



Water stress affects *Solanum lycopersicum* “Moneymaker” infection by “*Candidatus Liberibacter solanacearum*” in a haplotype-specific manner

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Abstract

“*Candidatus Liberibacter solanacearum*” (Lso) is a phloem-limited bacterial pathogen transmitted by psyllid. In the USA, the haplotypes A and B are transmitted by the tomato psyllid, *Bactericera cockerelli*, and are responsible for economic damage to the solanaceous crop industry. In tomato, haplotypes A and B cause diseases with differing degrees of severity, yet their underlying mechanisms are not well understood. The role that abiotic stress plays in disease development has not been characterized. In the present study, we evaluated whether water stress influenced the development of symptoms associated with these haplotypes in tomato (*Solanum lycopersicum* “Moneymaker”). First, pot-grown tomato plants were subjected to either a control or a water-stress regime, then they were assigned to one of three infection treatments (Lso-free, LsoA, or LsoB) under laboratory-controlled conditions. Symptom development was monitored for up to 8 weeks following infection. Results of this experiment revealed that water stress significantly reduced the plant water potential and was the primary driver of reduced height, with infection only having an effect in later weeks. Water stress also increased the detectability of Lso throughout the plant and across three timepoints (weeks 4, 6, and 8 after infection). This increase in Lso-positive tissues suggests that water stress creates a more homogenous distribution of Lso throughout the plant. More noticeably, water stress significantly reduced the severity of the disease associated with haplotype A but not B. Overall, these findings revealed the existence of haplotype-specific interactions between Lso infection and water stress on the tomato health. This work highlights the influence of abiotic factors on plant health.

Keywords Abiotic stress · *Bactericera cockerelli* · Disease epidemiology · Plant-pathogen interactions · Psyllid

Introduction

“*Candidatus Liberibacter solanacearum*” (Lso) is a phloem-limited, gram-negative, fastidious bacterial pathogen vectored by psyllids (Munyanza et al. 2007; Hansen et al. 2008). Several haplotypes of Lso have been identified worldwide associated with different host plants and psyllid vectors. In North America, the haplotypes LsoA and LsoB infect

solanaceous plants (Nelson et al. 2011; Lin et al. 2012). In potato plants, both LsoA and LsoB, cause zebra chip with symptoms that include stunting, chlorosis, decreased vigor, necrosis, and early death (Swisher-Grimm et al. 2018; Harrison et al. 2019). Additionally, tubers from infected plants develop characteristic stripes when fried. In tomato plants, the symptoms associated with these two haplotypes can be first observed around three to four weeks post-infection and include leaf deformation and chlorosis. As the disease develops, LsoA-infected tomato plants develop small leaves on the apical meristem, new growth from axillary meristems, and become stunted; however, LsoB-infected plants develop more severe symptoms, including necrosis and plant death (Mendoza Herrera et al. 2018).

LsoA and LsoB are vectored by the tomato psyllid (also known as the potato psyllid), *Bactericera cockerelli* (Hemiptera: Triozidae) (Šulc) (Munyanza et al. 2007; Hansen et al. 2008). This insect is native to the USA-Mexico border but

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has expanded its geographical range (Butler and Trumble 2012). Today, it is commonly found from Peru to Southern Canada, New Zealand, and Western Australia (Vereijssen 2022), and the invasion of these regions was accompanied by the introduction of Lso. Differences in the interaction between these haplotypes and their insect vector were also noted: in laboratory studies, both haplotypes reduced the fecundity of infected females, but LsoB also caused increased nymphal mortality (Yao et al. 2016). The negative effects these bacterial haplotypes have on host plants and vectors might be difficult to reconcile with their rapid spread and prevalence in the affected areas. Because the outcome of the interaction between microbes and eukaryotic hosts lies along the parasite-mutualistic continuum depending on the host context (Drew et al. 2021), biotic or abiotic conditions, such as water stress, can influence Lso infection and prevalence.

Water stress is one of the most critical abiotic stresses limiting crop productivity worldwide, causing significant yield reductions and economic losses amounting to millions of dollars annually (Sinclair and Rufty 2012). Water stress occurs when plants experience changes in water availability. Those changes can result from different conditions, such as excessive water (waterlogging), insufficient water, and situations when water is present but physiologically unavailable to the roots, such as in the case of high-salinity soils (Wu et al. 2022; Manghwar et al. 2024; Yanhong et al. 2025). Plants under deficit water stress mount a series of responses that allow them to conserve water (Osakabe et al. 2014). Upon water stress, abscisic acid (ABA) levels increase, triggering a series of signaling events mediated by increases in cytosolic Ca^{2+} and accumulation of reactive oxygen species (ROS) leading to stomatal closure (Liu et al. 2022). Transcriptional reprogramming also occurs (Liu et al. 2023); plants under water stress regulate the expression of genes involved in the synthesis and response to ABA, the production of osmoprotectant molecules, and of other defense compounds (Krasensky and Jonak 2012; del Carmen Martínez-Ballesta et al. 2013). Since water stress has profound effects on the plant physiology, it can also affect the plant interaction with insects and pathogens (Huberty and Denno 2004; Tariq et al. 2012; Zarattini et al. 2020). Therefore, it is increasingly important to understand the relationship between water-stressed plants, herbivorous insects, and plant pathogens. The effect of water stress on the plant interaction with other organisms, in particular insects, is difficult to predict because the outcomes can depend on the type of stress (continuous vs pulsed), its intensity, duration, etc., as well as the insect guild, hence the variability in the literature regarding the outcome of water stress (Huberty and Denno 2004; White 2009; Sconiers et al. 2020). For example, a study evaluating the performance of *Rhopalosiphum padi* on wheat plants under continuous water-stress ranging

