## Title

Characterizing the effects of deficit irrigation on soil borne diseases of processing tomatoes and evaluating tools for disease management under water scarcity



## Author

Beaulieu, Justine

## Publication Date

2023

Peer reviewed|Thesis/dissertation

Characterizing the Effects of Deficit Irrigation on Soil Borne Diseases of Processing Tomatoes and Evaluating Tools for Disease Management Under Water Scarcity

By

JUSTINE BEAULIEU

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Plant Pathology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Cassandra L. Swett, Chair

David Rizzo

Mallika Nocco

Committee in Charge

2023

Dedicated to my partner, Jacob, who agreed to come with me on this journey, and my son, Willem, who had no choice but made everything more fun.

## Acknowledgments

First and foremost, I would like to thank my major professor, Dr. Cassandra Swett, for the opportunity to conduct research in her lab. Thank you for the mentorship, guidance, and support over the years; I am a better scientist because of you. I would also like to thank my committee members Drs. David Rizzo and Mallika Nocco for their invaluable feedback. Thanks also go to other faculty members including Dr. Thomas Gordon, Richard Bostock, and Amisha Poret-Peterson for their open doors and incredible expertise. None of my research would have been possible without the guidance I received from the UC ANR Farm Advisors Gene Miyao, Tom Turini, and Brenna Aegerter and Zach Bagley from the CTRI. Your decades of work with tomato growers informed much of this research and helped me understand California processing tomato production. The field work component of this research would not have been possible without the help from Bryan Pellissier and Lexi Sommers-Miller. You two are the greatest and I would stand in a field to pick your brain forever if I could. I am also grateful to Maria Tuccori, who is always there with a hug and a compliment.

This work required a lot of field, greenhouse, and lab work. I could not have done it without the countless hours contributed by other (current and former) Swett Lab members. A huge thank you to Beth Hellman, Rino Oguchi, Erin Helpio, Kelley Flores, Elver Lopez Raymundo, Mrinalini Narayan, Emma Centeno, Alyssa Brackrog, Greg Sugawara, Harrison Powell, Karla Espinoza, Daisy Huang, Anni Divney, Megan Kozel, Aimee Hopkins, Hannah Josifek, Fernando Rodriguez, Sarah Suriano, Ashly Lord, Laurel Schmidt, Forrest Wilcox, Cooper Calvin, Rachel Hallmark, Brian Cain, Kacey Zimmerman, Megan Gastelum, Claire Theberge, Anna Erichsen, and Ashley Brown. Special thanks go to Drs. Johanna del Castillo and Kelley Paugh for their guidance and to Myles Collinson for his ability to bring out the funny in every situation. You're next!

I cannot express enough gratitude to my friend and partner, Jacob. Thank you for agreeing to come with me on this journey and move our lives across the country. You have given me so much support and grace over the last five years. I am looking forward to life after graduate school with you. Thanks also goes to my mother, Roselin, who has helped us in so many ways, big and small, especially since the birth of our son. Thank you for keeping me caffeinated and catching everything that falls between the cracks. Of course, I would be remiss if I didn't acknowledge the unconditional love I've received from our dog, Boba. She is always there for snuggles anytime I need a "Boba break". Thank you to my family including my brother, father, stepmother, and in-laws for checking in regularly. Your support has been lovely. Thank you also to my best gal pals for always encouraging me, even when I was doubtful myself. Last but not least, I want to thank my fellow graduate students and fossils for the coffee dates and happy hours. I cannot wait to see the amazing things you'll accomplish.

**Abstract**

California produces 99% of the nation's processing tomatoes and 26% of global production. Due to increasing water scarcity, deficit irrigation (DI) is a common practice in which growers irrigate to replace only a fraction of evapotranspiration (ET) needs starting at fruit ripening. However, this practice may enhance losses from soil borne diseases. This work attempted to enable the use of DI under disease pressure by first evaluating its cumulative effects on soil borne disease development, water stress, plant nutrition, and yields in a naturally infested field and determining if soil management practices can influence DI impacts on plant health (Chapter 1). We observed increased disease symptoms (vine decline, stem rot, and reduced red marketable fruit) under DI. *Fusarium oxysporum* f. sp. *radicis-lycopersici* (Fusarium crown and root rot, Forl) and *F. noneumartii* (Fusarium stem rot and vine decline, FRD) were the predominant pathogens isolated. The latter was isolated only from plants grown in the DI treatment, suggesting disease enhancement of this pathogen under DI. Because fungicides do not effectively manage soil borne pathogens and methyl bromide fumigation is highly restricted, we wanted to determine if cultivar-based management is effective in reducing disease development and yield losses under DI. We examined the effects of DI FRD in four cultivars with putative tolerance and evaluated whether greater FRD sensitivity under DI was related to water stress tolerance traits (Chapter 2). We observed enhanced FRD disease development under DI and found that cultivars with better water stress tolerance performed better under DI and FRD disease pressure indicating that appropriate cultivar selection can be a useful management tool. To better understand the microbial basis for increased disease symptoms under DI we used culture-dependent methods and amplicon sequencing to explore possible enhancement of soil borne pathogens under two DI treatments and to determine the effects of composted soil amendments and cover cropping on fungal root microbial communities; additionally, putative facultative Fusarium pathogens dominant in the ecosystem were tested for pathogenicity

(Chapter 3). *Fusarium brachygibbosum* isolates caused stem lesions on seedlings, suggesting that it is a facultative pathogen of tomato. With amplicon sequencing, we did not observe an effect of DI on fungal diversity or abundance, however we did observe an effect of compost amendment and cover cropping. Characterization of bacterial root microbial communities is forthcoming and may provide us with a better understanding of the effects of DI and soil management. Overall, this work confirms that DI can enhance losses caused by soil borne disease and informs management decisions regarding the importance of appropriate cultivar selection and soil management techniques for growers facing reduced water allocations and disease pressure.

**Contents**

**Chapter 1: Determining the effects of deficit irrigation on processing tomato health and interactions with soil health management**

## 1. Introduction

Tomatoes (*Solanum lycopersicum*) are grown either for fresh consumption or for processing into products such as paste, sauces, juices, and soups. In 2018 fresh and processing tomatoes were grown on approximately 14.3 million acres worldwide, yielding 268.8 million tons of fruit (Food and Agriculture Organization, 2021). California is a key contributor to processing tomatoes worldwide and domestically, growing 11% of the worldwide supply (Food and Agriculture Organization 2021) and at least 94% of the processing tomatoes consumed within the U.S. (USDA NASS 2021).

In California, processing tomatoes are planted between February and June, and harvested between June and October; they are grown from 110 to 140 days depending on the cultivar. The crop is commonly irrigated starting at planting, until 1-4 weeks prior to harvest depending on soil type, after which water is reduced or cut to promote ripening. Nearly all tomato farms are irrigated using drip lines buried 20-45 cm below the soil line; some farms continue to use furrow irrigation, but productivity is generally higher using drip (Mukherjee et al. 2023). The amount of irrigation water applied is determined based on crop water use or potential crop evapotranspiration (ET) requirements (Miyao et al., n.d.), which is a measure of the amount of water lost to the atmosphere by transpiration from the plant and evaporation from surrounding soil (Itier 1996).

California receives little to no summer rain, so crops are irrigated with surface water stored in reservoirs and ground water. However, California agriculture faces challenges with increasingly severe cyclic droughts. The period between 2000 and 2021 was the driest 22-year period over the last millennium (Williams et al. 2022) and snowpack was only 53% of the statewide average as of April 1, 2020, calculated from data collected over the previous 71 years (CA Department of Water Resources 2020). Surface water is allocated to growers by state regulators; allocations to California producers in many regions dipped as low as 0% several times over the last decade, resulting in less available land for food production and increased water costs. In some counties, such as Fresno, the top processing tomato producing county in the state (USDA NASS 2021), growers have received 50% or less of their requested agricultural water annually in 1977, 1990-1994, 2001, 2007-2010, 2012-2016, 2018, and 2020-2022 and received 0% water allocations in two of the last five years (CA Department of Water Resources).

California growers need water-saving strategies to produce tomatoes with less water. One available method is known as “deficit irrigation” (DI); while the term has been defined in several ways in the literature (Chai et al., 2016; Expósito and Berbel, 2017), in general it consists of reducing irrigation to the point where it no longer replaces 100% of the water lost to evapotranspiration (ET) (Fereres and Soriano 2007). The practice can reduce yields, but ideally not to levels that negate water savings benefits and can lead to improvements in fruit quality (Zegbe-Domínguez et al. 2003; Lu et al. 2019). In processing tomatoes, growers reduce irrigation by 60-80% potential crop ET around fruit ripening approximately eight weeks before harvest; some further reduce approximately four weeks before harvest. In general, growers stop irrigation two weeks before harvest (*pers comm.* Tom Turini).

Current deficit irrigation recommendations are based on studies conducted in disease-free settings. Previous work suggests that disease risk increases when irrigation is reduced (Del Castillo Múnera et al. 2019a, b) or when plants are water stressed (Ragazzi et al., 1995; Parsons et al., 2010; and Swett, 2020); thus, DI practices under pathogen-infested conditions may need to be adapted to mitigate disease-enhancing effects. Given DI timing, mid- to late-season diseases are likely the most affected, reducing canopy cover, exposing fruit to sunburn and rot, and leading to economically damaging yield losses. In California, common processing tomato pathogens causing mid- to late-season disease include *Fusarium oxysporum* f. sp. *lycopersici* (Fol), which causes Fusarium wilt; *Fusarium oxysporum* f. sp. *radicis lycopersici* (Forl), causing Fusarium crown and root rot (FCR); both *F. noneumartii* and *F. martii*, causing Fusarium stem rot and vine decline (FRD); *Verticillium dahliae*, which causes Verticillium wilt; *Sclerotium rolfsii*, causing Southern blight; *Phytophthora capsici*, which causes Phytophthora crown and root rot; tomato spotted wilt virus (TSWV); *Clavibacter michiganensis*, causing bacterial canker; and root knot nematode. The Fusarium pathogens (Fol, Forl, *F. noneumartii*, and *F. martii*) are among the most destructive tomato pathogens in California processing tomatoes.

In cases where drought stress increases risk to soil borne pathogens there may be management practices that can be used to protect yields. The negative impact of drought conditions on soil health, particularly soil structure, and in turn soil water holding capacity is well documented (Montanearella et al., 2015). Additionally, soil with poor organic content can restrict crop root growth and exploration of the soil for water and nutrients, further exacerbating crop water stress (Gregory 1988). One method of helping soil maintain its structure and water holding capacity is the application of organic amendments (Baveye et al. 2007; Hudson et al., 1994; Rasool et al., 2008; Rawls et al., 2003; and Zhou et al., 2009). This

practice has also been shown to increase yields, soil porosity, water retention, and hydraulic conductivity (Hirich et al. 2014; Eden et al. 2017; Głąb et al. 2020). Studies examining the relationship between organic soil amendments and DI demonstrate increased crop water use efficiency under DI without negative impacts on tomato and watermelon yields when biochar and humus were used, respectively (Agbna et al. 2017; Qin and Leskovar 2020). The potential for soil amendments to mitigate negative effects of DI on crop health under pathogen pressure has received little to no attention but may offer a valuable water-disease co-management tool.

To fill knowledge gaps surrounding DI use under pathogen pressure and provide guidance in downstream water scarcity adaptations for CA tomato growers, the objectives of this study were to 1a) evaluate the cumulative effects of deficit irrigation (DI) on soil borne disease development, water stress, plant nutrition, and yield quality impacts in a naturally infested field over sequential seasons, 1b) within this, characterize mid- to late-season root/stem rot and vine decline pathogen communities interacting with DI, and 2) assess the influence of soil nutrient management methods over sequential seasons on soil volumetric water content, soil and plant nutrient status, plant water stress, fruit yield and quality, and root/stem rot and vine decline under DI to determine if soil management practices can influence DI impacts on plant health.

## 2. Methods

### *2.1 Experimental design*

Field trials took place in 2019 and 2020 at the Russell Ranch Sustainable Agriculture Facility in Yolo County (38.54320644018775, -121.87000109999997), a region where approximately 15% of CA tomatoes are grown (USDA NASS, 2023). This area typically experiences hot dry summers and cooler wet winters. The field soil is classified as a Rincon silty

clay loam (Rg). The trial was arranged in a split plot RCBD; irrigation treatment was the main plot, and the field (14 ha) was divided into two halves; each half was assigned an irrigation treatment (100% or 60% potential crop ET, corresponding to "Well-Watered" (WW) and "Deficit" (DI) treatments, respectively) (Supp. Fig. 1). Within each irrigation treatment there were two soil amendment treatments, with each amendment allocated to three rows within each of the three blocks. Rows were approximately 185 m long and 1.5 m wide. Heinz tomato seedlings (H1662) were planted 0.3 m apart. For the purposes of this study, observations were conducted in the southernmost of the three rows within each treatment in each block for a total of 12 experimental rows. As this cultivar was Fusarium wilt-resistant, our studies focused on other stem/root rot and vine decline diseases.

Within each evaluated row, two 60 m disease evaluation subplots were established for a total of 6 subplots per amendment x irrigation treatment. Starting locations of subplots were decided by random number generation with numbers corresponding to paces down the rows starting 15 m from the head of each row. The two replicated subplots in each row were separated by 15 m; subplots closest to the irrigation header were called the "header" subplots and the subplots closest to the row ends were called the "end" subplots.

*2.2 Irrigation Treatments*

One drip irrigation line (2.5 cm) was buried at approximately 20 cm deep along the middle of each bed. Emitters were spaced every 30 cm. Irrigation treatments were selected based on commercial practice (*pers comm,* Tom Turini) and preliminary studies (Swett et al., *unpublished data*). Irrigation scheduling was based on evapotranspirative (ET) needs of the plants as measured by an onsite Tule system (Oakland, CA), which monitors actual ET in the

field ($ET_a$) along with the volume of irrigation applied. Plants in both irrigation treatments received enough water to replace 100% of their evapotranspirative (ET) needs until approximately 47 days preharvest in 2019 and 63 days preharvest in 2020 (Table 1). At this point the two irrigation treatments diverged; rows in the "Well-Watered" (WW) treatment continued to receive 100% of the irrigation hours recommended by Tule while rows in the "Deficit" (DI) plot received only 60% of the Tule-recommended irrigation hours. Irrigation was stopped completely 24 and 31 days preharvest in 2019 and 2020, respectively (Table 1).

To confirm that the DI treatment resulted in reduced soil moisture, or volumetric water content (VWC), one sensor (TEROS10, METER Group) was buried approximately 30 cm deep halfway between the drip line and edge of the bed in two blocks per irrigation treatment for a total of eight sensors (Supp. Fig. 1). Sensors measured soil VWC in 15-minute increments between Jun 16 and Aug 31 of 2020. Sensor data revealed clear differences between the WW and DI treatments in both soil amendments (Fig. 1) corresponding with the timing of the deficit treatment onset and the end of irrigation.

*2.3 Soil amendment treatments*

There were two soil amendment treatments within each block: "Synthetic Only" (no compost control + 404 Mg N/ha through drip) and "Synthetic & Compost", (404 Mg N/ha through drip + poultry manure compost at approximately 4.5 Mg/ha with a winter cover crop) (Table 2). The compost amendment was applied in the fall prior to transplanting. Synthetic fertilizer was added as needed through the season.

*2.4 Plant water stress*

To evaluate treatment effects on plant stress, midday stem water potential was measured 0- and 3-weeks post DI-onset in 2020 using a pressure bomb (Model 615, PMS Instrument Co., Albany, OR). A fully developed leaflet from a young branch was covered with a foil-laminate bag (Stem Water Potential Bag, PMS Instrument Co.) for approximately 15 min before excision and measurement. One leaflet was selected from each of three randomly selected plants in each block per amendment x irrigation treatment. Plants were marked so that measurements could be taken from the same plant at each time point.

*2.5 Soil and plant nutrition*

We assessed soil and plant nutrients in collaboration with the Scow lab to evaluate soil amendment treatment effects and to address the possibility that nutrient deficiencies in DI plants were a confounding effect. A 1.5-in. auger was used to collect a composite sample of three cores per row from each amendment x irrigation treatment in every block just prior to planting. Soil was sieved (2 mm) and analyzed for nitrate, phosphorus, and potassium. Soil nitrate was determined by extraction with 2.0 M KCl and analyzed on a liquid injection flow analyzer (Hofer 2013). Phosphorus (Olsen-P) was estimated through extraction of phosphate with 0.5 M sodium bicarbonate adjusted to pH 8.5, then reduced with ascorbic acid. Absorbance of the resulting solution was read at 880 nm. Soil exchangeable potassium was determined using inductively coupled plasma atomic emission spectrometry (Thomas 1982). Soil total carbon and nitrogen were determined using air-dried and ball-milled soil with a dry combustion elemental analyzer (ECS 4010 Costech Elemental Analyzer).

To evaluate plant NPK uptake, tomato leaves were collected at early flowering. The fourth tomato leaf from the top was sampled (Maynard and Hochmuth 2007); 30 leaves were

collected per row, dried at 60° C, ground to 2 mm, and analyzed for total N, P, and K according to the methods of Jones and Benton (2001), and Carlson et al. (1990).

*2.6 Soil water holding capacity*

To determine whether soil amendment influenced soil water holding capacity, measurements were taken as described in Wang et al. (2019). Briefly, intact soil cores were collected in July each year to 30 cm (3 per row), and water retention was measured on intact cores at -33 and -1500 kPa on a pressure plate apparatus, pressures which correspond to field capacity and permanent wilting point, respectively. Water holding capacity was defined as the difference between field capacity and permanent wilting point.

*2.7 Mid- to late-season vine decline and stem rot quantification*

Plants were said to have vine decline when all branches were symptomatic (turgor loss and/or necrotic leaves); incidence was quantified as the percentage of plants in the two subplots per row (out of 10 plants). Change in decline incidence between years was calculated as the difference between each year. Area under the disease progress curve (AUDPC) values were calculated based on decline incidence treating block as replicate to create an average per treatment. Stem rot incidence and severity were measured by evaluating the extent of stem rot from the belowground tissue through the crown and aboveground stem. In 2019 only the belowground tissue was examined; in 2020 the crown and aboveground tissue was included. A subset of symptomatic plants was collected for pathogen community characterization in both years, (described further below).

Fruit from the excavated plants was collected and sorted into three categories: Red marketable (red/pink fruit), green (all green), and damaged (red/pink fruit with any rot,

including blossom end rot and sunburn). Fruit from each group was then weighed and the percent of total yield was calculated per group by dividing their weights by the total fruit yield. Approximately 0.5 kg of red marketable fruit per treatment per block was taken for quality analysis (hue, Brix, and pH) by the Processing Tomato Advisory Board (Davis, CA).

