6.0 ± 2.53ab	6.4 ± 0.43a
TSH28	0.6 ± 0.34b	3.2 ± 1.57a	1.7 ± 0.69b	2.0 ± 0.88a	3.0 ± 1.32abc	3.2 ± 0.63a
TSH18	1.2 ± 0.61ab	3.8 ± 1.86a	1.8 ± 0.71b	2.8 ± 1.15a	3.3 ± 1.38abc	3.8 ± 0.70a
P-Value	0.0020	0.0157	0.0062	0.2890	0.0031	0.8980

Note: Incidence percent is the percent of a 100 fruit random sample with any bacterial spots, spots larger or smaller than 5 mm, "split" or "not split". Means in the same column followed by the same lowercase letter are not significantly different at $P \leq 0.05$, Tukey's Honestly Significant Difference. All data and standard errors processed on the lognormal distribution to meet normality assumptions and back transformed using ILINK. SE, standard error of the mean.

Table 3. Spearman's ranked correlation (r_s) coefficients for foliar standardized area under the disease progress curve (sAUDPC) and bacterial spot incidence and disease severity index (DSI) on fruit in tomato cultivars foliar inoculated with *Xanthomonas gardneri* 7 to 10 d after transplanting at the University of Guelph, Ridgetown, ON, 2016–2018.

Cultivar		sAUDPC × DSI	sAUDPC × any	sAUDPC × < 5 mm	sAUDPC × ≥ 5 mm	sAUDPC × not split	sAUDPC × split
All	r_s	0.01[a]	−0.02	0.15	0.01	0.22	−0.02
	P	0.9647	0.8728	0.1220	0.8854	0.0223	0.8690
CC337	r_s	−0.32	−0.32	−0.08	−0.33	−0.13	−0.30
	P	0.3126	0.3061	0.7940	0.2906	0.6876	0.3515
N3306	r_s	0.28	0.35	0.05	0.27	0.47	0.19
	P	0.3839	0.2643	0.8873	0.3949	0.1225	0.5486
H5108	r_s	−0.32	−0.31	0.27	−0.48	−0.43	−0.21
	P	0.3079	0.3230	0.3995	0.1121	0.1667	0.5193
H9706	r_s	0.06	0.20	−0.32	0.26	0.39	0.08
	P	0.8542	0.5339	0.3070	0.4094	0.2063	0.7951
H1178	r_s	−0.71	−0.68	−0.16	−0.52	0.12	−0.66
	P	0.0102	0.0158	0.6092	0.0800	0.7129	0.0185
Hypeel 696	r_s	0.37	0.33	0.44	0.11	0.50	0.12
	P	0.2356	0.3006	0.1509	0.7287	0.0952	0.7038
H3406	r_s	−0.20	−0.22	0.01	−0.21	0.20	−0.10
	P	0.5419	0.4845	0.9828	0.5128	0.5339	0.7530
TSH28	r_s	−0.11	−0.19	0.39	−0.27	0.04	−0.25
	P	0.7292	0.5567	0.2116	0.3902	0.8970	0.4291
TSH18	r_s	0.36	0.43	0.72	0.43	0.64	0.51
	P	0.2453	0.1667	0.0077	0.1634	0.0261	0.0877

[a]*Rs* values in the first row reflect the relationship between variables summed over all treatments.

The lack of relationship between foliar sAUDPC and incidence and severity of bacterial spot on fruit supports results of several studies reporting significant treatment effects on foliar bacterial spot disease intensity, but few or no treatment effects on fruit disease intensity for bacterial spot (Abbasi et al. 2002; Al-Dahmani et al. 2003; Obradovic et al. 2004; Ji et al. 2006). For example, Abbasi et al. (2002) found that application of yard waste

Table 4. Spearman's ranked correlation (r_s) coefficients for foliar standardized area under the disease progress curve (sAUDPC) measured in tomato cultivars foliar inoculated with *Xanthomonas gardneri* 7 to 10 d after transplanting, and bacterial spot incidence and disease severity index (DSI) on fruit inoculated with *X. gardneri* at the reproductive stage, University of Guelph, Ridgetown ON, 2016–2018.

Cultivar		sAUDPC × DSI	sAUDPC × any	sAUDPC × < 5 mm	sAUDPC × ≥ 5 mm	sAUDPC × not split	sAUDPC × split
All	r_s	0.27[a]	0.32	0.25	0.34	0.29	0.25
	P	0.0047	0.0007	0.0081	0.0003	0.0025	0.0108
CC337	r_s	0.17	0.24	0.02	0.26	0.14	0.16
	P	0.6006	0.4520	0.9615	0.4222	0.6747	0.6189
N3306	r_s	0.05	0.12	0.10	0.22	0.01	0.01
	P	0.8707	0.7099	0.7473	0.4970	0.9738	0.9643
H5108	r_s	0.14	0.30	0.37	0.34	0.30	0.40
	P	0.6670	0.3512	0.2402	0.3408	0.3512	0.1938
H9706	r_s	0.59	0.66	0.42	0.24	0.37	0.03
	P	0.0417	0.0205	0.1686	0.4530	0.2353	0.9385
H1178	r_s	0.32	0.52	0.57	0.60	0.45	0.77
	P	0.3146	0.0829	0.0548	0.0384	0.1433	0.0031
Hypeel 696	r_s	0.46	0.53	0.26	0.53	0.54	0.50
	P	0.1279	0.0729	0.4182	0.0768	0.0729	0.0999
H3406	r_s	0.49	0.47	0.29	0.49	0.43	0.42
	P	0.1243	0.1454	0.3953	0.1243	0.1854	0.1927
TSH28	r_s	0.26	0.32	0.24	0.35	0.33	−0.01
	P	0.4183	0.3121	0.4491	0.2635	0.2973	0.9774
TSH18	r_s	0.29	0.26	0.12	0.25	0.27	0.32
	P	0.3675	0.4151	0.7142	0.4399	0.4021	0.3065