from well watered to severe found that aphid performance decreased as the magnitude of the water stress on the plants increased (Kansman et al. 2022). Similarly, the fecundity of *R. padi* was reduced when feeding on water-stressed barley plants (Leybourne et al. 2022). However, *Myzus persicae* and *Brevicoryne brassicae* had higher fecundity on *Brassica oleracea* plants under continuous medium water stress than on control or highly water-stressed plants (Tariq et al. 2012). On pulse water-stressed plants, both aphid species performed better than on control or highly water-stressed plants, but not as well as under medium water stress (Tariq et al. 2012). These are just some of the abundant examples in the literature of the differential effect of water stress on sap-feeding insects. Part of this range of effects can be linked to the plant's adaptive responses to the stress.

Since water stress affects the interacting insects by modifying the availability of hosts or their suitability, it also plays a key role in the transmission of pathogens and potentially influences the epidemiology of vector-borne diseases (van Munster 2020). For instance, there was increased transmission of *Xylella fastidiosa* when its vector, the glassy-winged sharpshooter, acquired the pathogen from water-stressed grapevine under no-choice conditions; however, under choice conditions, the vector preferred well-watered plants resulting in reduced transmission (Del Cid et al. 2018). In another study, there was a correlation between watering levels and *Soybean mosaic virus* (Family: *Potyviridae*) transmission by soybean aphids and virus load on soybean plants: both were lower on plants under drought compared to saturated conditions (Nachappa et al. 2016). Similarly, aphid transmission of *Turnip yellows virus* (Family: *Solemoviridae*) to *Arabidopsis thaliana* plants was reduced under water deficit (Yvon et al. 2017). In the case of Lso and its vector, *B. cockerelli* exhibited a higher nymphal survival rate on pot-grown tomato water-stressed plants, producing a larger number of adult offspring than on pot-grown non-water-stressed plants (Huot and Tamborindéguy 2017), whereas continuously stressed pot-grown potato plants had a lower titer of Lso (Cohen et al. 2023).

Considering the direct and indirect effects of abiotic conditions on plant diseases, evaluating the effect of water stress on Lso infection is necessary to better understand the epidemiology of the diseases this pathogen causes. In this study, we evaluated the role of water stress in the development of symptoms associated with LsoA and LsoB infection in tomato plants. We also evaluated the distribution of the pathogen in the infected plants. Because water stress weakens plants, we hypothesized that water stress would lead to more severe disease symptoms; however, because LsoA and LsoB display different levels of pathogenicity in tomato, we hypothesized that the effect of water stress could differ depending on the Lso haplotype.

Materials and methods

Plants and insect colony maintenance

Tomato plants, *Solanum lycopersicum* L. “Moneymaker” (Thompson & Morgan Inc., Jackson, NJ), were grown from seeds in 9 × 9 cm pots with Jolly Gardener ProLine C25 soil (Oldcastle Lawn & Garden, Atlanta, Georgia) in a plant room. Three weeks post-planting, the plants were fertilized with Miracle-Gro Water-Soluble Tomato Plant Food at the label rate (18–18–21 NPK; Scotts Miracle-Gro Company, Marysville, OH).

Colonies of Lso-free, LsoA-, and LsoB-infected tomato psyllids were maintained on tomato plants in insect-proof cages (BioQuip, Compton, CA). DNA was extracted from psyllids using the 10% CTAB method (Mendoza Herrera et al. 2018). The infectious status and haplotype of the colonies were confirmed regularly by PCR using the Lso 16S rDNA and SSR-1 primers, respectively (Lin et al. 2012). All plants and colonies were maintained at room temperature on light shelves with a photoperiod of 16:8 h (light:dark).