*2.8 Characterizing pathogen communities associated with late season vine decline*

A subset of symptomatic plants was collected from the four amendment x irrigation treatments in both years except for the Synthetic & Compost – 60% ET treatment in 2019 (Table 3). Roots were examined for root knot nematode galls. Leaves with speckling or stunted growth in addition to leaves from plants with spotted fruit were tested for TSWV using Agdia (Elkhart, IN) immunostrip tests. Leaves from plants with cracked stem tissue or spotted fruit were tested for bacterial canker using Agdia immunostrip tests as well. As Beet Curly Top Virus (BCTV) and Phytophthora crown and root rot are not known to occur in this region and characteristic symptoms were not observed (Davis et al., 2013a; Davis et al., 2013b), no diagnostic tests were conducted for these diseases (Fig. 2 and Table 4).

To diagnose stem/root rot diseases, healthy-diseased margins in stem tissue were excised and surface disinfested by rinsing with tap water then 0.1% Tween (Sigma Aldrich, St. Louis, MO), dipping in 70% ethanol for 30s then 20% bleach (Clorox, Oakland, CA) for 2 min. Tissue (1 cm segments) was then either placed on growth media for fungal isolations or incubated (24°C, 46% RH, 12:12 L:D for 10 days) for Southern blight evaluations. Broad fungal diagnosis was conducted using the general growth medium 1/10 potato dextrose agar (1/10 PDA + tet) (3.9 g potato dextrose, 16.1 g agar, 1 L distilled water) amended with 0.3 g tetracycline in 10 cm diameter Petri dishes. For Fusarium disease diagnosis, tissue was placed

on Fusarium selective media (FSM) (15 g Bactone Peptone, 1 g KH2PO4 monobasic, 0.5 g MgSO4 – 7H2O, 20 g agar, 0.6 g PCNB (Terraclor 75%), 0.1 g ampicillin, 0.3 g streptomycin sulfate, and 1 L deionized water). Plates were sealed with parafilm and incubated (24°C, 46% RH, 12:12 L:D for 3-7 days).

Dominant emerging fungi were sub-cultured to 1/10 PDA and 0.6% KCl agar (6g KCl, 14 g agar, 1 L distilled water) (Fusarium only) and grown for 3-7 days (24°C, 46% RH, 12:12 L:D) then grouped based on colony morphological characteristics. Subcultures were identified to genus based on spore morphology and ontogeny when possible. Fusarium isolates were further identified to species complex. Isolates with longer monophilids were identified as members of the *F. solani* species complex (FSSC) and isolates with short monophialids were identified as *F. oxysporum.* DNA from a subset of isolates representing each morphological group or species complex (≥ 3/group) was extracted using PrepMan Ultra (Thermo Fisher Scientific, Waltham, MA). The internal transcribed sequence (ITS) gene forward primer ITS1 (5´-TCCGTAGGTGAACCTGCGG- 3) and reverse primer ITS4 (5´-TCCGTAGGTGAACCTGCGG- 3') were amplified as described in Liu et al. (1999). TEF analysis was conducted for *Fusarium* spp. using the translation elongation factor 1-alpha (TEF) gene forward primer EF1 (5' – ATGGGTAAGGA(A/G)GACAAGAC – 3') and reverse primer EF2 (5' – GGA(G/A)GTACCAGT(G/C)ATCATGTT – 3') (O'Donnell et al. 1998). Amplified PCR products were cleaned using ExoSAP-IT (Thermo Fisher Scientific, Waltham, MA) and Sanger sequenced using the ITS4 reverse primer (Quintara Bio, Hayward, CA). Resulting sequences were identified using NCBI BLAST (https://blast.ncbi.nlm.nih.gov). Tef sequence analysis was conducted using Mycobank (https://www.mycobank.org) and the Fusarium ID library

(http://www.fusariumdb.org). The identity of *F. oxysporum* isolates as *F. oxysporum* f. sp. *lycopersici* (Fol) was evaluated using the SIX 3 gene region forward primer (5' – CCAGCCAGAAGGCCAGTTT – 3') and reverse primer (5'-GGCAATTAACCACTCTGCC-3') (Van Der Does et al., 2008).

*Fusarium oxysporum* isolates that did not have the amplified SIX3 region were not Fol, indicating identity as either non-pathogen saprophytes or *F. oxysporum* f. sp. *radicis lycopersici* (Forl). There were 23 and 43 *F. oxysporum* isolates that did not have the amplified SIX3 region in 2019 and 2020, respectively; 19 and 17 isolates from 2019 and 2020, respectively, were further evaluated for formae speciales ID in Forl phenotyping trials using cultivars with and without the FR gene that conveys resistance to Forl (Fazio et al., 1999) and the I3 gene conveying resistance to Fol race 3 (McGrath and Maltby, 1988). Because SIX3 false negatives can occur (Wang et al., 2023), we included several isolates with and without the F3 R gene to Fol race 3. For these assays, we selected N6428 (no FR but does have resistance to Fusarium wilt race 3 – F3), HM4909 (FR but no F3), and Brandywine (no FR or F3). Known isolates of both pathogens, Fol (CS3) and Forl (CS141), were used as positive controls and non-inoculated plants served as negative controls.

For each isolate, three plants were inoculated per cultivar for a total of nine plants per isolate. Cultivars were grouped together, and isolate x plant replicates were randomized within each cultivar. Seeds were surface disinfested with 70% ethanol for 10 min, 50% sodium hypochlorite for 10 min, then rinsed with sterile water. Disinfested seeds were sown in 3.8L pots filled with pre-moistened UC Mix (Davis, CA). Pots were watered to saturation and at post-emergence were placed on a drip irrigation system with a photoperiod of 12 h per day. Spore

suspensions of each isolate were made by scraping mycelium on the surface of 10 7-day old PDA plates that were flooded with approximately 5 mL 0.5% KCl. The resulting liquid was filtered through two layers of sterile cheesecloth. Suspensions were diluted to 1 x $10^5$ spores/mL by adding 700 mL 0.1% water agar. When plants were three weeks old, 50 mL of this suspension was poured onto the substrate around the base of the plant. For negative controls, 0.1% water agar without spores was used. Plants were maintained in the greenhouse at 18-32°C 12:12 L:D with standard irrigation and drip fertilizer as needed. They were monitored until symptoms were observed in plants inoculated with the positive controls at 80-90 days after inoculation. Isolates were identified as Forl if they caused stem rot in non-FR plants but not in the FR plants. Isolates were identified as Fol if they caused wilt and chlorosis in the non-F3 plants but not the F3 plants. Isolates were identified as non-pathogens of tomato if we did not observe stem rot in non-FR plants or wilt and chlorosis in non-Fol plants. The incidence of dominant pathogens was quantified by treatment across years. This was calculated by dividing the number of collected plants with each disease per treatment across years by the total number of samples collected in that treatment across years.

*2.10 Statistical Analyses*

Analyses were conducted in RStudio v. 2023.06.1+524 (Rstudio Team, 2020). To establish whether data were normal, quantile-quantile plots were created using each dataset. ANOVA (stats package) was used for parametric data and Kruskal-Wallis (stats package) for nonparametric data. Differences in all analyses were considered significant based on a *P* value of 0.05 or lower. Soil amendment and irrigation treatments were used as fixed variables and block was used as a random variable. Interaction terms were removed from models if found to

be non-significant. We analyzed soil and plant nutrients and water holding capacity using ANOVA (lme4 package; factorial ANOVA). Stem water potential was also analyzed using ANOVA (lme4 package; factorial ANOVA) keeping time points separated. To analyze the effects of deficit irrigation (DI) (Obj. 1), we compared differences between the WW and DI irrigation treatments within the grower standard soil amendment plots (synthetic fertilizer only). To analyze the effects of soil amendments on DI (Obj. 2), we evaluated differences between the Synthetic Only and Synthetic & Compost treatments only within the DI plots.

Disease treatment effects were calculated based on percentage (incidence) data derived from each block, treating block as replicate, for data collected at harvest each year. Percentage data were transformed using an arcsine square root transformation. Years were kept separate to observe change over time. Disease incidence was analyzed using ANOVA (lme4 package; factorial ANOVA). If header subplots (those closest to the irrigation header) were found to be significantly different from end subplots (those farthest from the irrigation header), they were analyzed separately. Irrigation and soil amendment treatments were considered fixed effects while block was considered random. Change in decline incidence over time was calculated as the percent change from 2019 to 2020. Area under the disease progress curve (AUDPC) was calculated for vine decline based on incidence data treating block as replicate. The effects of DI and soil amendment on yield biomass and fruit quality were assessed using fruit weight (Mg/ha) and PTAB results (hue, Brix, and pH), respectively, derived from each block, treating block as replicate, for a total of three replicates in each year.

## 3. Results

### *3.1. Diagnosis of diseases detected in field study*

We collected 26 and 55 symptomatic plants and recovered 24 and 51 isolates in 2019 and 2020, respectively (Table 3). *Fusarium oxysporum* was the predominant species diagnosed in both years, isolated from 21 and 37 samples and 88% and 95% of all Fusarium isolates in 2019 and 2020, respectively. With the *in-planta* phenotyping assays, most of this group was further delineated as *F. oxysporum* f. sp. *radicis lycopersici* (Forl, Fusarium crown and root rot), which was found in every treatment and accounted for 82% of the total diagnoses across years (Table 4). The remaining *F. oxysporum* isolates were identified as non-pathogenic. Another identified pathogen was *Fusarium noneumartii* (Fusarium stem rot and vine decline, FRD), which was only isolated from plants in the deficit irrigation treatment, accounting for 18% of the total diagnoses across years (Table 4). These were the only pathogens found and together accounted for 100% of the diagnoses based on stem lesion analyses. Fusarium wilt (*Fusarium oxysporum* f. sp. *lycopersici*), Verticillium wilt (*Verticillium dahliae*), bacterial canker (*Clavibacter michiganensis*), root knot nematode, Southern blight (*Sclerotium rolfsii*), tomato spotted wilt virus (TSWV), and Phytophthora crown and root rot (*Phytophthora capsici*) were not detected in either year.

### *3.2 Effects of deficit irrigation on plant health and fruit production under synthetic amendments*

#### *3.2.1 Disease effects of DI*

*Vine decline.* We focused on vine decline at harvest rather than at earlier time points because incidence was low until the end of the season. Across all treatments, 13-67% and 87-90% of evaluated plants developed vine decline at harvest in 2019 and 2020, respectively ($P$ = 0.0001

for year). In 2019 there was higher decline incidence at harvest in header subplots than end subplots ($P$ = 0.011), so these were analyzed separately. Although vine decline more than doubled under DI in both subplots, differences were not significant ($P$ = 0.192 and $P$ = 0.184 in 2019 and 2020, respectively) (Table 5). We did not observe more decline under DI in 2020 ($P$ = 0.648), however incidence was high in both irrigation treatments. Although we observed higher decline incidence in 2020 under both irrigation treatments and the percent change under the WW treatment was almost double that in the DI treatment (67% vs 37% in 2019 and 2020, respectively), differences were not significant ($P$ = 0.240) (Table 5). Area Under the Disease Progress Curve (AUDPC) was calculated for decline incidence in destroying plots across both irrigation treatments keeping years separate. Even though AUDPC values were higher under DI, differences were not significant in either year ($P$ = 0.214 and $P$ = 0.132 in 2019 and 2020, respectively) (Table 6).

*Any stem rot.* Although we observed stem rot symptoms at the second time point after DI onset, we focused on stem rot incidence at harvest to be consistent with the time point used for vine decline data. At harvest, stem rot developed in all treatments in 40-97% of plants ($P$ = 0.0001 for year) (Table 7). All plants with stem rot had rot below the soil line in 2019. While in 2019 we observed approximately 40% stem rot incidence in both irrigation treatments with no treatment effect ($P$ = 0.695), in 2020 approximately 50% more plants developed stem rot under DI ($P$ = 0.038) (Table 7). Between years, any stem rot increased under DI more than two times more than it increased under WW ($P$ = 0.024).

*Belowground stem rot.* Across treatments, belowground stem rot developed in all treatments in 40-93% of plants ($P$ < 0.001 for year) (Table 7). The change between years was also greater

under DI in 2020 ($P$ = 0.026). Deficit irrigation did not influence belowground rot incidence in 2019 ($P$ = 0.695), however we observed an increase under DI in 2020 ($P$ = 0.026) (Table 7). Between years, belowground rot increased under DI at more than twice the rate we observed under WW, although differences were not significant ($P$ = 0.070) (Table 7).

*Crown rot.* Crown rot incidence was evaluated only in 2020. Across treatments, 20-93% of plants developed crown rot. Incidence was higher in end subplots than in header subplots ($P$ = 0.009) thus were analyzed separately. Regardless, we observed an approximately two- and threefold increase in crown rot incidence under DI in both subplots, although differences were significant only in end subplots ($P$ = 0.043) (Table 7).

*Aboveground stem rot.* Aboveground stem rot incidence was also evaluated only in 2020. Across treatments, 0-67% of plants developed rot above the soil line. As we observed more aboveground stem rot in end subplots ($P$ = 0.046) subplots were analyzed separately. No differences between aboveground stem rot incidence were observed in header subplots (in fact we did not observe aboveground stem rot under DI at all), however we observed a five-fold increase under DI in the end subplots ($P$ = 0.007) (Table 7). Taken together, stem rot incidence (across categories) was greater under DI in the second year, with a significant cumulative effect of DI treatment across the two years.

*3.2.2 Quantification of* Fusarium *pathogens by irrigation treatment*

In the Synthetic Only treatment, *Fusarium oxysporum* f. sp. *radicis lycopersici* (Forl) was recovered from 36.4% of symptomatic plants under WW (n = 11 averaged across years) and 34.6% of symptomatic plants under DI (n = 13 averaged across years) (Table XX). *Fusarium*

*noneumartii* (Fusarium stem rot and vine decline, FRD) was recovered from 0% of symptomatic plants under WW and 11.5% of symptomatic plants under DI (Table 8).

*3.1.4 Effects of DI on fruit yield and quality*

There were 23% and 27% less total fruit yields under DI in 2019 and 2020, respectively, however differences were not significant ($P$ = 0.175 and 0.094, respectively) (Table 9). We observed less red marketable fruit under DI in 2020 ($P$ = 0.029) and more damaged fruit under DI in both years ($P$ = 0.022 and 0.050, respectively) (Table 10). No differences in green marketable fruit were observed under DI in either year ($P$ = 0.197 and 0.507, respectively). Additionally, we did not observe differences between irrigation treatments for any fruit quality response variable (Table 11).

*3.2.3 Abiotic effects of DI - plant stem water potential and soil and plant nutrient levels*

We observed lower stem water potential in the plants under DI by the third week post DI-onset ($P$ = 0.025), signifying a water stress effect of the deficit treatment in 2020 (Table 12). In terms of soil nutrients, there was more soil nitrate under WW in 2019 ($P$ < 0.0001), but no other differences were observed between the irrigation treatments (Table 13). Additionally, we did not observe an effect of DI on leaf nutrient uptake in either year (Table 14), which addresses the possibility that disease differences between the irrigation treatments were confounded by differences in nutrient levels.

*3.3 Effects of soil amendment on plant health and yield under DI*

*3.3.1 Effects of soil amendment on disease development*

*Vine decline.* Although amendment treatment did not influence vine decline incidence in 2019 ($P$ = 0.721), there was less decline under compost in 2020 ($P$ = 0.023) (Table 15). This

relationship is reflected in the percent change in decline incidence between years, which was 11 times lower in the Synthetic & Compost treatment (differences were not significant *P* = 0.124) (Table 15). In 2019, the Area Under the Disease Progress Curve (AUDPC) was higher in the Synth & Comp treatment, although differences were not significant (*P* = 0.752). Conversely, in 2020 we observed a lower AUDPC value in the Synth & Comp treatment, although differences were not significant (*P* = 0.077).

*Any stem rot.* Combining all stem rot metrics together, there were no significant differences between the two amendments, although stem rot incidence (across all categories) was typically lower in the Synthetic & Compost treatment than in the Synthetic Only treatment. While we observed almost 50% more stem rot in the Synthetic & Compost treatment vs. the Synthetic Only treatment in 2019, we observed almost 20% less stem rot in the Synthetic & Compost treatment vs. the Synthetic Only treatment in 2020, although amendment treatment differences were not significant (*P* = 0.139 and 0.162, for the Synthetic & Compost treatment and the Synthetic Only treatment, respectively) (Table 17). Overall, there was approximately a three-fold increase in stem rot incidence in the Synthetic Only (53% increase) compared with the Synthetic & Compost treatment (17% increase), although differences were not significant (*P* = 0.152) (Table 17).

*Belowground stem rot.* In 2019 we observed approximately 30% less belowground rot under Synthetic & Compost than Synthetic Only, although differences were not significant (*P* = 0.139) (Table 17). In 2020, more belowground stem rot was observed in the end subplots (*P* = 0.024) thus subplots were analyzed separately; within the header and end subplots there was no significant effect of soil amendments (*P* = 0.642 and 0.063 for header and end subplots,

respectively). While the change in belowground stem rot incidence over time was not different between amendments, there was a trend for greater increase in the Synthetic Only treatment (49%) than in the Synthetic & Compost treatment (22%) ($P$ = 0.268). There was more crown and aboveground stem rot observed in end subplots vs. header subplots ($P$ = 0.001 and 0.002 for crown and aboveground stem rot, respectively) thus subplots were analyzed separately for both analyses. Although 6-17% more crown rot was observed under the Synthetic Only treatment across subplots, differences were not significant ($P$ = 0.500 and 0.456 for header and end subplots, respectively) (Table 17). Differences in aboveground stem rot were not significant ($P$ = 0.121 and 0.606, respectively) (Table 17).

*3.3.2 Effects on* Fusarium *disease under DI by soil amendment treatment*

*Fusarium oxysporum* f. sp. *radicis lycopersici* (Forl) was recovered from 34.6% of symptomatic plants in the Synthetic Only treatment under DI (n = 13 averaged across years) and 38.5% of symptomatic plants in the Synthetic & Compost treatment under DI (n = 6.5 averaged across years) (Table 8). *Fusarium noneumartii* was recovered from 11.5% of symptomatic plants in the Synthetic Only treatment and 23.1% of symptomatic plants in the Synthetic & Compost treatment (Table 8).

*3.3.3 Effects of soil amendment on fruit yield and quality*

Although we did not observe differences between the soil amendments in terms of fruit yield ($P$ = 0.451) (Table 18), there was a trend of less total and percent red marketable fruit and greater incidence of damaged fruit in Synthetic Only than in Synthetic & Compost ($P$ = 0.451, 0.064, and 0.067, respectively) (Tables 18 and 19). Soil amendment did not influence fruit

quality of hue and pH but there was higher Brix under Synthetic & Compost vs. Synthetic Only ($P$ = 0.043) (Table 20).