[a]*Rs* values in the first row reflect the relationship between variables summed over all treatments.

compost doubled foliar AUDPC for bacterial spot compared with the control, but at harvest, the increased rate of foliar disease was not reflected in higher disease incidence on fruit, which remained at the same incidence as control plants. Research on chemical management of bacterial spot using kasugamycin, acibenzolar-S-methyl, and copper hydroxide showed that even when reductions in foliar AUDPC compared with the nontreated control are achieved, there is no effect on the incidence of bacterial spot on fruit (Trueman 2015). Similarly, in the current study 'Hypeel 696', 'H9706', and 'H3406' had lower foliar sAUDPC than 'TSH18,' but severity of bacterial spot on fruit among these cultivars was not different. Furthermore, in the 100-fruit random plot samples of the fruit inoculated experiment, 'H3406' had higher incidence of "small" lesions than 'TSH18'. Thus, sAUDPC values are a poor predictor of bacterial spot intensity on fruit.

Environmental conditions, especially temperature, rain, and wind are important factors in bacterial spot outbreaks (Gardner and Kendrick 1923; Jones et al. 2014). As the cultivars evaluated in this study ranged from early to late maturing, one possibility is that incidence and severity of bacterial spot on fruit were confounded by growth stage at the time environmental conditions were optimum for flower or fruit infection by *X. gardneri*. However, in our statistical analysis, environmental conditions (i.e., location) were treated as a random effect. Data was collected over 3 yr with variable environmental conditions (Simonton et al. 2021) yet still passed the COVTEST, allowing data from all 3 yr to be grouped together, and indicating the effect of different environmental conditions was not so impactful. Little is known about the infection processes of *X. gardneri* on tomato flowers or fruit. For *Xanthomonas campestris* pv. *vesicatoria*, Bashan and Okon (1985) used scanning electron microscopy to observe pathogen multiplication and infection in inoculated pepper plants and found the fruit surface and ovaries hosted relatively few bacteria, while dead flowers and the wart area were populated by the pathogen. Naegele and Hausbeck (2020) found that root rot resistance to *P. capsici* was a poor predictor of fruit rot resistance in pepper, which could be explained by the existence of a major shared multiple quantitative trait loci (QTL) for both root fruit rot resistance and the presence of other fruit rot specific QTL, resulting in a differential response to infection among roots and fruit (Naegele et al. 2014). A similar relationship for tomato QTL and *X. gardneri* resistance has not been investigated.

A challenge during the completion of this study was the rate of abortion when reproductive clusters were

handled, which ranged from 21% to 72% in the field. The basal level of flower abortion is highly variable in tomatoes and related species, and specific basal abortion rates for tomato are not known (Wubs et al. 2007). The natural rate of abortion of untouched clusters was not measured in the current study, so the impact of applying liquid to the reproductive clusters as part of the inoculation process on the abortion rate, and in turn on these results, is not known. High abortion rates also disrupted attempts to validate field results in greenhouse trials as fewer than 10 fruits were recovered when the trial was replicated in a greenhouse (data not shown). Effects of *X. gardneri* on flower and fruit abortion in tomato should be explored in future research.

This research evaluated host resistance to *X. gardneri* in nine commercial processing tomato cultivars commonly grown in Ontario. 'H1178' is reported to have tolerance to *Xanthomonas* spp. (HeinzSeed 2021), but in the current study tolerance to foliar defoliation or fruit symptom development caused by *X. gardneri* was not observed in this cultivar. As little is known about the mechanism of tolerance reported by the breeder and how this was determined, it is difficult to speculate why our results differ from those reported by the seed company, but one possibility is that testing conditions were different from typical Ontario growing conditions or that previous testing was completed with BSX that did not include *X. gardneri*.

Bacterial spot is an economically important disease of tomatoes because of damage to both foliage and fruit. This study demonstrated a poor relationship between foliar sAUPDC and fruit disease intensity among nine commercial processing tomato cultivars. Thus, as new management methods for this disease are evaluated, the limitations of assessing only tomato foliage for bacterial spot should be acknowledged. This includes tomato breeding programs, which are motivated to use historic datasets and high-throughout phenotyping methods to predict and assess resistance (Liabeuf and Francis 2017; Bernal et al. 2021). Future research on the mechanisms of *X. gardneri* fruit infection and abortion would be beneficial to aid in the development of effective management and resistance breeding assessment techniques and better understand impacts of this disease on total and marketable yield.

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