Water and infection treatments

Figure 1 is a representation of the experiment. Four-week-old tomato plants were moved from the plant room to the

laboratory and randomly assigned to one of two watering regimes: control plants (C) received 75 mL of water twice weekly, while water-stressed plants (S) received 25 mL once weekly, corresponding to pulsed water stress. This time-point is referred to as “start.” Each plant was on top of an individual dish to collect any water flowing from the pots. The plants were maintained in the laboratory for the remainder of the experiment under similar conditions as previously stated but they were maintained inside insect cages to avoid any unwanted insect herbivory. Two weeks after the watering regimes were started, the plant water potential was measured using a pressure chamber (model 615; PMS Instrument Company, Albany, OR) according to the manufacturer’s instructions. Tomato plants with a reading below -0.6 MPa are considered to be water stressed (Hsiao 1973) as there is a well-documented inverse relationship between tomato plant water potential (Ψ_w) and chamber pressure ($r^2 = -0.99$) (Duniway 1971).

After measuring the water potential, the plants under each water regime were further assigned to one of the following infection treatments: (1) Lso-free (F, uninfected), (2) LsoA (A), or (3) LsoB (B). Each plant was infested with five adult male psyllids from their respective “infection treatment” colony. The psyllids were placed inside a mesh bag on the lowest true leaf of the plant. Plants within the same infection treatment were caged together for the remainder of the experiment to prevent any psyllid escape or accidental

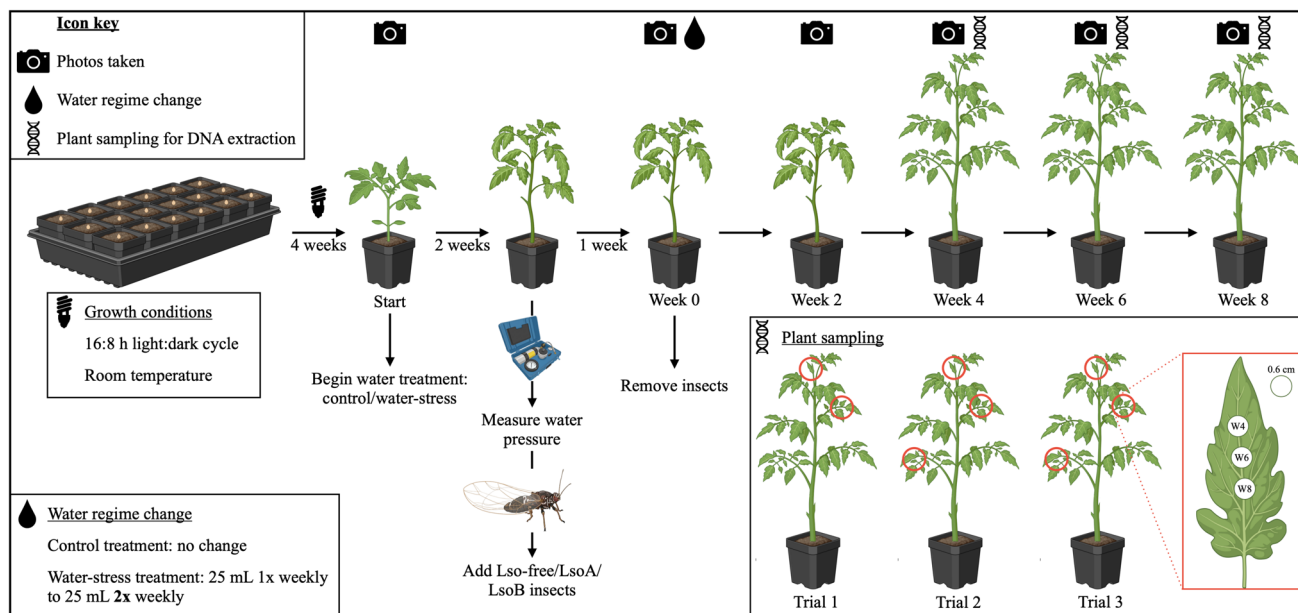


Fig. 1 Schematic of the experiment. The water droplet icon represents when the water regime changed. The camera and DNA icons represent the weeks when photos were taken and samples for DNA purification collected. The plant sampling occurred differently for each independent trial, illustrated in the bottom right insert titled “Plant sampling.” The red circles indicate where the samples were

collected. For trial 1, top or middle leaf samples were collected depending on the week and Lso treatment. For trial 2, samples were collected from top-, middle-, and bottom-leaves at every time point. For trial 3, disks were collected from the same top-, middle-, and bottom-leaf at each time point using a 0.6 cm cork borer

infestation or infection. Within the cages, the plants were maintained in their individual dish but grouped by water treatment on large trays by groups of six: two columns of three rows of plants. After 1 week (3 weeks after the initiation of the water treatment), the psyllid-infested leaf was cut from the plant to remove the psyllids. The removal of psyllids from the plants is considered “week 0.” In the end, there were six combinations of “water treatment” and “infection treatment”: control Lso-free (CF), control LsoA (CA), control LsoB (CB), water-stress Lso-free (SF), water stress LsoA (SA), and water-stress LsoB (SB).