*3.3.4 Effects of soil amendment on soil water holding capacity and plant stem water potential*

We did not observe an effect of soil amendment on water holding capacity under DI with a yearly average of 19.0% and 19.3% in the Synthetic Only and Synthetic & Compost treatments, respectively ($P$ = 0.492) (Table 21). Stem water potential data from 0- and 3-weeks post DI-onset were significantly different ($P$ = 0.003) and was analyzed separately. We did not observe an effect of soil amendment on stem water potential under DI at 0 weeks post DI-onset ($P$ = 0.923) or 3 weeks post DI-onset ($P$ = 0.870) (Table 22). In fact, soil VWC sensors suggest that soil volumetric water content in the compost-amended plots were dryer than the synthetic plots (Fig. 1).

*3.2.5 Effect of amendments on soil and plant nutrient status*

While we observed higher soil nutrients (nitrate, phosphorus, potassium, but not total N) in the Synthetic & Compost treatment across both years, differences were not significant (Table 23). Generally, leaf nutrients were slightly lower in the Synthetic & Compost treatment, but once again differences were not significant in either year (Table 24).

**4. Discussion and Conclusion**

*4.1 Structure of pathogen communities under study*

Overall, these studies captured the effects of deficit irrigation (DI) and soil amendment on Fusarium diseases specifically Fusarium crown and root rot (FCR) and Fusarium stem rot and vine decline (FRD). Other diseases were tested for but were not detected. As symptoms of FcR

and FRD are not distinguishable in the field, rot and decline could be due to either one or both pathogens. Fungal isolations indicate that *Fusarium oxysporum* f. sp. *radicis lycopersici* was the primary pathogen responsible for the disease symptoms under 100% ET, although incidences were similar under DI.

*4.2 Deficit irrigation influences disease development in a naturally infested field.*

We observed increased vine decline, stem rot (any stem rot, belowground stem rot, crown rot, and aboveground stem rot) along with reduced red marketable fruit under deficit irrigation (DI) in an Forl and FRD co-infected field. It is noteworthy that FRD was only detected in the DI treatment, suggesting disease enhancement of this pathogen under DI. FRD is an important emerging problem causing major economic losses in California tomato growing regions. Controlled studies are needed to better understand DI-FRD interactions, as explored further in Chapter 2. These findings are consistent with other work in experimental trials have demonstrating DI-mediated enhancement of Phytophthora crown and root rot under DI in tomato (Del Castillo et al., 2019b), Fusarium wilt in cotton (Ragazzi et al., 1995) and Fusarium ear rot in corn (Parsons et al., 2010). Given that this study took place in a naturally infested field, we had little to no control over disease presence. As we did not detect viruses or bacterial diseases such as Tomato Spotted Wilt Virus (TSWV) and Beet Curly Top Virus (BCTV) and bacterial canker, as well as other fungal diseases such as Fusarium wilt, Southern blight, and Verticillium wilt, we are unable to comment on effects of DI on these other important tomato diseases. More work needs to be done to elucidate the effects of DI on both fungal and non-fungal diseases.

There are several possibilities that may account for increased Fusarium-driven stem rot under DI. Firstly, DI reductions in soil VWC could alter the rhizosphere environment and subsequently the root microbiome. DI-mediated effects on the rhizosphere between plant defenses and pathogens could include changes in chemotaxis, root entry, and colonization by beneficials, opportunists, and pathogens (Raaijmakers et al. 2009; Berendsen et al. 2012; Rahman et al. 2021). A better understanding of the root microbial communities and the influence of deficit irrigation on their activity could elucidate whether such changes are occurring as explored further in Chapter 3. Additionally or alternatively, plant water stress could be indirectly influencing the rhizosphere microbial community by altering the volume or content of root exudates, which attract microbes to roots (Preece and Peñuelas 2016). For example, drought stress can increase cumulative total organic carbon exuded by crested wheatgrass roots compared to the unstressed control (Henry et al. 2007) and similar results were observed in corn (Somasundaram et al. 2009). We observed clear differences in stem water potential by three weeks post-DI onset, signifying greater water stress in the DI tomatoes and indicating potential for altered root exudates. As root exudate content and volume can influence the rhizosphere and pathogen germination (Ruan et al., 1995; Steinkellner et al., 2005), it is possible that water stress can influence root colonization by pathogens.

Another possibility is that irreversible alterations in plant defense caused by abiotic stress (in this case, drought stress) could be inhibiting the tomato plant ability to recognize and respond to pathogens. Known as “predisposition”, this has been shown to increase host susceptibility (Bostock et al., 2005; Bostock et al. 2014). Examples of abiotic stress increasing pathogen virulence can be found across diverse fungal and oomycete diseases in agricultural,

horticultural, and forest systems. Abiotic stresses include water stress, such as with Phytophthora root rot in safflower (Duniway, 1977), water saturation, as with Phytophthora root rot on alfalfa (Kuan and Erwin, 1980), salinity stress, as with Phytophthora root rot on chrysanthemum (MacDonald JD, 1982), drought stress, as with fungal forest diseases (Desprez-Loustau et al., 2006) and tomato (DiLeo et al. 2010), and cold stress, as with diseases of fruit and nut trees (Marek et al., 2013). Predisposition occurs due to the "crosstalk" between abscisic acid (ABA), a phytohormone upregulated as a response to these environmental stressors and salicylic acid (SA), the phytohormone responsible for systemic acquired resistance in plants (Bostock et al., 2005). In our study, which produced drought stress, it is possible that the upregulation of ABA stemmed production of SA, resulting in increased susceptibility to Fusarium-driven stem rot.

*4.3 Effect of organic amendment-deficit irrigation interactions on plant health*

We hypothesized that an organic soil amendment could buffer against enhanced disease under DI due to increased soil water holding capacity *i.e.,* retention via organic matter addition. Vine decline under DI was lower in plots amended with compost; we also observed less fruit damage (although not significantly due to low replication). Although disease mitigating effects were observed, we did not see a treatment effect on soil water holding capacity or stem water potential. Authors of a recent meta-analysis concluded that organic matter has a negligible effect on soil available water (Minasny and McBratney 2018). Future work examining the effects of organic amendments should include measurements of soil organic matter.

*4.4 Field metrics for irrigation studies.*

Interpreting results relied heavily on establishing clear differences between our irrigation treatments. Confirming treatment differences is tantamount for interpreting results in field studies as plant water stress can trigger responses such as increased root growth (to access more water), or responses such as stomatal closure and leaf curling that enable plants to decrease water use thus reducing or eliminating the stress (Bodner et al. 2015). Additionally, factors such as soil texture, porosity, and percent organic matter can influence how much moisture a soil retains and how much plants can access (Vereecken et al. 2014; Rasheed et al. 2022). In short, differences in irrigation treatments may not necessarily translate to differences in the water accessible by the plant or consequently plant water stress.

Much of the previous work studying the effects of deficit irrigation on plant disease have neglected to include metrics such as soil volumetric water content (VWC), soil matric potential, and/or stem water potential (Swett 2020). While the current study incorporated soil VWC and stem water potential measurements only in the second year, we were able to see that our irrigation applications resulted in clear differences between our 100% and 60% ET treatments for both response variables. Achieving reliable measurements, however, can be challenging. Soil is a heterogeneous medium that can change drastically over short distances, particularly in terms of soil moisture (Dobriyal et al. 2012; Zhu et al. 2012; Vereecken et al. 2014; Rasheed et al. 2022). Such variability is usually captured with large sample sizes, but tools used for metrics such as VWC, stem water potential, and soil matric potential can be cost and time prohibitive. Other tools such as remote sensing and aerial imagery may provide more efficient ways of capturing treatment efficacy and differences in the future, as explained further in Chapter 2.

*4.5 Deficit irrigation and fruit quality metrics.*

In the processing tomato industry, higher soluble solids translate to sweeter fruit while lower hues translate to redder fruit; these quality traits are valued by tomato processors. A cited benefit of DI is the resulting increase in soluble solids (Brix) and decreased hue (Zegbe-Domínguez et al. 2003; Lu et al. 2019), however we did not observe any appreciable differences in fruit quality between the irrigation treatments. Additionally, we observed significant differences in fruit quality parameters between the two years; 2020 fruit had higher Brix yet higher hue (less red color). This could be explained by season length differences between the two years – not only was the 2020 season 12 days longer, but also the plants went an additional week without irrigation at the end of the season (as evidenced by no green fruit that year). While studies by Zegbe et al (2003) and Lu et al. (2019) observed reduced yields under DI, they also observed increased Brix and the former study observed increased red fruit color (decreased hue). This tradeoff between yield and fruit quality is often reported as true among growers (*pers comm,* Gene Miyao), however we did not observe this in our own work.

*4.6 Future studies to refine water use-disease co-management*

For growers with limited water supplies and higher disease pressure from soil borne pathogens, the extent to which deficit irrigation is implemented could significantly influence water use efficiency and yield losses. In our work we reduced irrigation by 40% ET to ensure treatment differences, but many growers choose to reduce irrigation by only 20-25% ET and not always at once but gradually once fruit has started ripening (*pers comm,* Tom Turini). Irrigation at these levels could strike a balance between water savings and yield losses. Studies to evaluate disease effects at lower DI levels are needed to test this hypothesis. Moving

forward, managing the negative effects of DI on plant disease will be important for future water savings. Use of cultivars with greater disease resistance and water stress tolerance, as explained for FRD in Chapter 2, could also help manage DI-disease enhancement.

**Literature Cited**

Agbna G.H.D., Dongli S., Zhipeng L., Elshaikh N.A., Guangcheng S., Timm L.C. (2017). Effects of deficit irrigation and biochar addition on the growth, yield, and quality of tomato. Sci Hortic (Amsterdam) 222:90-101.

Baveye, P.C. (2007). Soils and runaway global warming: terra incognita. J of Soil and Water Cons 62:139A-139A.

Berendsen R.L., Pieterse C.M.J., Bakker P.A.H.M. (2012). The rhizosphere microbiome and plant health. Trends Plant Sci 17:478-486.

Bodner G., Nakhforoosh A., Kaul H. (2015). Management of crop water under drought: a review. Agron Sustain Dev 35:401-442.

Bostock R.M. (2005). Signal Crosstalk and Induced Resistance: Straddling the Line Between Cost and Benefit. Annu Rev Phytopathol 43:545-580.

Bostock R.M., Pye M.F., Roubtsova T.V. (2014). Predisposition in Plant Disease: Exploiting the Nexus in Abiotic and Biotic Stress Perception and Response. Annu Rev Phytopathol 52:517-549.

CA Department of Water Resources (2020). California Snow Water Content. Online. https://cdec.water.ca.gov/reportapp/javareports?name=PLOT_SWC. Accessed 5 Aug. 2023.

Carlson R.M., Cabrera R.I., Paul J.L., Quick J., Evans R.Y. (1990). Rapid direct determination of ammonium and nitrate in soil and plant tissue extracts. Commun Soil Sci Plant Anal 21:1519-1529

Chai Q., Gan Y., Zhao C., Xu H.L., Waskom R.M., Niu Y., Siddique K.H. (2016). Regulated deficit irrigation for crop production under drought stress. A review. Agronomy for sustainable development 36:1-21.

Davis R., Miyao G., Subbarao K., Stapleton J., Aegerter B. (2013a). Curly Top. Online. https://ipm.ucanr.edu/agriculture/tomato/curly-top/. Accessed 4 August 2023.

Davis R., Miyao G., Subbarao K., Stapleton J., Aegerter B. (2013b). Phytophthora Root Rot. Online. https://ipm.ucanr.edu/agriculture/tomato/phytophthora-root-rot/. Accessed 4, August 2023.

Del Castillo Múnera J., Belayneh B., Ristvey A., Koivunen E.E., Lea-Cox J., Swett C.L. (2019a). Enabling adaptation to water scarcity: Identifying and managing root disease risks associated with reducing irrigation inputs in greenhouse crop production – A case study in poinsettia. Agric Water Manag 226:105737.

Del Castillo Múnera J., Belayneh B., Lea-Cox J., Swett C.L. (2019b). Effects of set-point substrate moisture control on oomycete disease risk in containerized annual crops based on the tomato-*Phytophthora capsici* pathosystem. Phytopathology 109:1441-1452.

Desprez-Loustau M.L., Marçais B., Nageleisen L.M., Piou D., Vannini A. (2006). Interactive effects of drought and pathogens in forest trees. Annals of forest science 63:597-612.

DiLeo M.V., Pye M.F., Roubtsova T.V., Duniway J.M., MacDonald J.D., Rizzo D.M., Bostock R.M. (2010). Abscisic acid in salt stress predisposition to Phytophthora root and crown rot in

tomato and chrysanthemum. Phytopathology 100:871-879.

Dobriyal P., Qureshi A., Badola R., Hussain S.A. (2012). A review of the methods available for estimating soil moisture and its implications for water resource management. J Hydrol 458-459:110-117.

Duniway J.M. (1977). Predisposing effect of water stress on the severity of Phytophthora root rot in safflower. Phytopathology 67:884.

Eden M., Gerke H.H., Houot S. (2017). Organic waste recycling in agriculture and related effects on soil water retention and plant available water: a review. Agron Sustain Dev 37:1-21.

Expósito A., Berbel J. (2017). Sustainability implications of deficit irrigation in a mature water economy: A case study in southern Spain. Sustainability 9:1144.

Fazio G., Stevens M.R., Scott J.W. (1999). Identification of RAPD markers linked to Fusarium crown and root rot resistance (Frl) in tomato. Euphytica 105:205-210.

Fereres E., Soriano M.A. (2007). Deficit irrigation for reducing agricultural water use. Journal of Experimental Botany 58:47-159.

Food and Agriculture Organization (2021). Worldwide Tomato Yield Data. Online. http://www.fao.org/faostat/en/#data/QC. Accessed 4 August 2023.

Foster E.J., Del Grosso S.J., Cotrufo M.F., Ramlow M. (2019). Broadcast woody biochar provides limited benefits to deficit irrigation maize in Colorado. Agric Ecosyst Environ 269:71-81.

Głąb T., Żabiński A., Sadowska U., Gondek K., Kopeć M., Mierzwa-Hersztek M., Tabor S., Stanek-Tarkowska J.S. (2020). Fertilization effects of compost produced from maize, sewage sludge and biochar on soil water retention and chemical properties. Soil Tillage Res 197:104493.

Gregory P. (1988). Growth functioning of plant roots. In: Russell's Soil Conditions and Plant Growth, 11th edn. pp 113–167.

Henry A., Doucette W., Norton J., Bugbee B. (2007). Changes in Crested Wheatgrass Root Exudation Caused by Flood, Drought, and Nutrient Stress. J Environ Qual 36:904-912.

Hirich A., Choukr-Allah R., Jacobsen S.E. (2014). Deficit irrigation and organic compost improve growth and yield of Quinoa and Pea. J Agron Crop Sci 200:390-398.

Hofer S. (2013). Determination of Ammonia (Salicylate) in 2M KCl soil extracts by Flow Injection Analysis. QuikChem Method 12-107-06-2-A. Loveland, CO.

Hudson B.D. (1994). Soil organic matter and available water capacity. J Soil Water Conserv 49:189-194.

Itier B. (1996). Measurement and estimation of evapotranspiration. In: Sustainability of irrigated agriculture. Dordrecht: Springer Netherlands. pp 171–191.

Jones J. (2001). Laboratory Extraction of Cl, NO3, PO4, K, and SO4 from Plant Tissue. In: Guide for Conducting Soil tests and Plant Anal pp 228–229.

Kuan T.L., Erwin D.C. (1980). Predisposition effect of water saturation of soil on Phytophthora root rot of alfalfa. Phytopath 70:981-986.

Liu Y.J., Whelen S., Hall B.D. (1999). Phylogenetic relationships among ascomycetes: evidence from an RNA polymerse II subunit. Molecular biology and evolution, 16:1799-1808.

Lu J., Shao G., Cui J., Wang X., Keabetswe K. (2019). Yield, fruit quality and water use efficiency of tomato for processing under regulated deficit irrigation: A meta-analysis. Agric Water Manag 222:301-312.

MacDonald J.D. (1982). Effect of salinity stress on the development of Phytophthora root rot of

chrysanthemum. Phytopath 72:214-219.

Marek S.M., Yaghmour M.A., Bostock R.M. (2013). Fusarium spp., Cylindrocarpon spp., and environmental stress in the etiology of a canker disease of cold-stored fruit and nut tree seedlings in California. Plant Dis 97:259-270.

Maynard D., Hochmuth G. (2007). Knott's Handbook for Vegetable Growers. John Willy & Sons, Inc., Hoboken, NJ.

McGrath D.J., Maltby J.E. (1988). Fusarium wilt race 3 resistance in tomato. Research and Development Conference on Vegetables, the Market, and the Producer 247.

Minasny B., McBratney A.B. (2018). Limited effect of organic matter on soil available water capacity. Eur J Soil Sci 69:39-47.

Miyao G., Goodell P.B., Davis R.M., Hembree K.J., Natwick E.T., Ploeg A.T., Aegerter B.J., Lanini W.T., Stapleton J.J., Stoddard C.S., Subbarao K.V., Trumble J.T., Zalom F.G. Revised continuously. *UC IPM Pest Management Guidelines: Tomato*. UC ANR Publication 3470. Davis, CA.

Montanearella L., Bardraoui M., Chude V. et al. (2015) Status of the World's Soil Resources (SWSR) - Main Report. Online. http://www.kerwa.ucr.ac.cr/handle/10669/78011. Accessed 5 Aug. 2023.

Mukherjee S., Dash P.K., Das D., Das S. (2023). Growth, yield and water productivity of tomato as influenced by deficit irrigation water management. Environ Process 10.

O'Donnell K., Corby K., Cigelnik E., Ploetz R.C. (1998). Multiple evolutionary origins of the fungus causing Panama disease of banana: Concordant evidence from nuclear and mitochondrial gene genealogies. Proc Nat Acad of Sci 95.5:2044-2049.

Parsons M.W., Munkvold G.P. (2010). Associations of planting date, drought stress, and insects with Fusarium ear rot and fumonisin B1 contamination in California maize. Food Additives and Contaminants 27:591-607.

Posit team (2023). RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. URL http://www.posit.co/.

Preece C., Peñuelas J. (2016). Rhizodeposition under drought and consequences for soil communities and ecosystem resilience. Plant Soil 409:1-17.

Qin K., Leskovar D.I. (2020). Assessments of humic substances application and deficit irrigation in triploid watermelon. HortSci 55:716-721.

Raaijmakers J.M., Paulitz T.C., Steinberg C., Alabouvette C., Moénne-Loccoz Y. (2009). The rhizosphere: A playground and battlefield for soilborne pathogens and beneficial microorganisms. Plant Soil 321:341-361.

Ragazzi A., Moricca S., Dellavalle I., Mancini F. (1995). Infection of cotton by *Fusarium oxysporum* f. sp. *vasinfectum* as affected by water stress. Phytoparasitica 23:315-321.

Rahman N.S.N.A., Hamid N.W.A., Nadarajah K. (2021). Effects of abiotic stress on soil microbiome. Int J Mol Sci 22.

Rasheed M.W., Tang J., Sarwar A., Shah S., Saddique N., Usman M.U., Imran Khan M. Nawaz S., Shamshiri R.R., Aziz M., Sultan M. (2022). Soil moisture measuring techniques and factors affecting the moisture dynamics: A comprehensive review. Sustain 14:11538.

Rasool R., Kukal S.S., Hira G.S. (2008). Soil organic carbon and physical properties as affected by long-term application of FYM and inorganic fertilizers in maize–wheat system. Soil and Till Res, 101:31-36.

Rawls W.J., Pachepsky Y.A., Ritchie J.C., Sobecki T.M., Bloodworth H. (2003). Effect of soil organic carbon on soil water retention. Geoderma 116:61-76.

Ruan Y., Kotraiah V., Straney, D.C. (1995). Flavonoids stimulate spore germination in *Fusarium solani* pathogenic on legumes in a manner sensitive to inhibitors of cAMP-dependent protein kinase. MPMI-Molec Plant Microbe Inter 8:929-938.

Somasundaram S., Rao T.P., Tatsumi J., Iijima M. (2009). Rhizodeposition of mucilage, root border cells, carbon and water under combined soil physical stresses in *Zea mays* L. Plant Prod Sci 12:443-448.

Steinkellner S., Mammerler R., Vierheilig H. (2005). Microconidia germination of the tomato pathogen *Fusarium oxysporum* in the presence of root exudates. J of Plant Inter, 1:23-30.

Swett C.L. (2020). Managing crop diseases under water scarcity. Phytopathology 58:387-406.

Thomas G.W. (1982). Exchangeable cations. In: Methods of soil analysis: Part 2. Chemical and microbiological properties. ASA Monograph Number 9. pp 159–165.

USDA NASS (2021). Quick Stats. Tomatoes, in the Open, Processing - Production, Measured in Tons. Online. https://quickstats.nass.usda.gov Accessed 4 August 2023.

van Der Does H.C., Lievens B., Claes L., Houterman P.M., Cornelissen B.J., Rep M. (2008). The presence of a virulence locus discriminates *Fusarium oxysporum* isolates causing tomato wilt from other isolates. Environ. Micro. 10:1475-1485.

Vereecken H., Huisman J.A., Pachepsky Y., Montzka C., Van Der Kruk J., Bogena H., Weihermüller L., Herbst M., Martinez G., Vanderborght J. (2014). On the spatio-temporal dynamics of soil moisture at the field scale. J Hydrol 516:76-96.

Wang C., Zheng Y., Liu Z., Qian Y., Li Y., Yang L., Liu S., Liang W., Li J. (2023). The secreted FolAsp

aspartic protease facilitates the virulence of *Fusarium oxysporum* f. sp. *lycopersici*. Front Microbiol 14:1103418.

Wang D., Li C., Parikh S.J., Scow K.M. (2019). Impact of biochar on water retention of two agricultural soils – A multi-scale analysis. Geoderma 340:185-191.

Williams A.P., Cook B.I., Smerdon J.E. (2022). Rapid intensification of the emerging southwestern North American megadrought in 2020–2021. Nat Clim Chang 12:232-234.

Zegbe-Domínguez J.A., Behboudian M.H., Lang A., Clothier B.E. (2003). Deficit irrigation and partial rootzone drying maintain fruit dry mass and enhance fruit quality in “Petopride” processing tomato (*Lycopersicon esculentum*, Mill.). Sci Hortic (Amsterdam) 98:505-510.

Zhou, L.M., Li F.M., Jin S.L., Song Y. (2009). How two ridges and the furrow mulched with plastic film affect soil water, soil temperature and yield of maize on the semiarid Loess Plateau of China. Field Crops Res. 113:41-47.

Zhu Q., Liao K., Xu Y., Yang G., Wu S., Zhou S. (2012). Monitoring and prediction of soil moisture spatial-temporal variations from a hydropedological perspective: A review. Soil Res 50:625-637.

**Figures**

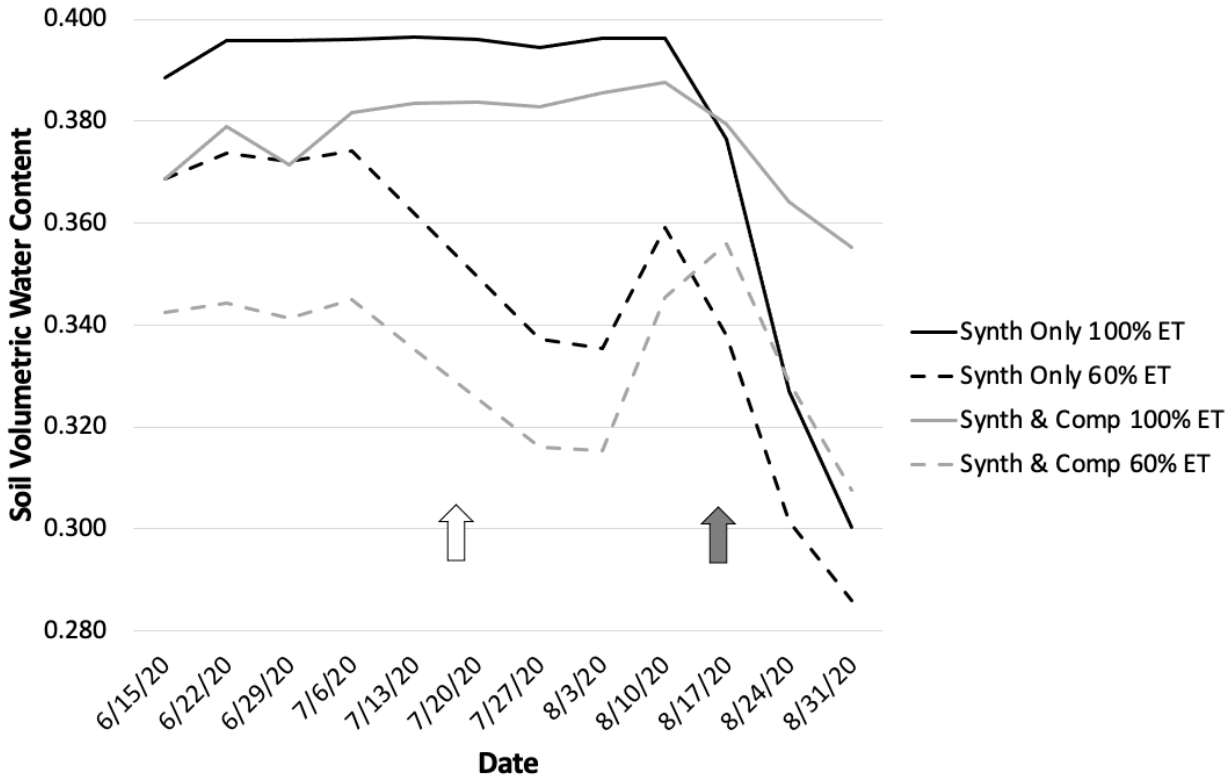



**Figure 1.** Volumetric water content (VWC) of soil in the four treatments at 30 cm deep. Sensors measured soil moisture in 15-minute increments between Jun 16 and Aug 31 of 2020. The white arrow indicates when the deficit irrigation treatment began (7/13/20); the gray arrow shows when irrigation was stopped completely for all treatments (8/14/20).

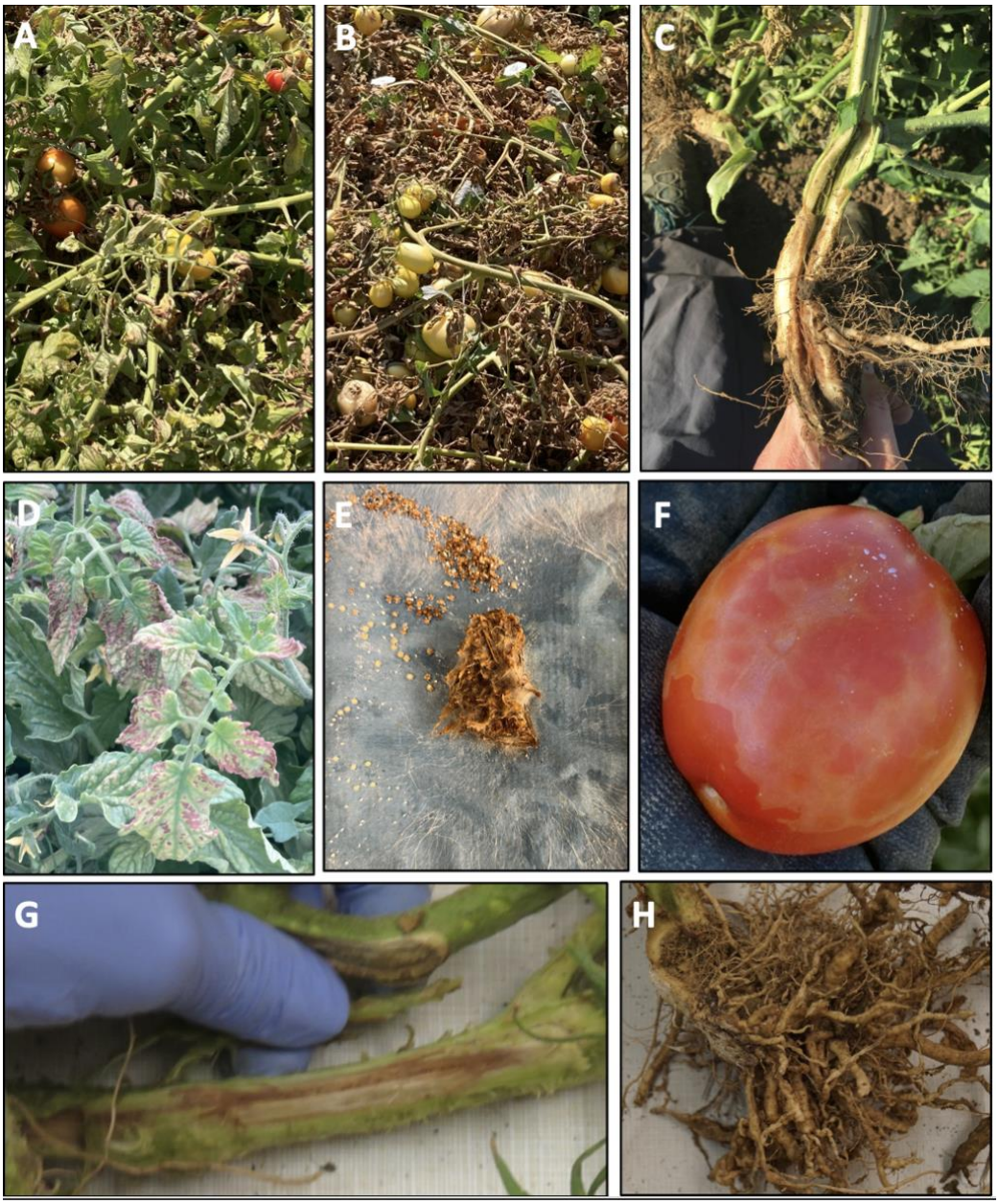



**Figure 2.** Common disease symptoms and signs of processing tomatoes in California. Early vine decline (A), advanced vine decline (B), stem rot (C), leaf speckling (D), mycelia and/or sclerotia on stems (E), chlorotic fruit spots (F), stem streaking (G), and root galls (H).

**Tables**

**Table 1.** Field trial dates in 2019 and 2020.

| Activity | 2019 | 2020 |
|---|---|---|
| Soil samples collected | Mid-April | Mid-April |
| Transplant | 29-Apr | 22-Apr |
| Leaves collected for nutrient analyses | Early June | Early June |
| Soil collected for nutrient analyses | 2-Jul | 29-Jun |
| DI starts | 24-Jul | 13-Jul |
| Stem water potential measurement | NA | 14-Jul |
| Disease rating 1 (T0) | 24-Jul | 10-Jul |
| Disease rating 2 | 14-Aug | 31-Jul |
| Stem water potential measurement | NA | 3-Aug |
| Cut water | 16-Aug | 14-Aug |
| Total days under DI | 23 | 32 |
| Disease rating 3 | 26-Aug | 24-Aug |
| Harvest | 9-Sep | 14-Sep |
| Total days w/out water | 24 | 31 |
| Season length | 133 | 145 |

**Table 2**. Composition of the two soil amendment treatments.

| Treatment | Compost (Mg/ha) | Synthetic fertilizer (Mg N/ha) |
|---|---|---|
| "Synthetic only" | - | 404 |
| "Synthetic & Compost" | Poultry manure (4.5)[a] | 404 |

[a] The compost amendment was applied in the fall prior to transplanting.

**Table 3.** Number of symptomatic plants with root/stem rot diagnosed in each treatment in 2019 and 2020.

| | 2019 | | 2020 | |
|---|---|---|---|---|
| Treatment | Plants | Isolates | Plants | Isolates |
| Synthetic Only – 100% ET | 11 | 9 | 11 | 8 |
| Synthetic & Compost – 100% ET | 4 | 3 | 16 | 15 |
| Synthetic Only – 60% ET | 11 | 12 | 15 | 14 |
| Synthetic & Compost – 60% ET | 0 | NA | 13 | 14 |
| Totals | 26 | 24 | 55 | 51 |

**Table 4.** Number of samples diagnosed with each disease evaluated in 2019 and 2020. Diseases detected in plants with different symptom categories.

| | | | | # of samples diagnosed | |
|---|---|---|---|---|---|
| Disease tested[a] | Tested with[b] | Stem rot | Vine decline | 2019 (n = 26) | 2020 (n = 51) |
| TSWV | Fruit symptom and immunostrip | No | No | 0 | 0 |
| Southern Blight | Incubation of stem tissue | No | No | 0 | 0 |
| Verticillium wilt | Isolation on PDA, ITS seq ID if detected | No | No | 0 | 0 |
| Forl | Isolation on FSM, TEF seq ID if detected, phenotyping | Yes | Yes | 12 | 15 |
| FRD | Isolation on FSM, TEF seq ID if detected | Yes | Yes | 3 | 3 |
| Fol | Isolation on FSM, SIX ID | No | No | 0 | 0 |
| Bacterial canker | Immunostrip | No | No | 0 | 0 |
| RKN | Examination of roots | No | No | 0 | 0 |

[a] TSWV = Tomato spotted wilt virus; Forl = Fusarium crown and root rot (*Fusarium oxysporum* f. sp. *radicis-lycopersici*); FRD = Fusarium stem rot and vine decline (*Fusarium noneumartii*); Fol = Fusarium wilt (*Fusarium oxysporum* f. sp. *lycopersici*); RKN = Root knot nematode

[b] PDA = Potato dextrose agar; FSM = Fusarium selective media; ITS = internal transcribed spacer; TEF = Translation elongation factor; SIX = Secreted in xylem.

**Table 5.** Vine decline incidence at harvest in the Synthetic Only plots comparing the two irrigation treatments in 2019 and 2020 and the change between years.

| Year | Subplot[a] | Irrig (% ET) | Vine decline incidence (% plants)[bcd] | *P* value Irrig |
|---|---|---|---|---|
| 2019 | Header | 100% | 33 ± 10 a | 0.192 |
| | | 60% | 67 ± 20 a | |
| | End | 100% | 13 ± 10 a | 0.184 |
| | | 60% | 33 ± 10 a | |
| 2020 | Combined | 100% | 90 ± 10 a | 0.648 |
| | | 60% | 87 ± 10 a | |
| Change between years[e] | Combined | 100% | +67 ± 20 a | 0.240 |
| | | 60% | +37 ± 20 a | |

[a] Sublots (Header = "destroying" subplot closest to the beginning of the row, End = "destroying" plot farthest from the beginning of the row) were analyzed separately if significantly different. If not, subplots were analyzed together ("Combined").

[b] Incidence values reported here were quantified as the percent of plants with decline symptoms in "destroying" subplots at harvest each year.

[c] Plants were said to have vine decline when all branches were symptomatic (turgor loss and/or necrotic leaves).

[d] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[e] Change between years was calculated as the difference between incidence each year.

**Table 6.** Vine decline Area Under the Disease Progress Curve (AUDPC) in the Synthetic Only plots comparing the two irrigation treatments in 2019 and 2020.

| Year | Irrig (% ET) | Vine decline AUDPC[abc] | *P* value Irrig |
|---|---|---|---|
| 2019 | 100% | 0.47 ± 0.27 a | 0.214 |
| | 60% | 1.33 ± 0.62 a | |
| 2020 | 100% | 0.55 ± 0.49 a | 0.132 |
| | 60% | 1.53 ± 0.32 a | |

[a] AUDPC curves were calculated using incidence data from destroying subplots collected at three time points between DI onset and harvest.

[b] Plants were said to have vine decline when all branches were symptomatic (turgor loss and/or necrotic leaves).

[c] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

**Table 7.** Stem rot (any stem rot, belowground stem rot, crown rot, and aboveground stem rot) incidence as the percentage of symptomatic plants at harvest in Synthetic Only plots comparing the two irrigation treatments in 2019 and 2020[a].

| Symptom | Year | Plot | Irrig (% ET) | Rot (%)[b] | *P* value Irrig |
|---|---|---|---|---|---|
| Any stem rot | 2019 | Combined | 100%<br>60% | 40 ± 5 a<br>43 ± 6 a | 0.695 |
| | 2020 | Combined | 100%<br>60% | 63 ± 12 a<br>97 ± 3 b | 0.038 |
| | Change between years | Combined | 100% ET<br>60% ET | +23 ± 12 a<br>+53 ± 7 b | 0.024 |
| Belowground stem rot | 2019 | Combined | 100% ET<br>60% ET | 40 ± 10 a<br>43 ± 10 a | 0.695 |
| | 2020 | Combined | 100% ET<br>60% ET | 60 ± 10 b<br>93 ± 10 a | 0.026 |
| | Change between years[c] | Combined | 100% ET<br>60% ET | +20 ± 10 a<br>+49 ± 10 a | 0.070 |
| Crown rot[c] | 2020 | Header | 100% ET<br>60% ET | 20 ± 0 a<br>45 ± 27 a | 0.121 |
| | | End | 100% ET<br>60% ET | 33 ± 7 a<br>93 ± 7 b | 0.043 |
| Aboveground stem rot | 2020 | Header[c] | 100% ET<br>60% ET | 13 ± 7 a<br>0 ± 0 a | 0.114 |
| | | End | 100% ET<br>60% ET | 13 ± 13 a<br>67 ± 18 b | 0.007 |

[a] Stem rot incidence was quantified as the percent of five randomly selected plants per treatment with stem rot.