Following insect removal, the water regime for the water-stressed plants was changed to 25 mL of water twice weekly to account for plant growth. This new water regime was maintained throughout the rest of the experiment to prevent excessive plant mortality while maintaining water stress. Water was adjusted as needed for the control plants based on plant appearance, such as leaf curling, wilting, or soil dryness to ensure they were well watered. Any remaining free water in the dish under the plant was emptied prior to the next scheduled watering. The plants were maintained under their new respective water regimes for 8 weeks as previously described. Photos of the plants were taken at the “start” and at weeks 0, 2, 4, 6, and 8. Conditions of the photos were standardized: they were taken from the same position in the room, with the same lighting (no flash, ambient), angle, camera (iPhone 15 Pro Max, Apple Inc., Cupertino, CA, USA), and camera adjustments ($f/1.78$ aperture lowered by 1.1–0.7 stops). Sampling for DNA extraction occurred in weeks 4, 6, and 8. The experiment was performed three times independently (trials), each time with six plants per treatment, for a total of 108 plants. The spatial arrangement of plants was consistent throughout the trial, meaning plant 1 was always in the same location within the cage, but the location of each cage corresponding to the infection treatment was rotated between trials.

Verification of Lso-infection

Lso infection was assessed by PCR using the samples collected in weeks 4, 6, and 8. The plants were not assessed in weeks 0 or 2 because Lso titers are too low for reliable detectability before 4 weeks. In the first independent trial, a leaflet was sampled at each time point from the top tier part of the plants in the LsoB and Lso-free treatments. Samples from plants in the LsoA treatment were collected from the top-tier part of the plant at week 4, but from a middle-tier leaf at weeks 6 and 8, based on our previous determination of LsoA and LsoB distribution in tomato plants as the infection progressed (Mendoza Herrera et al. 2018). For the second and third independent trials, top-, middle-, and bottom-tier leaves were sampled from each plant at each time point; the only difference was that in the third independent trial,

leaf disks were collected from the same leaves each time (when possible). These changes were introduced to account for potential differences in Lso distribution in plants under water stress. For the third trial, the same leaves were subsequently sampled to evaluate the same leaf over time. DNA was extracted from the collected leaf samples and PCR was performed as mentioned before using the Lso 16S rDNA and SSR1 primers to confirm the presence of Lso and the haplotype.

Lso disease index and plant height

Observations and photos were taken at the beginning of the water treatment (start), and every 2 weeks starting at week 0. Using these observations and photos, the plants were scored in weeks 4, 6, and 8 based on the presence (1) or absence (0) of eight specific Lso symptoms (Table 1). Weeks 0 and 2 were not scored because Lso symptoms are not visible prior to week 4. The plants were scored additively as symptoms developed with the progression of the disease (Bock et al. 2010; Mendoza Herrera et al. 2018). A plant that died was automatically scored as a 10.

Plant height was measured relative to the 9 cm side of the square pots with ImageJ (version: 1.54 g) using the images taken throughout the experiment by tracing the stem length.

Data analysis

One plant from the uninfected control water regime was removed from data analysis due to improper infection status; so, data from 107 plants were analyzed for height and symptoms. Data analysis and figure generation were performed in R (version 4.5.1), RStudio (version

Table 1 Lso disease index describing the symptoms scored and the weeks when they are usually first observed. If a symptom was present, a value of 1 was assigned; otherwise, a value of 0 was assigned. Plants that died were automatically given a score of 10. The scoring system was additive throughout the disease progression

Lso Disease Index	
Symptom becomes observable in...	Symptom
Week 4	Apical meristem leaves are smaller
	Apical meristem leaves are discolored
	New growth from axillary meristem in the lower tier of the plant
Week 6	Apical meristem leaves stopped growing
	Necrosis begins to develop
Week 8	Discoloration throughout the plant
	Younger leaves are curling and yellowing
	Plant is dying

2025.09.0 + 387), Microsoft Excel (version 16.103.4), and BioRender; the figures were marked up in Apple Freeform (version 4.0) when needed.

Pressure chamber values were compared using a Wilcoxon rank-sum test (Mann–Whitney U), as the data violated the Shapiro–Wilks normality test ($p < 0.05$). Infection data was visualized as a heatmap in Microsoft Excel using two-color conditional formatting to display a gradient from yellow (0% Lso-positive samples) to red (100% Lso-positive samples).

Height data were analyzed by a three-way mixed ANOVA using the *rstatix* package, with water treatment and infection as between-subject factors and time as the within factor (height ~ water * infection * time + Error(plant/time)). All ANOVA assumptions were met. For the simple two-way interactions and simple-simple main effects, Bonferroni corrections were applied.

Disease scores were analyzed using a Cumulative Link Mixed Model (clmm) from the ordinal package in R using a logit link function. Plants in the control regime and Lso-free treatment (CF) were used as the reference. Different models were compared for their performance using the Akaike Information Criterion (AIC) and the Hessian value (Hess). The model with the lowest AIC (834.77) and Hess value (740) evaluated water treatment, infection, their two-way interaction and time as fixed effects, while trial was evaluated as a single random effect (model: score ~ water * infection + time + (1 | trial)). The model fitting performed used the Laplace approximation (nAGQ = 1). An estimated marginal means post-hoc was performed using the Sidak correction.

Results

Confirmation of water stress

The water potential of the plants was evaluated two weeks after the water treatments were initiated. The water treatment had a significant effect on the pressure recorded by the pressure chamber ($W = 212.5$, $p < 0.001$). This indicated that plants in the control treatment (mean = -0.39 MPa, standard deviation = 0.28 MPa, $n = 53$) had higher water potential compared to those in the water-stress treatment (mean = -1.02 MPa, standard deviation = 0.32 MPa, $n = 54$).

Water stress affected Lso distribution in plants, not the percentage of infected plants

Plant infection was confirmed using PCR. Every plant in the infected treatments tested positive at least once, i.e., all plants were infected. The Lso haplotype was also confirmed; all plants were infected with the corresponding haplotype. However, one control Lso-free plant in trial 2 was excluded because it tested positive for Lso infection.

In the first trial, by week 4, all plants in the LsoA and LsoB infection treatments tested positive for Lso infection (Table 2). A decrease in the number of plants testing positive was observed in the control treatment as the experiment progressed: by week 6, two-thirds of the LsoA-infected plants tested positive, and by week 8, one-third of the LsoA-infected and half of the LsoB-infected plants tested positive (Table 2). However, all the plants in the water-stress treatment continued to test positive.

Table 2. Heatmap of the percentage of plants testing positive for Lso for each treatment combination for each week tested, with red indicating 100% infection and yellow indicating 0% infection. Abbreviations:

CA: control treatment, LsoA-infected plants; CB: control treatment, LsoB-infected plants; SA: water-stress treatment, LsoA-infected plants; SB: water-stress treatment, LsoB-infected plants

Total Plant Infection per Week					
Trial	Week	CA	CB	SA	SB
Trial 1	Week 4	100%	100%	100%	100%
	Week 6	67%	100%	100%	100%
	Week 8	33%	50%	100%	100%
Trial 2	Week 4	100%	100%	100%	100%
	Week 6	67%	83%	67%	100%
	Week 8	100%	83%	100%	100%
Trial 3	Week 4	100%	83%	100%	100%
	Week 6	83%	67%	100%	100%
	Week 8	50%	50%	100%	100%

In the second trial, by week 4, all plants in the infected treatments tested positive for Lso. A reduction in the percentage of plants testing positive was also observed in this trial as the disease progressed, and this reduction was also greater in the plants under the control regime. Similar results were obtained for the third trial, with the exception that one plant in the LsoB control condition did not test positive at week 4, but by week 6, it tested positive and developed symptoms associated with Lso infection.

The analysis of the individual plant tiers revealed that LsoA and LsoB were first better detected in the top- and middle-tier samples, but as the weeks progressed, they were more detectable in the middle and bottom tiers of the plants (Table 3). Also, a greater level of detection was observed in the samples from the plants under the water-stress regime. At week 4, Lso was primarily detected in the top- and middle-tier samples, except for LsoB which was detectable

throughout the water-stressed plants. As the infection progressed, Lso was increasingly detectable on the middle and lower parts of the plants. However, Lso was more readily detectable in the plants under the water-stress regime.

Plant height was mainly affected by the water treatment

Before initiating the water and infection treatments, there were no statistically significant differences ($W = 1353.5$, $p = 0.63$) in height between the plants assigned to the control treatment (mean = 26 cm, standard deviation = 11.8 cm, $n = 53$) and water-stressed treatment (mean = 24.6 cm, standard deviation = 10.1 cm, $n = 54$).

After infection, the height of the plants in each of the six treatments was measured every 2 weeks. Their analysis revealed a statistically significant three-way interaction

Table 3. Heatmap of the percentage of plants testing positive at each sampling week and plant tier with red indicating 100% infection and yellow indicating 0% infection. The numbers in parentheses denote sample size when fewer than six samples were available because the plants had no remaining leaves in the corresponding tier. Abbreviations: CA: control treatment, LsoA-infected plants; CB: control treatment, LsoB-infected plants; SA: water-stress treatment, LsoA-infected plants; SB: water-stress treatment, LsoB-infected plants