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[c] Analyzed with Kruskal-Wallis for nonparametric data using RStudio v. 2023.06.1+524.

**Table 8.** Incidence of dominant pathogens Fusarium crown and root rot (Forl) and Fusarium stem rot and vine decline (FRD) by soil amendment and irrigation treatment averaged across years[abc].

| Amendment | Irrigation | No. of Samples[d] | Forl (%)[d] | FRD (%)[d] |
|---|---|---|---|---|
| Synthetic Only | 100% ET | 11.0 ± 0.0 | 36.4 ± 1.0 | 0.0 ± 0.0 |
| | 60% ET | 13.0 ± 2.0 | 34.6 ± 0.5 | 11.5 ± 1.5 |
| Synthetic & Compost | 100% ET | 10.0 ± 6.0 | 25.0 ± 0.5 | 0.0 ± 0.0 |
| | 60% ET | 6.5 ± 6.5 | 38.5 ± 2.5 | 23.1 ± 1.5 |
| Combined | 100% ET | 21.0 ± 6.0 | 31.0 | 0.0 |
| | 60% ET | 19.5 ± 8.5 | 35.9 | 15.4 |
| Synthetic Only | Combined | 24.0 ± 2.0 | 35.4 | 6.3 |
| Synthetic & Compost | Combined | 16.5 ± 12.5 | 30.3 | 9.1 |
| All treatments combined | | 40.5 | 33.3 | 7.4 |

[a] Incidence was calculated by dividing the number of plants with each disease by the total number of samples collected in each treatment.

[b] Symptoms included root/stem rot and often vine decline; fungi were isolated from stem rot margins.

[c] Pathogens were identified to species based on *in planta* phenotyping assays (Forl) and TEF sequence analysis (FRD).

[d] Averaged across years. The ± is the standard error of the mean.

**Table 9.** Average total yields in the Synthetic Only plots comparing the two irrigation treatments 2019 and 2020[ab].

| Year | Irrig (% ET) | Avg. Total Yield (Mg/ha)[c] | *P* value |
|---|---|---|---|
| 2019 | 100% | 226.6 ± 19.9 a | 0.175 |
| | 60% | 173.7 ± 16.2 a | |
| 2020 | 100% | 133.5 ± 11.2 a | 0.094 |
| | 60% | 97.6 ± 10.7 a | |

[a] Fruit from five plants in both "destroying" subplots under DI was harvested to calculate the average total yield.

[b] Variables were analyzed using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524.

[c] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

**Table 10.** Red marketable, green, and damaged fruit yields as percentages of total fruit yield in the Synthetic Only plots comparing the two irrigation treatments 2019 and 2020[a].

| Category | Year | Irrig | % of Total[b] | *P* value |
|---|---|---|---|---|
| Red Marketable | 2019 | 100% ET | 84.70 ± 2.17 a | 0.125 |
| | | 60% ET | 77.61 ± 1.71 a | |
| | 2020 | 100% ET | 86.50 ± 2.64 a | 0.029 |
| | | 60% ET | 69.00 ± 2.19 b | |
| Green Marketable | 2019 | 100% ET | 7.79 ± 1.51 a | 0.197 |
| | | 60% ET | 4.14 ± 1.29 a | |
| | 2020[c] | 100% ET | 1.02 ± 1.02 a | 0.507 |
| | | 60% ET | 0.39 ± 0.10 a | |
| Damaged | 2019 | 100% ET | 7.52 ± 0.66 b | 0.022 |
| | | 60% ET | 18.25 ± 1.65 a | |
| | 2020 | 100% ET | 12.49 ± 0.04 b | 0.050 |
| | | 60% ET | 30.61 ± 0.02 a | |

[a] Fruit from five plants in both "destroying" subplots under DI was harvested and sorted into three categories: Red marketable (red/pink fruit), green (all green), and damaged (red/pink fruit with any rot including blossom end rot and sunburn).

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[c] Variables were analyzed using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524.

**Table 11.** Hue, soluble solids (Brix), and pH of fruit harvested from Synthetic Only plots comparing the two irrigation treatments in 2019 and 2020[a].

| Category | Year | Irrig (% ET) | Average[b] | *P* value Irrig |
|---|---|---|---|---|
| Hue (degrees)[c] | 2019 | 100% | 21.67 ± 0.33 a | 0.099 |
| | | 60% | 22.33 ± 0.17 a | |
| | 2020 | 100% | 23.33 ± 0.44 a | 0.121 |
| | | 60% | 22.50 ± 0.00 a | |
| Brix (degrees)[c] | 2019 | 100% | 4.53 ± 0.12 a | 0.637 |
| | | 60% | 4.63 ± 0.03 a | |
| | 2020 | 100% | 5.00 ± 0.10 a | 0.609 |
| | | 60% | 5.07 ± 0.07 a | |
| pH | 2019[c] | 100% | 4.45 ± 0.04 a | 0.268 |
| | | 60% | 4.50 ± 0.10 a | |
| | 2020 | 100% | 4.34 ± 0.02 a | 0.073 |
| | | 60% | 4.44 ± 0.02 a | |

[a] Approximately 0.5 kg of harvested fruit that had been categorized as "red marketable" per Irrigation x Synthetic fertilizer treatment was taken to the Processing Tomato Advisory Board (PTAB) (Davis, CA) for analysis.

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[c] Variables were analyzed using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524.

**Table 12.** Stem water potential measurements across both soil amendments comparing the two irrigation treatments at 0- and 3-weeks post DI onset in 2020.

| Weeks post DI-onset[a] | Irrig (% ET) | Stem water potential $\psi_w$ (bar)[bcd] | *P* value *Irrig* |
|---|---|---|---|
| 0 | 100% ET | -5.9 ± 0.3 a | 0.878 |
| | 60% ET | -6.0 ± 0.5 a | |
| 3 | 100% ET | -7.1 ± 0.3 a | 0.025 |
| | 60% ET | -8.2 ± 0.4 b | |

[a] Sample sizes were as follows: 0 weeks post DI-onset: n = 38-45, 3 weeks post DI-onset: n = 22

[b] Midday stem water potential was measured using a pressure bomb (Model 615, PMS Instrument Co., Albany, OR).

[c] Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[d] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524.

**Table 13.** Soil nutrients (Nitrate, Phosphorus, Potassium, and Total N) measured pre-season across both soil amendments and irrigation treatments in 2019 and 2020.

| | | | | *P* values[ab] | |
|---|---|---|---|---|---|
| Year | Irrig (% ET) | Soil Amend | Nitrate[cd] | Irrig | Soil Amend |
| 2019 | 100% | Synth Only | 8.67 ± 0.7 a | < 0.0001 | 0.612 |
| | | Synth & Comp | 8.00 ± 0.6 a | | |
| | 60% | Synth Only | 5.00 ± 1.0 b | | |
| | | Synth & Comp | 6.00 ± 0.6 b | | |
| 2020 | 100% | Synth Only | 46.40 ± 2.9 a | 0.300 | 0.989 |
| | | Synth & Comp | 38.30 ± 14.8 a | | |
| | 60% | Synth Only | 28.07 ± 10.3 a | | |
| | | Synth & Comp | 35.90 ± 4.5 a | | |
| Year | Irrig (% ET) | Soil Amend | Phosphorus | Irrig | Soil Amend |
| 2019 | 100% | Synth Only | 5.00 ± 1.5 a | 0.268 | 0.153 |
| | | Synth & Comp | 7.33 ± 0.9 a | | |
| | 60% | Synth Only | 3.50 ± 1.5 a | | |
| | | Synth & Comp | 5.33 ± 1.5 a | | |
| 2020 | 100% | Synth Only | 14.33 ± 1.2 a | 0.398 | 0.746 |
| | | Synth & Comp | 12.00 ± 2.5 a | | |
| | 60% | Synth Only | 8.33 ± 5.0 a | | |
| | | Synth & Comp | 12.67 ± 0.9 a | | |
| Year | Irrig (% ET) | Soil Amend | Potassium | Irrig | Soil Amend |
| 2019 | 100% | Synth Only | 9.67 ± 2.2 a | 0.067 | 0.695 |
| | | Synth & Comp | 8.33 ± 1.2 a | | |
| | 60% | Synth Only | 2.00 ± 1.0 a | | |
| | | Synth & Comp | 6.57 ± 2.7 a | | |
| 2020 | 100% | Synth Only | 15.67 ± 1.5 a | 0.369 | 0.369 |
| | | Synth & Comp | 20.00 ± 0.6 a | | |
| | 60% | Synth Only | 14.67 ± 1.5 a | | |
| | | Synth & Comp | 15.67 ± 5.4 a | | |
| Year | Irrig (% ET) | Soil Amend | Total N | Irrig | Soil Amend |
| 2019 | 100% | Synth Only | NA | NA | NA |
| | | Synth & Comp | NA | | |
| | 60% | Synth Only | NA | | |
| | | Synth & Comp | NA | | |
| 2020 | 100% | Synth Only | 8.13 ± 0.7 a | 0.782 | 0.466 |
| | | Synth & Comp | 7.47 ± 4.1 a | | |

| | | |
|---|---|---|
| 60% | Synth Only | 8.87 ± 4.3 a |
| | Synth & Comp | 5.07 ± 0.5 a |

[a] Based on a significant difference of $P = 0.05$.

[b] There was an interaction between Irrigation and Soil Amendment for nitrate in 2019 ($P = 0.024$)

[c] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[d] Soil columns were collected in July using a 1.5-in. auger to collect 3 cores per row, which were composited into one sample.

**Table 14.** Leaf nutrient (NPK) uptake across soil amendments comparing the two irrigation treatments at early flowering in 2019 and 2020[a].

| | Leaf N (%) | | Leaf P (%) | | Leaf K (%) | |
|---|---|---|---|---|---|---|
| Irrig | 2019 | 2020 | 2019 | 2020 | 2019 | 2020 |
| 100% ET | 2.51 ± 0.22 a | 3.78 ± 0.25 a | 0.23 ± 0.01 a | 0.36 ± 0.03 a | 0.83 ± 0.14 a | 2.10 ± 0.24 a |
| 60% ET | 2.56 ± 0.18 a | 3.57 ± 0.29 a | 0.22 ± 0.01 a | 0.39 ± 0.02 a | 0.81 ± 0.15 a | 1.94 ± 0.21 a |
| *P* value Irrig | 0.860 | 0.577 | 0.384 | 0.362 | 0.928 | 0.614 |

[a] Composite sample numbers n = 10 (2019), n = 18 (2020).

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

**Table 15.** Vine decline incidence at harvest under DI comparing the two soil amendments in 2019 and 2020 and the change between years.

| Year | Amendment | Vine decline incidence (% plants)[abc] | *P* value |
|---|---|---|---|
| 2019[d] | Synth Only | 50 ± 18 a | 0.721 |
| | Synth & Comp | 60 ± 10 a | |
| 2020[d] | Synth Only | 87 ± 14 b | 0.023 |
| | Synth & Comp | 63 ± 15 a | |
| Change between years[e] | Synth Only | +37 ± 22 a | 0.124 |
| | Synth & Comp | +3 ± 21 a | |

[a] Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[b] Plants were said to have vine decline when all branches were symptomatic (turgor loss and/or necrotic leaves).

[c] Incidence values reported here were quantified as the percent of plants with decline symptoms in "destroying" plots at harvest each year.

[d] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524.

[e] Variables were analyzed using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524.

**Table 16.** Area Under the Disease Progress Curve (AUDPC) based on vine decline under DI comparing the two soil amendments in 2019 and 2020 and the change between years.

| Year | Amendment | Vine decline AUDPC[abc] | *P* value Amendment |
|---|---|---|---|
| 2019 | Synth Only | 1.33 ± 0.62 a | 0.752 |
| | Synth & Comp | 1.57 ± 0.42 a | |
| 2020 | Synth Only | 1.53 ± 0.32 a | 0.077 |
| | Synth & Comp | 0.77 ± 0.20 a | |

[a] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[b] Plants were said to have vine decline when all branches were symptomatic (turgor loss and/or necrotic leaves).

[c] AUDPC curves were calculated using incidence data from destroying subplots collected at three time points between DI onset and harvest.

**Table 17.** Stem rot incidence at harvest under DI comparing the two soil amendments in 2019 and 2020 and the change between years.

| Symptom | Year | Subplots | Amendment | Incidence (% of Plants)[ab] | *P* value Amend |
|---|---|---|---|---|---|
| Any stem rot[c] | 2019 | Combined | Synth Only | 43 ± 10 a | 0.139 |
| | | | Synth & Comp | 63 ± 10 a | |
| | 2020 | Combined | Synth Only | 97 ± 3 a | 0.162 |
| | | | Synth & Comp | 80 ± 10 a | |
| | Change between years | Combined | Synth Only | +53 ± 10 | 0.152 |
| | | | Synth & Comp | +17 ± 20 | |
| Belowground stem rot[c] | 2019 | Combined | Synth Only | 63 ± 10 a | 0.139 |
| | | | Synth & Comp | 43 ± 20 a | |
| | 2020 | Header | Synth Only | 85 ± 10 a | 0.642 |
| | | | Synth & Comp | 70 ± 20 a | |
| | | End | Synth Only | 100 ± 0 a | 1.000 |
| | | | Synth & Comp | 100 ± 0 a | |
| | Change between years | Combined | Synth Only | +49 ± 10 a | 0.268 |
| | | | Synth & Comp | +22 ± 30 a | |
| Crown rot[d] | 2020 | Header | Synth Only | 45 ± 20 a | 0.500 |
| | | | Synth & Comp | 28 ± 10 a | |
| | | End | Synth Only | 93 ± 10 a | 0.456 |
| | | | Synth & Comp | 87 ± 10 a | |
| Aboveground stem rot[c] | 2020 | Header[c] | Synth Only | 0 ± 0 a | 0.121 |
| | | | Synth & Comp | 15 ± 10 a | |
| | | End | Synth Only | 67 ± 20 a | 0.606 |
| | | | Synth & Comp | 58 ± 10 a | |

[a] Stem rot incidence was quantified as the percent of five randomly selected plants at harvest with stem rot.

[b] Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[c] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524.

[d] Variables were analyzed using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524.

**Table 18.** Total fruit yield under DI comparing the two soil amendments in 2020.

| Amendment | Total (Mg/ha) | *P* value Amend |
|---|---|---|
| Synthetic Only | 98.49 ± 10.7 a | 0.451 |
| Synthetic & Compost | 110.83 ± 7.9 a | |

**Table 19.** Red marketable, green, and damaged fruit biomass as percentages of total fruit yield under DI comparing the two soil amendments in 2020.

| Category | Amendment | Total % of Yield[ab] | *P* value Amend |
|---|---|---|---|
| Red Marketable[c] | Synthetic Only | 69 ± 2 a | 0.064 |
| | Synthetic & Compost | 78 ± 1 a | |
| Green[d] | Synthetic Only | 0 ± 0 a | 0.513 |
| | Synthetic & Compost | 0 ± 0 a | |
| Damaged[d] | Synthetic Only | 31 ± 2 a | 0.067 |
| | Synthetic & Compost | 21 ± 1 a | |

[a] Fruit from five plants in both "destroying" subplots under DI was harvested and sorted into three categories: Red marketable (red/pink fruit), green (all green), and damaged (red/pink fruit with any rot including blossom end rot and sunburn).

[b] Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[c] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524.

[d] Variables were analyzed using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524.

**Table 20.** Hue, soluble solids (Brix), and pH of fruit under DI harvested in 2019 and 2020.

| Category | Soil Amend | mean | *P* value Soil Amend |
|---|---|---|---|
| Hue | Synth | 22.5 ± 0.0 a | 0.487 |
| | Comp | 22.3 ± 0.6 a | |
| Brix | Synth | 5.07 ± 0.1 a | 0.043 |
| | Comp | 5.37 ± 0.1 b | |
| pH | Synth | 4.44 ± 0.0 a | 0.246 |
| | Comp | 4.38 ± 0.0 a | |

[z] Based on least square means significant difference *P* = 0.05.

[y] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[x] Approximately 0.5 kg of harvested fruit that had been categorized as "red marketable" per Soil Amendment x DI treatment was taken to the Processing Tomato Advisory Board (PTAB) (Davis, CA) for analysis.

**Table 21.** Soil water holding capacity under DI comparing the two soil amendments in 2019 and 2020 and years combined[a].

| Year | Soil Amend | Water holding capacity (%)[b] | *P* value Soil Amend |
|---|---|---|---|
| 2019 | Synth Only | 19.6 ± 0.6 a | 0.755 |
| | Synth & Comp | 19.4 ± 0.2 a | |
| 2020 | Synth Only | 19.2 ± 0.7 a | 0.160 |
| | Synth & Comp | 18.6 ± 0.9 a | |
| Years Comb. | Synth Only | 19.3 ± 0.4 a | 0.492 |
| | Synth & Comp | 19.0 ± 0.4 a | |

[a] Intact soil cores were collected to 30 cm (3 per row) in July of each year, and water retention was measured on intact cores at -33 and -1500 kPa on a pressure plate apparatus.

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

**Table 22.** Stem water potential measurements at 0- and 3-weeks post DI onset in 2020.

| Weeks post DI-onset[a] | Amendment | Stem water potential ψw (bar)[bc] | *P* value Soil Amend |
|---|---|---|---|
| 0[d] | Synth Only | -6.59 ± 0.44 a | 0.923 |
| | Synth & Comp | -5.59 ± 0.74 a | |
| 3[e] | Synth Only | -8.17 ± 0.41 a | 0.870 |
| | Synth & Comp | -8.30 ± 0.73 a | |

[a] Weeks were significantly different ($P = 0.003$). Sample sizes were as follows: 0 weeks post DI-onset: n = 16-22, 3 weeks post DI-onset: n = 10-12

[b] Midday stem water potential was measured using a pressure bomb (Model 615, PMS Instrument Co., Albany, OR).

[c] Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[d] Variables were analyzed using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524.

[e] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524.