Trial 1 Infection					
Time	Tier	CA	CB	SA	SB
Week 4	-	100%	100%	100%	100%
Week 6	-	67%	100%	100%	100%
Week 8	-	33%	50%	100%	100%
Trial 2 Infection					
Week 4	Top	100%	100%	100%	100%
	Middle	33%	83%	100%	100%
	Bottom	0%	17%	17%	83%
Week 6	Top	50%	33%	33%	67%
	Middle	17%	50%	50%	67%
	Bottom	33%	17%	33%	100% (5)
Week 8	Top	17%	67%	17%	83%
	Middle	83%	100% (4)	83%	100% (5)
	Bottom	50%	33%	83%	80% (5)
Trial 3 Infection					
Week 4	Top	83%	67%	100%	83%
	Middle	83%	67%	100%	83%
	Bottom	0%	0%	50%	67%
Week 6	Top	33%	17%	50%	33%
	Middle	50%	50%	83%	67%
	Bottom	17%	17%	83%	67%
Week 8	Top	50%	17%	50%	33%
	Middle	33%	50% (4)	100%	75% (4)
	Bottom	0%	17%	67%	83%

among water treatment, infection treatment, and time [$F(6.07, 306.46) = 8.58, p < 0.001$], and of the simple two-way interaction between the infection and time under the control and water-stress regime [$F(5.77, 14.0) = 14.0, p < 0.001$ and $F(6.75, 172.0) = 16.1, p < 0.001$, respectively]. There was also a statistically significant simple-simple main effect of time on the plant height for each treatment, infection combination (Online Resource 1). The significant differences among the different height means are shown in Fig. 2.

Throughout the experiment, the plants under control water regime were taller than the plants under water-stress regime. While the infection did not significantly affect the plant's height, by week 8, the Lso-free plants were significantly taller than LsoA- and LsoB-infected plants under control water regime, while the LsoB-infected plants were significantly shorter than the Lso-free and LsoA-infected plants under water-stress regime. These results indicate that water availability was the primary driver of plant growth, whereas the infection effects became apparent at week 8 and they depended on the Lso haplotype.

Water stress alleviated LsoA-related symptoms

The plants were scored as Lso-related symptoms developed. Symptom severity increased over time in all infected plants, but water stress significantly reduced disease expression

in LsoA-infected plants but not in LsoB-infected plants. Water treatment has a significant effect on the disease index, decreasing the odds of a higher Lso score (OR = 0.083, 95% CI [0.031, 0.222], $z = -4.20, p < 0.001$). Infection increased the odds of having a higher Lso score when compared to the Lso-free treatment, with LsoA- (OR = 2560.90, 95% CI [1080.78, 6067.42], $z = 12.44, p < 0.001$) and LsoB- (OR = 1460.39, 95% CI [719.96, 2960.38], $z = 11.91, p < 0.001$) infected plants scoring higher than the Lso-free treatment. Symptom severity increased over time with higher odds in week 6 (OR = 27.03, 95% CI [14.02, 52.11], $z = 8.78, p < 0.001$) and week 8 (OR = 301.47, 95% CI [129.70, 700.63], $z = 12.63, p < 0.001$) relative to week 4. There was a significant interaction between water-stress and LsoB infection (OR = 9.55, 95% CI [2.37, 38.50], $z = 3.30, p = 0.001$), while there was not a significant interaction between water-stress and LsoA-infection (OR = 0.68, 95% CI [0.28, 1.63], $z = -0.56, p = 0.573$) (Fig. 3).

These results indicated that both Lso haplotypes induced symptom development compared to the Lso-free plants, and that as the infection progressed, the symptoms increased. As shown by the post hoc results, LsoA-infected plants had a lower score when the plants were under water stress compared to the control regime. However, this reduction in symptoms under water stress was not observed in the LsoB-infected plants.

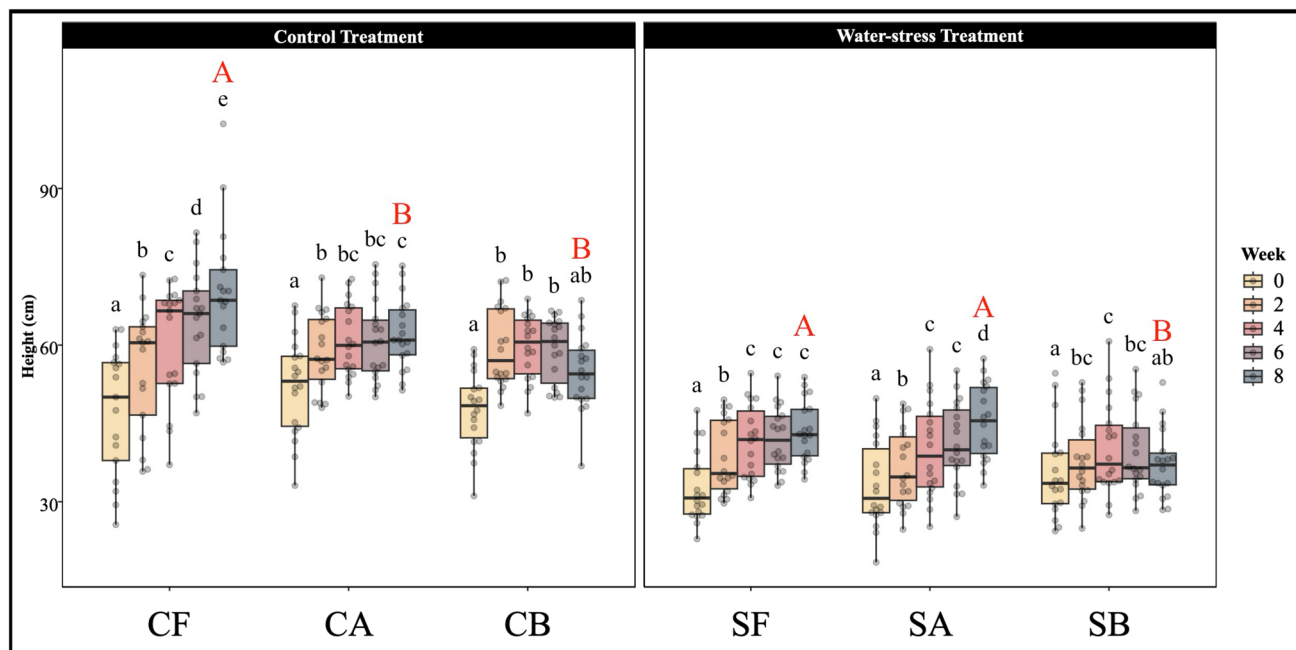


Fig. 2 Plant height (cm) across treatments and weeks. A three-way mixed ANOVA was performed. Week 0 corresponds to the removal of the insects and represents the beginning of the infection treatment ($n = 18$, except for CF $n = 17$). Different lowercase letters indicate statistically significant differences among the height of the plants within each treatment, while uppercase letters indicate differences in

plant height among infection treatments within each water treatment at week 8. Abbreviations: CF: control treatment, Lso-free plants; CA: control treatment, LsoA-infected plants; CB: control treatment, LsoB-infected plants; SF: water-stress treatment, Lso-free plants; SA: water-stress treatment, LsoA-infected plants; SB: water-stress treatment, LsoB-infected plants

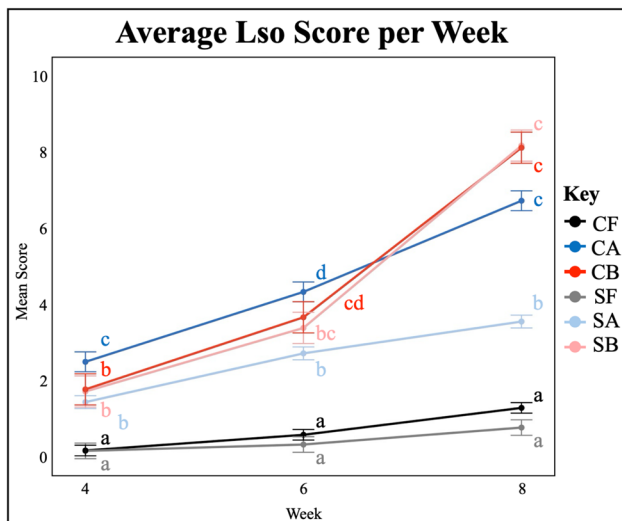


Fig. 3 Tomato plant scores across treatments and weeks. Week 4 coincides with Lso symptoms beginning to show ($n=18$, except for CF $n=17$). Different letters indicate statistically significant differences within weeks ($p<0.05$). Abbreviations: CF: control treatment, Lso-free plants; CA: control treatment, LsoA-infected plants; CB: control treatment, LsoB-infected plants; SF: water-stress treatment, Lso-free plants; SA: water-stress treatment, LsoA-infected plants; SB: water-stress treatment, LsoB-infected plants

Discussion

Water availability is one of the main limitations that plants face (Chieb and Gachomo 2023). In some cases, plant-associated microbes can help mitigate this constraint. Plant–microbe interactions can range from mutualistic to pathogenic, and their outcome often depends on the environmental conditions (Roossinck 2011, 2015). Several studies have reported beneficial effects conferred by viruses helping plants cope with water or temperature stress (Fernández-Calvino et al. 2014; Aguilar and Lozano-Duran 2022; Jaime et al. 2025). Just as microbes can influence the plant’s response to abiotic factors, the abiotic conditions can also impact disease development. For example, changes in the transcriptional profiles of plants under water stress can increase or decrease their susceptibility to infection (Shu et al. 2024).

Liberibacters are phloem-restricted bacteria that display a range of relationships with their hosts, from highly pathogenic, such as Lso, to commensal, such as “*Candidatus Liberibacter europaeus*” and “*Candidatus Liberibacter brunswickensis*” (Raddadi et al. 2011; Morris et al. 2024). The role of water stress in the development of diseases caused by these microbes remains poorly understood. Previously, it was demonstrated that water stress improved the quality of tomato plants as hosts for the vector of Lso (Huot and Tamborindéguy 2017).