**Table 23.** Soil nutrients (Nitrate, Phosphorus, Potassium, and Total N) under DI comparing the two soil amendments measured in July 2019 and June 2020[a].

| | Nitrate | | Phosphorus | | Potassium | | Total N |
|---|---|---|---|---|---|---|---|
| Soil Amend | 2019[b] | 2020[c] | 2019[c] | 2020[c] | 2019 | 2020 | 2020[c] |
| Synth Only | 5.0 ± 1.0 a | 28.1 ± 10.3 a | 26.0 ± 3.0 a | 37.0 ± 11.2 a | 115.5 ± 6.5 a | 169.0 ± 11.6 a | 8.9 ± 4.3 a |
| Synth & Comp | 6.0 ± 0.6 a | 35.9 ± 4.5 a | 29.0 ± 1.7 a | 40.3 ± 2.6 a | 127.3 ± 8.1 a | 182.3 ± 29.2 a | 5.1 ± 0.5 a |
| *P* value Soil Amend | 0.215 | 0.318 | 0.374 | 0.318 | 0.491 | 0.713 | 1.000 |

[a] Soil columns were collected in July using a 1.5-in. auger to collect 3 cores per row, which were composited into one sample n = 3 except for Synth Only treatment in 2019 (n = 2).

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[c] Variables were analyzed using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

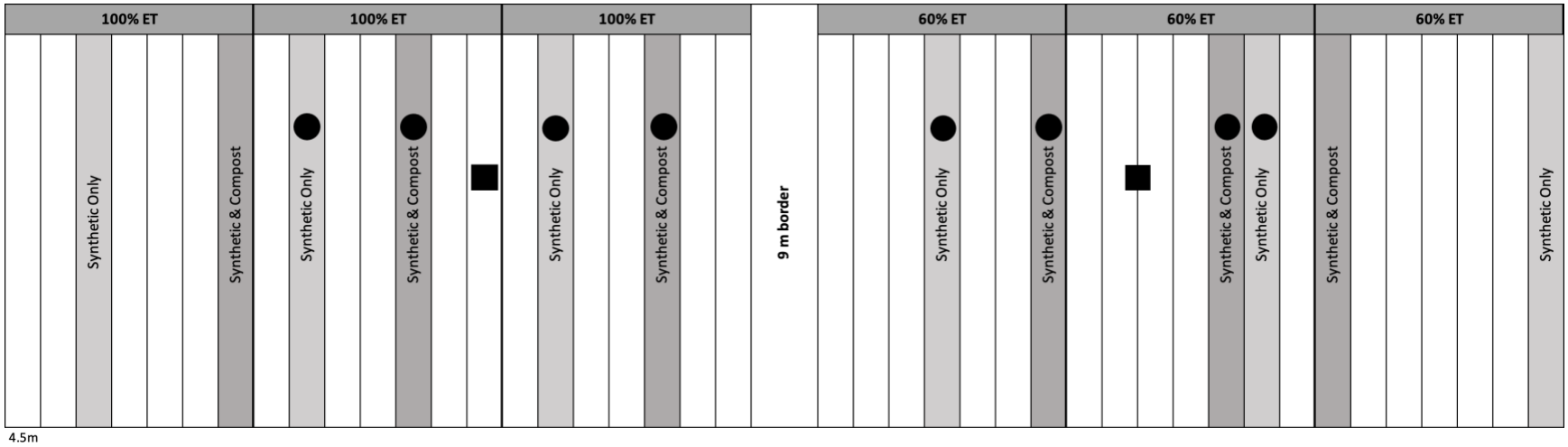
**Table 24.** Leaf nutrient (NPK) uptake under DI comparing the two soil amendments at early flowering in 2019 and 2020[a].

| | Nitrogen | | Phosphorus | | Potassium | |
|---|---|---|---|---|---|---|
| Soil Amend | 2019[b] | 2020[c] | 2019[c] | 2020[c] | 2019[c] | 2020[c] |
| Synth Only | 2.61 ± 0.2 a | 3.60 ± 0.4 a | 0.20 ± 0.0 a | 0.39 ± 0.0 a | 0.74 ± 0.2 a | 2.06 ± 0.3 a |
| Synth & Comp | 2.51 ± 0.3 a | 3.53 ± 0.4 a | 0.23 ± 0.0 a | 0.39 ± 0.0 a | 0.89 ± 0.2 a | 1.82 ± 0.3 a |
| *P* value Soil Amend | 0.802 | 0.659 | 0.173 | 0.965 | 0.346 | 0.31 |

[a] Thirty leaves were collected per treatment row.

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.

[c] Variables were analyzed using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524. Values in a column followed by the same letter are not significantly different ($P < 0.05$). The ± is the standard error of the mean.




**Supplemental Figure 1.** Field map representing the locations of irrigation and soil amendment treatments. The field was divided into two halves with one side corresponding to the 100% ET treatment and the other to 60% ET. An RCBD with three blocks made up of two soil amendment treatments per block was set up in each half field. Each soil amendment treatment was made up of three rows. Circles represent locations of soil volumetric water content sensors. Squares represent the locations of the soil volumetric water content data loggers.

## Ch. 2 Fusarium stem rot and vine decline management under water stress

### 1. Introduction

Processing tomatoes are grown for producing paste, sauces, juices, and soups. They are the second most consumed vegetable in the United States, second only to potatoes (USDA Economic Research Service, 2019). In 2020, California grew approximately 99% of the U.S. supply of processing tomatoes and 11% of the world supply (Anonymous, 2021), with 95,000 ha planted, producing 11.3 million tons (USDA NASS, 2021). In California, processing tomatoes are planted between February and June, and harvested between June and October. Nearly all tomato farms are irrigated using drip lines buried 8-18" below the soil line; some farms continue to use furrow irrigation, but productivity is demonstrably higher using drip (Mukherjee et al., 2023). The amount of irrigation water applied is often determined based on crop water use or crop evapotranspiration (ET) requirements (Miyao et al., n.d.) which is a measure of the amount of water lost to the atmosphere by transpiration from the plant and evaporation from surrounding soil (Itier, 1996).

Approximately one-third of production occurs in Fresno County alone, where growers rely on surface water allocated to them by water districts. California receives very little summer rain, so summer crops like processing tomatoes are irrigated with stored surface water released from snowpack over the summer. Reliance on surface water allocations is not uncommon south of the California Delta region and allocations have been as low as 0% within the last decade (Bureau of Reclamation, 2020), resulting in less available land for food production. Dwindling water allocations are motivating growers to reduce irrigation inputs across the state. One way to do this is called "deficit irrigation" (DI) which generally consists of

reducing irrigation to the point where it no longer meets the optimum (100%) evapotranspiration (ET) requirements of the crop. Not all crops are amenable to DI, but the practice works well for processing tomatoes. Irrigation is usually reduced to approximately 80% ET around 60 days preharvest; some further reduce to 60% ET around 30 days before harvest. The practice not only reduces water use but can also improve fruit soluble solids and color (Lu et al., 2019; Zegbe-Domínguez et al., 2003).

Problematically, recent studies indicate that DI can increase disease risk in a range of crops and growing conditions (Swett, 2020). In our own work, we have observed increased Phytophthora root rot (*Phytophthora capsici*) under reduced irrigation (Del Castillo Múnera et al., 2019). Additionally, Chapter 1 findings indicate that mid to late season vine decline caused by *Fusarium oxysporum* f. sp. *radicis lycopersici* and/or *Fusarium noneumartii* may be enhanced under reduced irrigation; in this study, *F. noneumartii* was only detected in tomatoes grown under DI, strongly implicating DI in disease enhancement. *Fusarium noneumartii*, the cause of Fusarium stem rot and decline (FRD), is a relatively new problem in California. This pathogen causes stem rot and premature vine decline, exposing fruit to sunburn and secondary rots, ultimately reducing yields. Based on Chapter 1 results, we hypothesized that DI enhances FRD in processing tomatoes.

While there are no commercial cultivars with complete resistance to *F. noneumartii*, field trials have demonstrated a wide range in vine decline severity and yield performance in existing cultivars under pressure from this pathogen (Brackrog, 2021; Paugh and Swett, 2022). Use of these better-performing cultivars is currently one of the only available FRD management tools. However, there is concern that increased stress under DI might influence

resistance and/or yield performance of these better performing cultivars. This led us to the question – will DI influence efficacy of cultivar-based management?

Numerous studies have demonstrated that water stress in plants enhances disease development. This includes studies of fungal diseases in forest trees (Desprez-Loustau et al. 2006), Phytophthora root rot in processing tomatoes (Ristaino and Duniway, 1989), charcoal rot in common bean (Mayek-Perez et al., 2002), and vine decline in processing tomatoes (see Ch. 1). It has been shown that tomato genotypes can vary in water stress tolerance traits with some highly stress tolerant genotypes (Alian et al., 2000; Sánchez-Rodríguez et al., 2011). We therefore hypothesized that cultivars with better FRD resistance/tolerance under DI is due, at least in part, to greater water stress tolerance.

Thus, the objectives of this study were to 1) learn whether deficit irrigation influences FRD development and associated yields, 2) determine whether cultivar-based management is effective in reducing FRD development and yield losses under DI, and 3) evaluate whether greater FRD sensitivity in certain cultivars is related to water stress tolerance traits.

## 2. Methods

### *2.1 Experimental design*

Field trials took place in 2021 and 2022 at the UC Davis Plant Pathology Field Station in Davis, CA (GPS: 38.5, -121.8). This area of CA is characterized by hot dry summers and cooler wet winters. The field soil is classified as a Yolo silty clay loam (Ys). There were two fields (70m long with 26 1.5 m-wide rows per field), one “fumigated” and the other “inoculated”. Specifically, the “fumigated” field was fumigated in the fall of 2020 with the maximum rate of

Pic-Clor 60 under a TIF tarp for 15 days. In each field the trial was arranged in a RCBD consisting of three blocks. Within each block there were two irrigation treatments, “Optimum” (100% potential crop ET) and “Deficit” (60% potential crop ET) made up of four rows each. One cultivar was planted to each row at 30 cm spacing and was replicated across both irrigation treatments and all three blocks for a total of six rows per cultivar within each field (Fig. 1). A row of H8504 seedlings were planted on either side of each field to serve as border rows. Cultivars ranging in FRD resistance and performance under pressure from *Fusarium noneumartii* (HM3887, SVTM9016, H5608, and N6428) were selected for this study (Brackrog, 2021; Paugh and Swett, 2022) (Fig. 2). One 15-plant “monitoring” subplot was randomly placed in the eastern and western halves of each row and were used for yield evaluations (decline data also collected – see Supp. Tables) throughout the year whereas the areas outside of the monitoring subplots were used for destructive canopy health and stem rot evaluations used for disease analyses.

*2.2 Irrigation Treatments*

One drip irrigation line was buried at an approximate depth of 15 cm along the middle of each bed. Emitters were spaced every 30 cm. Irrigation treatments were based on evapotranspirative (ET) needs of the plants as measured by an onsite Tule system (Oakland, CA), which monitors actual ET in the field ($ET_a$) along with the volume of irrigation applied. Irrigation levels were selected based on commercial practices by processing tomato growers (*pers comm,* Tom Turini) and previous studies (Swett and Gaudin, *unpublished*). Plants in both irrigation treatments received enough water to replace 100% of their ET needs until approximately 56 and 49 days preharvest in 2021 and 2022, respectively (Supp. Table 1). At

this point the two irrigation treatments diverged; rows in the "Optimum" side of the field continued to receive 100% of the irrigation hours recommended by Tule while rows in the "Deficit" side received only 60% of the Tule recommended irrigation hours. Irrigation was stopped completely 28 days preharvest in both years. To confirm that the deficit irrigation treatment resulted in reduced soil moisture, sensors (TEROS10, METER Group) were buried throughout both fields approximately 30 cm deep halfway between the drip line and edge of the bed (Fig. 1). In both years, 14 and 16 sensors were used in the fumigated and inoculated fields, respectively. In some cases, multiple sensors were placed within rows to account for water pressure variability down the row (see Chapter 1). Soil moisture was measured in 15-minute increments between 5/28 and 8/20 in 2021 and between 6/25 and 8/13 in 2022. Based on these measures, DI resulted in a .001 – 0.060 $cm^3/cm^3$ reduction in soil VWC across years and fields (Fig. 3).

*2.3 Seedling inoculation*

Seedlings were provided by TS&L Seed Company (Woodland, CA) in 2021 and AgSeeds Unlimited (Woodland, CA) in 2022. Seedling trays (~400 cell) were dipped into a *F. noneumartii* spore suspension (1 x $10^6$ spores/mL 0.1% water agar (WA)) for 1 min and allowed to sit overnight before machine transplantation the following day. Spore suspensions were prepared by using 0.5% potassium chloride (KCl) to scrape 1-week old cultures of pure culture isolate *F. noneumartii* (CS109) on potato dextrose agar (39 g potato dextrose in 1 L water) (PDA) through two layers of sterile cheesecloth. A hemocytometer was used to enumerate spore concentration and calculate dilutions, which were made using 0.1% WA the following day, immediately before inoculation.

*2.4 Plant water stress*

To evaluate treatment effects on plant water stress, midday stem water potential (plant water stress) and blossom end rot (BER) incidence (an abiotic symptom of water stress) were measured in the fumigated field. Stem water potential was measured in all cultivars at 3 and 6-weeks post deficit irrigation (DI) onset in 2021 and at 2 and 7-weeks post DI onset in 2022 using a pressure bomb (Model 615, PMS Instrument Co., Albany, OR). In the easternmost monitoring plot in each row within block 2, a fully developed leaflet from a young branch was covered with a foil-laminate bag (Stem Water Potential Bag, PMS Instrument Co.) for approximately 15 min before excision and measurement. One leaflet was selected from each of three randomly selected plants. Plants were marked so that measurements could be taken from the same plant each time. Blossom end rot (BER) incidence was quantified by dividing the biomass of fruit with BER (Fig. 3) by the total biomass of fruit in the harvested monitoring plots.

*2.5 Soil and leaf nutrient analyses*

The soil and plant nutrients N, P, and K in each field (fumigated vs. inoculated) were measured to ensure that yield differences observed between the fields were the result of disease and not nutrient deficits. Additional nutrients (Ca, Mg, and Na) were tested at time points 2 and 3 in 2022. Composite soil samples were collected on 5/5/21, 6/17/21, 8/3/21, 8/23/21, 4/5/22, 7/7/22, and 8/24/22. To collect the soil samples, the top layer of organic matter was removed then a 2.5 cm diameter soil corer was used to collect the top 15 cm of soil from 10 locations in a diagonal transect across each field in a NE to SW direction. In 2021, samples were analyzed by the UC Davis Analytical Lab for all dates except 8/23/21, which was

analyzed by Ward Laboratories, Inc. (Kearney, NE). In 2022, samples were analyzed by Dellavale Laboratory, Inc. (Fresno, CA) (Supp. Table 2). For plant nutrient analysis, leaf samples were collected on 8/3/21 and 8/23/21, 7/12/22 and 8/24/22. One healthy (disease and insect damage-free) fully formed leaflet from a young branch was collected from 10 plants in each cultivar x irrigation treatment for a total of 30 leaves per treatment and a total of 8 composite samples per field. All leaf samples were analyzed by Ward Laboratories, Inc. (Kearney, NE) (Supp. Table 3).

*2.6 Vine decline and stem rot quantification*

Aboveground (vine decline) disease evaluations were conducted on 7/7/21, 8/5/21, 8/26/21, 6/30/22, 7/21/22, and 8/22/22 in both fields. A random number generator was used to select five plants in each row for a total of 120 plants in each field at each timepoint. Each plant was excavated, and each plant was evaluated (presence/absence) for early decline (some, but not all branches experiencing necrosis), and advanced decline (all branches experiencing necrosis) (Fig. 4). Additionally, plants were evaluated for the presence of belowground (BG) stem rot as an indication of pathogen infection and for crown and aboveground (AG) stem rot as an indication of infection progress (severity).

Disease analysis was based on percentage data derived from excavated plants in each block, treating block as replicate. Area Under the Disease Progress Curve (AUDPC) was calculated for advanced decline in the excavated plants. The incidence of “any stem rot” was calculated as the proportion of plants with either BG stem rot, crown rot, or AG stem rot (Fig. 4) to the total number of evaluated plants. Because there was a lack of treatment differences in terms of BG stem rot, crown rot, and AG stem rot incidence, our analysis focused on “any

stem rot" incidence (Fig. 4). We focused on disease data from the second time point in both years (8/6/21 and 7/21/22) as there was little disease at the first time point and many plants were dead by the third time point, making disease evaluations challenging.

*2.7 Fungal isolations and molecular identification*

Within each year, at least five symptomatic plants from each cultivar in each irrigation treatment per block in the fumigated field were collected for diagnostics except that plants were collected from the inoculated field only in 2021. This served to confirm whether disease was due solely to *F. noneumartii* in the inoculated field and define whether other diseases were present in either field. Fungal isolations were conducted as described in Chapter 1. *Fusarium oxysporum* was the primary species recovered from symptomatic tissue in the fumigated field, although *F. noneumartii* was isolated once in 2022 (Supp. Table 4). In 2021 *F. oxysporum* was present in 47% and 20% of diseased plants in the 100% ET and 60% ET treatments, respectively. In 2022, *F. oxysporum* made up 70% and 60% of plants in the 100% ET and 60% ET treatments, respectively (Supp. Table 4). None of the *F. oxysporum* isolates selected for SIX3 PCR amplified. Because these isolates came from symptomatic tissue, they were tentatively diagnosed as *F. oxysporum* isolates as *F. oxysporum* f. sp. *radicis lycopersici* (Forl), the pathogen responsible for Fusarium crown and root rot in tomato (Supp. Table 4). No other pathogens were recovered from the fumigated field.

Not surprisingly, plants in the inoculated field were primarily infected by *F. noneumartii*, with an average of 30% and 20% recovery in the 100% ET and 60% ET treatments, respectively (Supp. Table 5). The only other species identified was *F. oxysporum*, which was on

average identified in 20% and 5% of plants in the 100% ET and 60% ET treatments, respectively, however identity as Forl or non-pathogens was not further evaluated.

*2.8 Yield and fruit quality evaluations*

Fruit from each monitoring plot closest to the header of each row was mechanically harvested using a HM Blackweller small plot harvester, and total fruit was weighed on the harvester. Because vine decline can expose fruit to sunburn and rot, total fruit yields (red marketable (red/pink) fruit, green fruit, sunburned, blossom end rot (BER), and damaged) were evaluated in each treatment (Fig. 3). The BER category was included to be sure that decreased irrigation alone was not contributing to this abiotic disease. A 19 L bucket was used to collect a representative subset from each plot to sort into the four categories and fruit in each category was weighed. Approximately 0.5 L of red marketable fruit from each treatment was analyzed for quality by the Processing Tomato Advisory Board at the Campbell's Cannery (Dixon, CA) (hue, Brix, and pH).

*2.9 Statistical analysis*

All analysis was conducted in RStudio v. 2023.06.1+524 (Rstudio Team, 2020). To determine whether deficit irrigation could influence Fusarium stem rot and vine decline (FRD) (Obj. 1), we analyzed symptoms, yield, and quality metrics keeping cultivars separate evaluating both the fumigated and inoculated fields. To determine whether cultivar-based management is effective in reducing FRD influence (Obj. 2), we analyzed the inoculated field alone along with the differences between fields. the same metrics combining cultivars and focusing on the inoculated field. Total yield biomass, sorted fruit categories (percent red marketable, green, sunburned, BER, and damaged), and fruit quality parameters (hue, Brix,

and pH) were analyzed using data from both the fumigated and inoculated treatments. Both analyses used incidence data from time point 2 to maximize the irrigation treatment effects without suffering high plant mortality towards the end of the season due to the pathogen treatment effect. To determine if poor cultivar performance is linked to lower water stress tolerance (Obj. 3), analyses of stem water potential and BER incidence associated with irrigation treatments in the fumigated treatment were conducted, keeping years and time points separated and treating irrigation as a fixed variable.

Years for disease and yield data were analyzed separately and combined unless there was a significant Year x treatment effect. To establish whether data were normal, quantile-quantile plots were created for each model. ANOVA (stats package) was used for parametric data and Kruskal-Wallis (stats package) for nonparametric data. Differences in all analyses were considered significant based on a *P* value of less than 0.05. Percentage data were transformed using an arcsine square root transformation. Disease incidence analyses were conducted using ANOVA (lme4 package). Irrigation was considered a fixed effect and Block was considered random in all analyses while Pathogen was considered a fixed effect only in Objective 2 analyses. Area under the disease progress curve (AUDPC) was calculated for advanced decline incidence, treating block as replicate. The effects of deficit irrigation on yield (total yield, fruit categories, and yield reductions – the difference in treatment yields between fields) was assessed using fruit weight (kg/ha), derived from each block, treating block as replicate, for a total of three replicates in each year. If ANOVA was significant for an irrigation effect, treatment means were compared using Dunnett's test treatment 100% ET as the

control. If ANOVA was significant for a cultivar effect, treatment means were compared using Tukey's pairwise means comparisons.

## 3. Results

### *3.1 Does deficit irrigation (DI) influence Fusarium stem rot and vine decline (FRD) development and associated yields of processing tomatoes?*

To examine the influence of DI on Fusarium stem rot and vine decline (FRD) development and associated yields in processing tomatoes, we monitored symptom development in four cultivars with a range of putative FRD tolerance between DI onset and harvest with and without pathogen pressure. Vine decline was observed only in the inoculated treatment, where it was observed in both years and both irrigation treatments. While we did not observe significant increases in vine decline under DI in any cultivar (Table 1), we did observe several trends. Firstly, there was less total decline and advanced decline under DI in SVTM9016 in both years. Cv H5608 was similarly unaffected by DI except for a 22% increase in advanced decline under DI in 2021. Cvs N6428 and HM3887 were most affected by DI; within N6428 total decline incidence increased under DI by 135% and advanced decline incidence increased three-fold in 2021. Within HM3887 we observed ~18% increase in total decline and advanced decline incidences in 2021 along with a 30% increase in advanced decline incidence under DI in 2022. We also did not observe a significant effect of DI on Area Under the Disease Progress Curve (AUDPC) values for advanced decline incidence for all cultivars. Trends were similar to the above for H5608; however, AUDPC was higher under DI for SVTM9016 in both years and lower or near identical under DI for HM3887 and N6428 (Table 2).

We defined the incidence of “any stem rot” as the proportion of plants with either belowground stem rot, crown rot, or aboveground stem rot within the total number of evaluated plants (n = 30 plants per cultivar per field). We observed higher incidence of “any stem rot” in the inoculated treatment compared with the fumigated treatment across all cultivars ($P$ = < 0.0001 – 0.002) (Table 3). “Any stem rot” development was enhanced under DI in the inoculated treatment for HM3887 (both years) and N6428 (2021), based on significant differences between each treatment and/or significant pathogen x irrigation interactions. In general, “any stem rot” incidence was higher under DI across all cultivars in 2021, however differences were significant only in HM3887 ($P$ = 0.024) (Table 3). In 2022 there was a trend of lower “any stem rot” incidence under DI, although differences were not significant.

Total yields were calculated by harvesting and weighing fruit in the monitoring subplots. DI influenced total yields only in the case of H5608 in 2022 in the fumigated field where there was a 37% reduction under DI ($P$ = 0.012) (Table 4). However, there was a general trend of reduced yields under DI in this cultivar across pathogen treatments and years (except for the inoculated treatment in 2022). Total yield biomass in SVTM9016 was ~40% lower under DI in 2021 across both pathogen treatments, but 8% (fumigated) and 86% (inoculated) higher under DI in 2022. The opposite was true for N6428 in which we observed 10% (fumigated) and 22% (inoculated) higher total yields under DI in 2021 but 3% (fumigated) and 10% (inoculated) lower total yields under DI in 2022. Total yields were consistently lower under DI in the HM3887 cultivar in both pathogen treatments and in both years and yields were reduced by 50% under DI in the inoculated treatment in 2022 ($P$ = 0.035) (Table 4). This trend is supported by total yield differences between the fumigated and inoculated fields under each irrigation

treatment (Table 5) in which we observed a bigger difference in total yields between the inoculated and fumigated plants only in the HM3887 cultivar ($P$ = 0.039). Otherwise the yield differences between the fields were not significantly different.

A random subset of harvested fruit was collected from each row in 19 L buckets and sorted into four categories. We observed a lower percentage of red marketable fruit under DI only in the H5608 cultivar in the fumigated field in 2022 (10% reduction) ($P$ = 0.013) (Table 6). There was a trend of less red marketable fruit under DI in H5608 and HM3887 across pathogen treatments. We observed a trend of less red marketable fruit under DI in the SVTM9016 cultivar, but only in the inoculated treatment (29% and 5% reductions in 2021 and 2022, respectively). While we observed a trend of increased sunburned fruit under DI in both pathogen treatments across all cultivars, differences were significant only in the HM3887 cultivar in the inoculated treatment in 2022 ($P$ = 0.050) (Table 7. There was significantly less damaged fruit under DI in the N6428 cultivar in the fumigated treatment in 2021 ($P$ = 0.020) (Table 8), but no other effects or trends emerged. Similarly, we did not observe an effect of DI on fruit quality metrics (hue, Brix, or pH) (Table 9-11).

*3.2. Is cultivar-based management effective in reducing FRD incidence and yield losses under DI?*

To determine whether cultivars that perform well under *F. noneumartii* pressure can maintain that performance under DI, we evaluated plant health in our four cultivars under DI and pathogen pressure focusing on *F. noneumartii* symptoms (vine decline and stem rot) along with yield biomass and fruit quality. In terms of vine decline, we observed an effect of cultivar on advanced decline ($P$ = 0.008, years combined) with higher advanced decline incidence in

HM3887 and SVTM9016 (Table 12). Although there was an effect of cultivar on total decline (*P* = 0.038, years combined), means comparisons using Tukey's HSD did not resolve the differences. There was no effect of irrigation on either metric, however we observed increased advanced decline incidence under DI in HM3887 (25% increase) and N6428 (7-fold increase) while incidence decreased in SVTM9016 (50% decrease) and remained unchanged in H5608 (Table 12). Similar trends were observed with total decline; we observed ~33% higher total decline incidence under DI in HM3887 and N6428 but decreased incidence under DI in SVTM9016 (18% decrease) and H5608 (6% decrease). Area Under the Disease Progress Curve (AUDPC) for advanced decline significantly varied by year (*P* < 0.001) and were analyzed separately (Table 13); there was no effect of irrigation (*P* = 0.335 in 2021 and *P* = 0.204 in 2022) or cultivar (*P* = 0.934 in 2021 and *P* = 0.221 in 2022). There was no effect of cultivar on "any stem rot" development (*P* = 0.102 in 2021 and *P* = 0.337 in 2022); we observed higher incidence of "any stem rot" for all cultivars under DI in 2021 (*P* = 0.024), but not in 2022 (*P* = 0.337) (Table 14).

There was an effect of cultivar on total yield biomass in both years (*P* = 0.017 in 2021 and *P* = 0.010 in 2022) and when years were combined (*P* = 0.014) (Table 15). Total yields were generally highest in the SVTM9016 cultivar and lowest in HM3887 across both irrigation treatments in both years. Total yield biomass was reduced under DI in both years in the fumigated treatment (*P* = 0.035 in 2021 and *P* = 0.076 in 2022) (Supp. Table 6), but not in the inoculated treatment, where yield biomass was higher under DI in N6428 in 2021 and in SVTM9016 and H5608 in 2022. These trends are supported by the total yield differences between the fumigated and inoculated treatments where we observed an effect of cultivar in

2022 (*P* = 0.008) and when years were combined (*P* = 0.012) (Table 17), however differences were generally greatest in HM3887 and least in SVTM9016 in both years.

We did not observe an effect of irrigation (*P* = 0.470 in 2021 and *P* = 0.376 in 2022) or cultivar (*P* = 0.254 in 2021 and *P* = 0.372 in 2022) on percent red marketable fruit. However, we observed a trend of less red marketable fruit in HM3887 than in the other cultivars under 100% ET (19-38% less) and 60% ET (20-30% less) in 2021 (Table 19). Additionally, we observed a trend of less red marketable fruit under DI in SVTM9016 in 2021 (29% reduction) and years combined (17% reduction). There was an effect of cultivar on percent sunburned fruit in 2021 (*P* = 0.012) and in years combined (*P* = 0.015) with the most sunburned fruit in the HM3887 cultivar and the least in N6428 (Table 18). There was no effect of irrigation, although a trend of increased sunburn was observed under DI in both years. We observed the most damaged fruit in HM3887 compared to the other cultivars when years were combined (*P* = 0.031), although the trend can be seen in 2021 and 2022 as well (Table 19). There was no effect of irrigation, however there was a trend of higher percent damaged fruit under DI in SVTM9016 in 2021 (3-fold increase) and 2022 (77% increase).

We observed an effect of cultivar on the three fruit quality metrics used (hue, Brix, and pH). There was an effect of cultivar on hue in 2022 (*P* = 0.040) with the reddest fruit observed in H5608 (Table 20). We observed an effect of cultivar on Brix (soluble solids) in both years (*P* = 0.031 in 2021 and *P* = 0.035 in 2022) and when years were combined (*P* = 0.009), although Tukey's HSD was unable to resolve differences (Table 21). The highest Brix values (highest sugar) were observed in the HM3887. Similarly, there was an effect of cultivar on fruit acidity (pH) in both years (*P* = 0.019 in 2021 and *P* = 0.002 in 2022) and when years were combined (*P*

< 0.001) (Table 22). Ideal pH values are between 4.30 and 4.45 (*pers comm,* Zach Bagley); pH values for the SVTM9016 cultivar were generally lower and were within that ideal range (*P* = 0.019 in 2021 and *P* = 0.002 in 2022); pH values for the other cultivars were higher than the ideal range in each year and years combined.

*3.3. Are cultivars with better performance under FRD pressure more water stress tolerant?*

Midday stem water potential and blossom end rot (BER) incidence was measured in the fumigated field as indicators of water stress. By three weeks post DI onset in 2021 we observed more plant water stress under DI in HM3887 (*P* < 0.001) and SVTM9016 (*P* = 0.042) (Table 25). Conversely, there was less water stress under DI in N6428 (*P* = 0.031) and H5608 (*P* = 0.001). At six weeks post DI onset there were no treatment effects, however the trend of increased water stress in HM3887 and SVTM9016 and decreased water stress in N6428 and H5608 continued. By two weeks post DI onset in 2022 we observed more plant water stress under DI in HM3887 (*P* = 0.011). There was no effect of DI on plant water stress in the other three cultivars. By seven weeks post DI onset we observed more plant water stress under DI in HM3887 (*P* = 0.011), N6428 (*P* = 0.072), and H5608 (*P* = 0.029).

We observed higher blossom end rot (BER) incidence under DI (*P* = 0.050) in all cultivars except for HM3887 in 2021 (Table 24). There was an effect of cultivar in both years (*P* < 0.001). Incidence was highest in the SVTM9016 cultivar across both years; we observed the highest incidence of BER in N6428 and H5608 in 2021 but not in 2022. HM3887 had the lowest BER incidence in both years, regardless of irrigation treatment.

**4. Discussion and Conclusion**

Taken together, these studies indicate that deficit irrigation (DI) can enhance Fusarium stem rot and vine decline (FRD) disease development and yield losses caused by *Fusarium noneumartii* in processing tomatoes and that appropriate cultivar selection continues to be a useful management under DI. Additionally, our results indicate that cultivars with better performance under FRD pressure are more water stress tolerant while cultivars with poor performance are less water stress tolerant under DI. Stem water potential and BER incidence data suggest that water stress tolerance could be an important trait for cultivars to maintain FRD disease resistance or at least prevent cultivars from becoming more susceptible.

The most significant effects of DI were in HM3887. We observed a trend of increased total and advanced decline under DI only in this cultivar and a trend of lower total yields under DI regardless of pathogen presence. Additionally, HM3887 was the only cultivar in which we observed significantly more sunburned fruit under DI. In the absence of water stress and pathogen pressure, this cultivar performed well, and we observed the lowest stem rot frequency and best fruit quality of the four cultivars. However, this cultivar appears to be quite susceptible to *F. noneumartii* even without the additional stress of DI. In fact, disease symptoms were so prevalent, and yields were so poor in the inoculated field that the effects of DI were sometimes lost as both irrigation treatments resulted in symptoms in all plants.

Reduced pathogen tolerance under water stress is a well-studied phenomenon known as “predisposition”. This term generally applies to an abiotic stress that irreversibly alters a plant’s ability to recognize and respond to pathogens, resulting in increased pathogen virulence (Bostock, 2005; Bostock et al., 2014). In these trials, however, seedling roots were dipped into the inoculum before transplanting and the deficit irrigation *i.e.,* water stress

treatment did not start until 78 days later. While plants may not have been predisposed to pathogen infection by the DI treatment, the resulting water stress may have exacerbated colonization. Reduced susceptibility or improved tolerance to one stressor resulting from the defense response to another stressor is known as “cross-tolerance”. This appears to occur only in cases where induced systemic resistance (ISR) is triggered via wounding or when the challenging pathogen utilizes stomata for plant entry *e.g.,* bacteria. In these cases, reactive oxygen species (ROS) are created that help protect the plant from water stress and pathogen infection by triggering stomatal closure (Ben Rejeb et al., 2014), which is not the case here.

Under water deficit, plants respond in a myriad of ways that can differ between species and even genotypes. These differences involve maintaining physiological processes, gene regulation, and metabolic pathways (Fang and Xiong, 2015). An example of this can be found in Alian et al. (2000), in which tomato cultivars under water stress maintained fresh weights similar to the control plants but with differing osmotic adjustment responses. In other work, authors found that water stress sensitive cultivars had decreased shikimate pathways and phenolic compound production while tolerant cultivars had increased organic compound synthesis (Sánchez-Rodríguez et al., 2011). Additionally, improved responses to salt stress were observed in grafted tomatoes with specific scion cultivars (Santa-Cruz et al., 2002). These factors should be considered in breeding efforts to develop FRD tolerant cultivars.

Blossom end rot (BER) is a common abiotic disease of tomato in which a lack of calcium causes rot at the blossom end of the fruit, resulting in yield losses (Saure, 2001). During the growing season, nutrients are delivered to processing tomatoes via driplines, known as fertigation. Because DI reduces the volume of water supplied to plants, it is possible that this

results in less nutrients like calcium delivered to plants via the drip system or less soil moisture to aid in nutrient uptake from the soil. Additionally, drought stress itself can reduce calcium absorption, even when it is readily available in the soil (Feng et al., 2023). As an unexpected outcome of this study, in a pathogen-free setting, we observed higher BER incidence under DI in 2021, however this finding supports previous work where increased BER was observed under reduced irrigation practices in tomato (Taylor et al., 2004; Zegbe et al., 2007). Additionally, Adams and Ho (1993) observed a linear reduction in calcium uptake with increasing salinity (like water stress in terms of plant response) in tomatoes. Others have argued that physiological differences in the number and functionality of xylem vesicles could influence BER incidence in plants (Belda et al., 1996; Ho et al., 1993), leaving room for the possibility that cultivars with more numerous and/or functional vesicles may also be more water stress tolerant.

Another unexpected outcome of this study a low resident population of (tentative) *Fusarium oxysporum* f. sp. *radicis lycopersici* (Forl), the cause of Fusarium crown and root rot of tomato, in the fumigated field. Because none of the cultivars used have Forl resistance we believe that this did not influence results in any particular cultivar. A third unexpected result of the study was smaller yield differences between the fumigated and inoculated field under DI than under well-watered conditions for SVTM9016 and H5608, however this result can be explained by their strong performance in the fumigated field under well-watered conditions and their comparatively poor performance under pathogen pressure under the same irrigation treatment, especially in 2022.

Because fungicides do not effectively manage soil borne pathogens and methyl bromide fumigation is highly restricted, processing tomato growers with *F. noneumartii* pressure need effective management tools. Growers who have adopted DI because of reduced water allocations additionally contribute water stress to the system. Based on this study, SVTM9016, N6428, and H5608 had some tolerance to FRD in at least one year. Because growers select between cultivars favored by processors, options are limited and may not include any of these "more tolerant" options. In these cases, alternative management strategies such as incorporating organic soil amendments to buffer against water stress, incorporating beneficials or biocontrols to promote microbial community diversity, and using anaerobic soil disinfestation or solarization to reduce pathogen pressure could be useful.

**Literature cited**

Adams P., and Ho L.C. (1993). Effects of environment on the uptake and distribution of calcium in tomato and on the incidence of blossom-end rot. Plant and Soil. 154:127-132.

Alian A., Altman A., and Heuer B. (2000). Genotypic difference in salinity and water stress tolerance of fresh market tomato cultivars. Plant Sci. 152:59–65.

Anonymous (2021). Worldwide Tomato Yield Data. Food and Agriculture Organization (FAO). Online. https://fao.org/faostat/en/#data/QC. Accessed 21 August 2023.

Belda R. M., Fenlon J. S., and Ho L.C. (1996). Salinity effects on the xylem vessels in tomato fruit among cultivars with different susceptibilities to blossom-end rot. J. Hortic. Sci. 71:173-179.

Ben Rejeb, I., Pastor, V., and Mauch-Mani, B. (2014). Plant responses to simultaneous biotic

and abiotic stress: Molecular mechanisms. Plants. *3*, 458–475.

Bostock, R.M. (2005). Signal Crosstalk and Induced Resistance: Straddling the Line Between Cost and Benefit. Annu. Rev. Phytopathol. *43*, 545–580.

Bostock, R.M., Pye, M.F., and Roubtsova, T.V. (2014). Predisposition in Plant Disease: Exploiting the Nexus in Abiotic and Biotic Stress Perception and Response. Annu. Rev. Phytopathol. *52*, 517–549.