Consequently, by influencing vector fitness, water stress can also indirectly affect the epidemiology of the diseases caused by these pathogens (Szczepaniec and Finke 2019).

One key finding of our study was the existence of a haplotype-specific effect of water stress on Lso infection. By week 4, LsoA-infected tomato plants under water stress developed milder Lso-associated symptoms compared to LsoA-infected plants under the control treatment. As the disease progressed, the difference in symptom severity increased (Fig. 3). However, water stress did not change the outcome of LsoB-infected tomato plants, as those plants developed typical symptoms associated with this haplotype, including death (Mendoza Herrera et al. 2018).

Similar results were observed when evaluating Lso symptoms in field-grown potato plants in years characterized by different irrigation and precipitation levels (O’Shaughnessy et al. 2022). Additionally, while greater seasonal precipitation resulted in increased potato yields, it did not affect the development of zebra chip symptoms in potato plants (Rho et al. 2022). Both studies evaluated infection caused by the concurrent infection with LsoA and LsoB, and in both cases, no correlation was observed between water availability and disease development in potato plants.

One hypothesis explaining the increased tolerance to LsoA conferred by water stress is that osmoprotectant molecules or other compounds produced during water stress could provide protection against this Lso haplotype. LsoA and LsoB deploy different strategies to infect plants (Levy et al. 2023) and, as a consequence, they were shown to induce different responses in tomato (Harrison et al. 2022). Molecules such as proline and trehalose, which accumulate during water stress (Chieb and Gachomo 2023), can contribute to a microbe’s pathogenicity (Christgen and Becker 2019). For example, trehalose accumulation reduced bacterial colonization by the bacterial wilt pathogen, *Ralstonia solanacearum*, indicating that water stress can provide protection against pathogens (MacIntyre et al. 2022).

A second key finding of this study was that Lso detection was improved under water stress. Typically, LsoA and LsoB are characterized by patchy distribution within plants (Mendoza Herrera et al. 2018). In trial 1, we obtained the expected distribution for each haplotype under control condition, but higher detection in water-stressed plants. To rule out that this difference was not due to differences in sampling locations because of changes in the architecture of the plant under water stress, we included the complete sampling at each week. In trial 2, we observed an unexpected reduction of Lso detection in week 6, which could be linked to the fact that LsoB-infected plants had fewer available leaves to sample, making it difficult to obtain up-, middle-, and bottom-tier samples. Therefore, for the third trial, leaf disks were collected which allowed us to

sample the same leaf over time. On average, under water stress, LsoA and LsoB were detected more consistently in different sections of the plants (Table 3). This finding could suggest that water stress may weaken plant defenses against Lso, enabling a stronger, faster and more extensive colonization. Several examples of pathosystems in which water stress increases the plant's susceptibility to the pathogen exist. For example, it was determined that water-stressed *Arabidopsis thaliana* plants were more susceptible to *Pseudomonas syringae* pv. *tomato*, because water stress downregulated transcription factors involved in the SA-mediated defense pathway (Choudhary and Senthil-Kumar 2022).

In the case of the effect of water stress on Lso detection, similar effects were observed for both haplotypes which were characterized by increased pathogen spread. However, symptom development did not differ for LsoB infection under control and water-stress conditions, whereas water stress was associated with reduced symptom severity in LsoA-infected plants. These results highlight the fact that symptom development is not directly correlated with the degree of plant colonization and indirectly with Lso titer. Furthermore, these results also indicate that the reduced incidence of disease symptoms in water-stressed tomato plants infected with LsoA was not linked to an increased resistance to this pathogen.

It is tempting to speculate that similar results, i.e., increased colonization under water stress and absence of a direct link between the degree of plant colonization and symptom development, might be valid for field conditions and other crops, not just tomato, as well as for other Lso haplotypes. Moreover, these results could also apply to other “Liberibacter” pathosystems, explaining why some species are commensal and not associated with disease development (Raddadi et al. 2011; Morris et al. 2024).

Finally, as expected, the plants were smaller under water stress than control treatment. While the uninfected plants grew throughout the experiment under the control treatment, the height of those under water stress plateaued by the fourth week after psyllid removal. In the case of LsoB infection, the plants stopped growing and then started dying independently of the water regime. However, while the height of the LsoA-infected plants under the control treatment plateaued after week 4, the plants under the water-stress treatment continued to grow. Overall, this study revealed that water stress could contribute to the epidemiology of Liberibacter diseases. Field studies should evaluate the role of water stress in the epidemiology of Lso diseases, specifically, evaluate if, as in pot studies, water stress enhances Lso colonization and psyllid development, which would contribute to increasing the number of bacterioliferous vectors and the spread of the pathogen.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of Interest The authors declare no competing interests.

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