Brackrog A. (2021). Characterizing cultivar resistance and pathogen-seed interactions for Fusarium falciforme (FSSC 3+4), an emerging vine decline and stem rot pathogen of California processing tomato. Master's thesis, University of California, Davis.

Bureau of Reclamation (2020). Summary of Water Supply Allocations. Online. https://www.usbr.gov/mp/cvp-water/allocations.html. Accessed 21 August 2023.

Del Castillo Múnera J., Belayneh B.E., Lea-Cox J.D., and Swett C.L. (2019). Effects of set-point substrate moisture control on oomycete disease risk in containerized annual crops based on the tomato–phytophthora capsici pathosystem. Phytopathology 109:1441–1452.

van der Does H., Lievens B., Claes L., Houterman P.M., Cornelissen B.J., and Rep M. (2008). The presence of a virulence locus discriminates Fusarium oxysporum isolates causing tomato wilt from other isolates. Environ. Microbiol. 10:1475–1485.

Desprez-Loustau M.L., Marçais B., Nageleisen, L.M. Piou, D., and Vannini A. (2006). Interactive effects of drought and pathogens in forest trees. Ann. For. Sci. 63:597-612.

Fang Y., and Xiong L. (2015). General mechanisms of drought response and their application in drought resistance improvement in plants. Cell. Mol. Life Sci. 72:673–689.

Feng D., Wang X., Gao J., Zhang C., Liu H., Liu P., and Sun X. (2023). Exogenous calcium: Its mechanisms and research advances involved in plant stress tolerance. Front. Plant Sci. 14:1143963.

Ho L.C., Belda R., Brown M., Andrews J., and Adams P. (1993). Uptake and Transport of Calcium and the Possible Causes of Blossom-end Rot in Tomato. J. Exp. Bot. 44:509–518.

Itier B. Measurement and estimation of evapotranspiration. In Sustainability of Irrigated Agriculture. Dordrecht: Springer Netherlands, 1996. 171–191.

Liu Y.J., Whelen,S., and Hall B.D. (1999). Phylogenetic relationships among ascomycetes: Evidence from an RNA polymerse II subunit. Mol. Biol. Evol. 16:1799–1808.

Lu J., Shao G., Cui J., Wang X., and Keabetswe L. (2019). Yield, fruit quality and water use efficiency of tomato for processing under regulated deficit irrigation: A meta-analysis. Agric. Water Manag. 222:301–312.

Mayek-Pérez N., García-Espinosa R., López-Castañeda C., Acosta-Gallegos J.A., and Simpson J. (2002). Water relations, histopathology, and growth of common bean (*Phaseolus vulgaris* L.) during pathogenesis of *Macrophomina phaseolina* under drought stress. Physiol Mol Plant Pathol. 60:185-195.

Miyao G., Goodell P.B., Davis R.M., Hembree K.J., Natwick E.T., Ploeg A.T., Aegerter B.J., Lanini W.T., Stapleton J.J., Stodard C.S., Subbarao K.V., Trumble J.T., Zalom F.G. Revised continuously. UC IPM Pest Management Guidelines: Tomato. UC ANR Publication 3470. Davis, CA.

Mukherjee S., Dash P.K., Das D., and Das S. (2023). Growth, Yield and Water Productivity of

Tomato as Influenced by Deficit Irrigation Water Management. Environ. Process. 10:1-21.

O'Donnell K., Corby Kistler H., Cigelnik E., and Ploetz R.C. (1998). Multiple evolutionary origins of the fungus causing Panama disease of banana: Concordant evidence from nuclear and mitochondrial gene genealogies. PNAS. 95:2044-2049.

Paugh K., and Swett C. (2022). Evaluation of processing tomato cultivars for tolerance to vine decline caused by Fusarium falciforme (FSSC 3 + 4, syn. F. noneumartii) in California. Plant Dis. Manag. Reports. 023.

Posit team (2023). RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. URL http://www.posit.co/.

Ristaino J.B. and Duniway J.M. (1989). Effect of preinoculation and postinoculation water stress on the severity of Phytophthora root rot in processing tomatoes. Plant Dis.

Sánchez-Rodríguez E., Moreno D.A., Ferreres F., Rubio-Wilhelmi M.D.M., and Ruiz J.M. (2011). Differential responses of five cherry tomato varieties to water stress: Changes on phenolic metabolites and related enzymes. Phytochemistry 72:723–729.

Santa-Cruz A., Martinez-Rodriguez M.M., Perez-Alfocea F., Romero-Aranda R., and Bolarin M.C. (2002). The rootstock effect on the tomato salinity response depends on the shoot genotype. Plant Sci. 162:825–831.

Saure M.C. (2001). Blossom-end rot of tomato (Lycopersicon esculentum Mill.) — a calcium- or a stress-related disorder? Sci. Hort. 90:193-208.

Swett C.L. (2020). Managing crop diseases under water scarcity. Phytopathology 58:387–406.

Taylor M.D., Locascio S.J., and Alligood M.R. (2004). Blossom-end rot incidence of tomato as

affected by irrigation quantity, calcium source, and reduced potassium. HortSci. 39:1110-1115.

USDA Economic Research Service (2019). Potatoes and tomatoes are the most commonly consumed vegetables. Online. https://www.ers.usda.gov/data-products/chart-gallery/gallery/chart-detail/?chartId=58340. Accessed 21 August 2023.

USDA National Agricultural Statistics Service (2021). Tomatoes, in the Open, Processing - Production, Measured in Tons. Online. https://quickstats.nass.usda.gov. Accessed 21 August 2023.

Zegbe-Domínguez J.A., Behboudian M.H., Lang A., and Clothier B.E. (2003). Deficit irrigation and partial rootzone drying maintain fruit dry mass and enhance fruit quality in "Petopride" processing tomato (*Lycopersicon esculentum*, Mill.). Sci. Hortic. (Amsterdam). 98:505–510.

Zegbe J.A., Hossein-Behboudian M., and Clothier B.E. (2007). Response of tomato to partial rootzone drying and deficit irrigation. Rev. Fitotec. Mex. 30:125-125.

## Figures

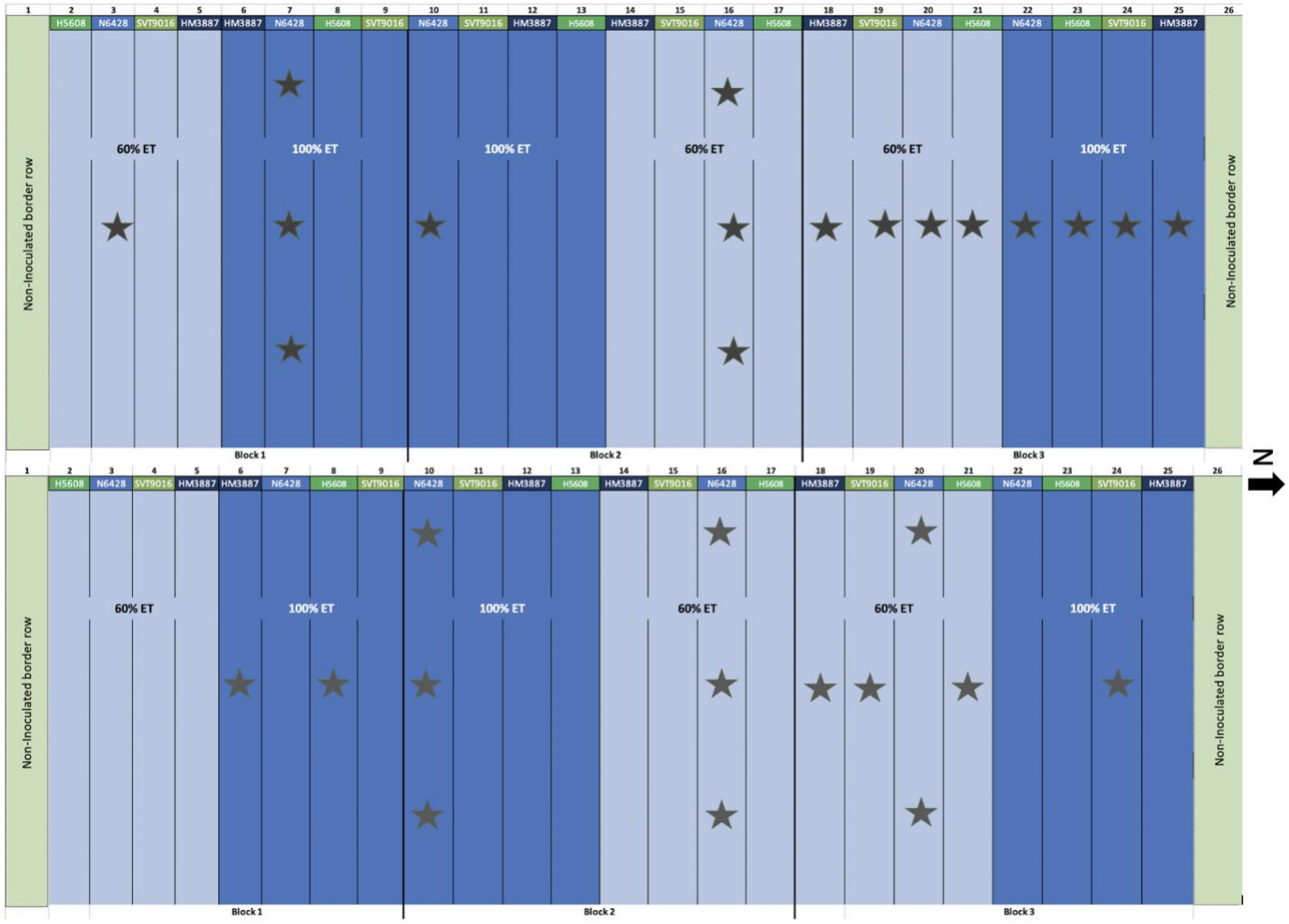



**Figure 1.** Layouts of the inoculated (top) and fumigated (bottom) fields in both years. Gray stars represent soil moisture sensor locations, which were buried approximately 30 cm deep halfway between the middles and edges of the rows.

| | | Yield | | |
|---|---|---|---|---|
| | | **Low** | **Moderate** | **High** |
| **Putative *Fusarium noneumartii* Tolerance** | **Tolerant** | | | N6428 |
| | **Moderate** | | SVTM9016 | H5608 |
| | **Susceptible** | HM3887 | | |

**Figure 2**. Putative *Fusarium noneumartii* tolerance and historical yields of the four cultivars chosen for this study based on previous field trials (Brackrog, 2021; Paugh and Swett, 2022).

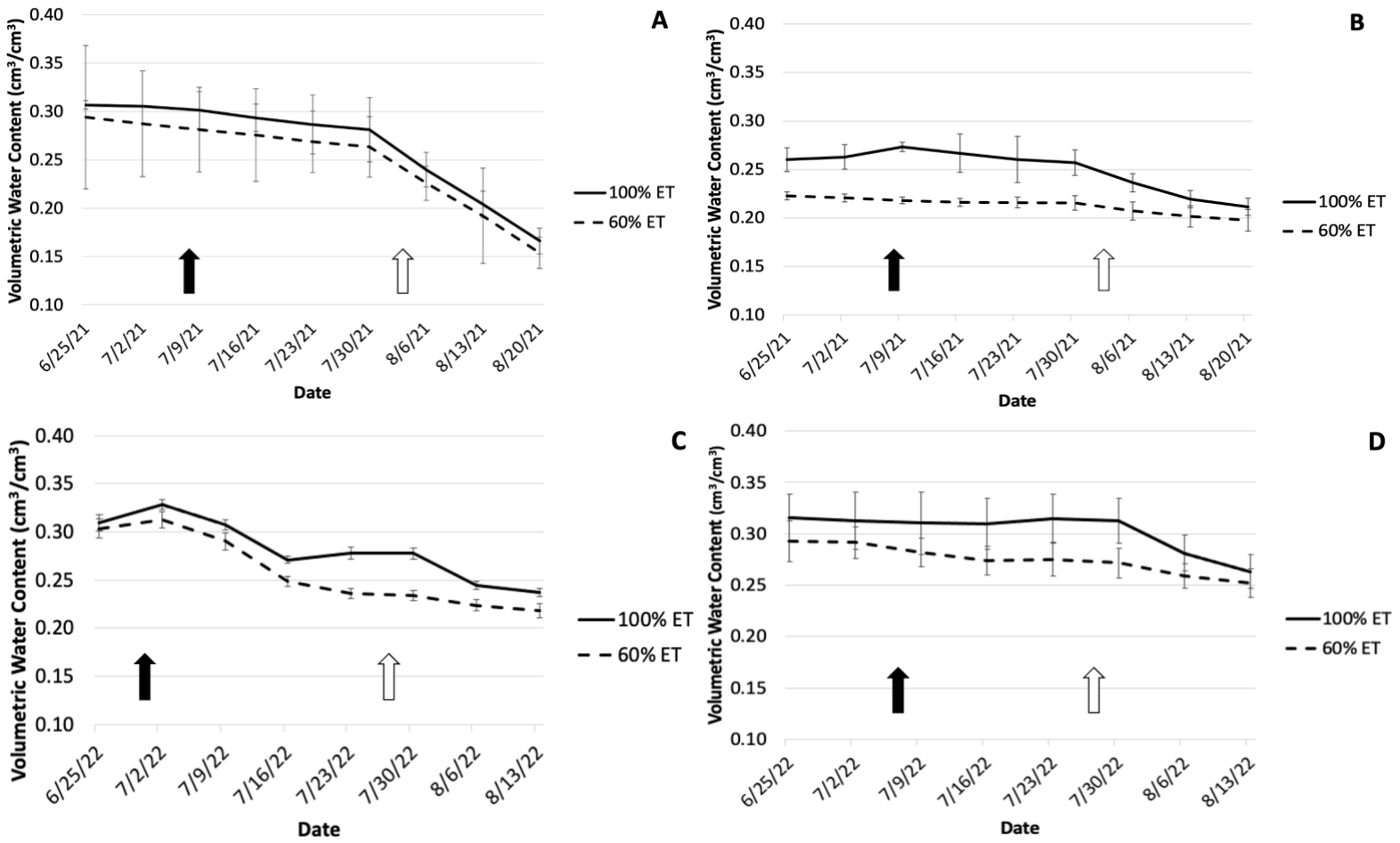



**Figure 3.** Soil moisture averaged across sensors in the (A) fumigated field in 2021 (n = 14), (B) inoculated field in 2021 (n = 16), (C) fumigated field in 2022 (n = 14), and (D) inoculated field in 2022 (n = 16). Solid black lines represent soil moisture in the 100% ET

treatment. Dashed black lines represent soil moisture in the 60% ET treatment. Black arrows represent when the deficit irrigation treatment began, white arrows represent when irrigation was stopped completely.

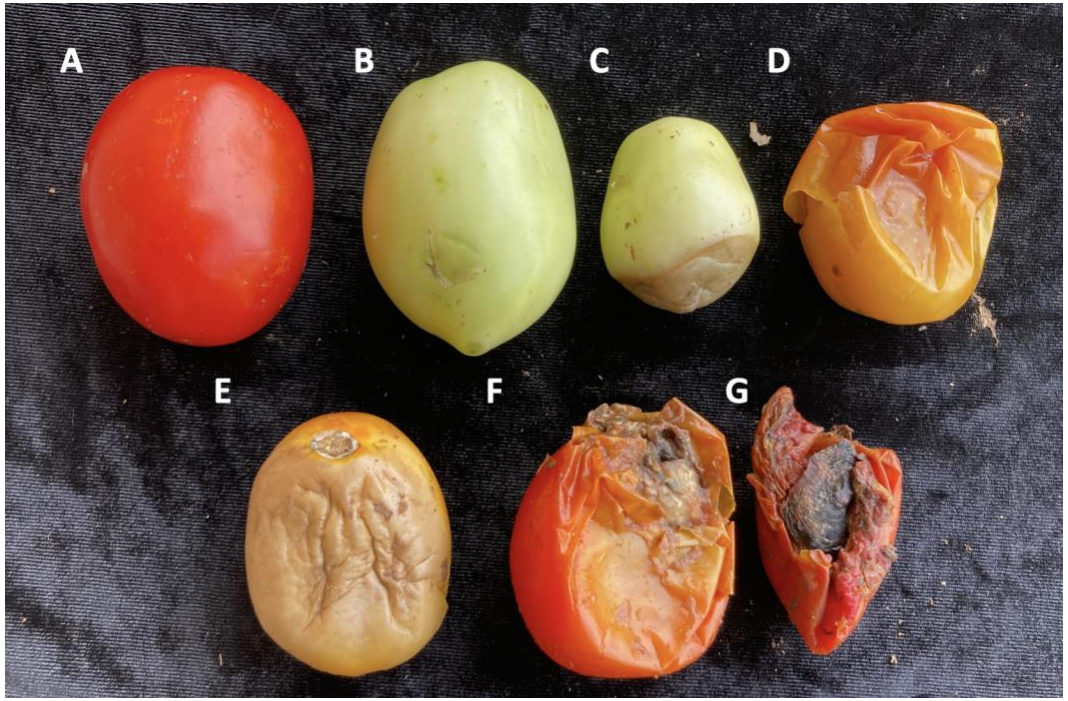



**Figure 4**. Representative fruit from the seven categories. Top row left to right: (A) Red marketable, (B) green marketable, (C) blossom end rot, and (D) loss of use (L/U). Bottom row right to left: (E) Sunburn, (F) sunburn with rot, and (G) rot.

**Figure 5.** From left to right, symptoms of early vine decline (some, but not all branches are necrotic) and advanced vine decline (all branches are necrotic).

**Tables**

**Table 1.** Vine decline (total vine decline and advanced decline) incidence as a proportion of plants with symptoms in all four cultivars in the inoculated field (years separated and combined).

| | | Total Decline (%)[ab] | | | | Advanced Decline (%)[ac] | | | |
|---|---|---|---|---|---|---|---|---|---|
| Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 | HM3887 | SVTM9016 | N6428 | H5608 |
| 2021 | 100% | 67 ± 18 a | 40 ± 31 a | 20 ± 12 a | 53 ± 18 a | 33 ± 13 a | 40 ± 31 a | 7 ± 7 a | 27 ± 18 a |
| | 60% | 93 ± 7 a | 33 ± 18 a | 47 ± 7 a | 53 ± 27 a | 55 ± 16 a | 13 ± 7 a | 20 ± 12 a | 33 ± 18 a |
| | *P* value Irrig | 0.355 | 0.801 | 0.145 | 0.727 | 0.372 | 0.531 | 0.464 | 0.727 |
| 2022 | 100% | 53 ± 24 a | 73 ± 7 a | 47 ± 18 a | 80 ± 12 a | 47 ± 27 a | 47 ± 13 a | 0 ± 0 a | 20 ± 12 a |
| | 60% | 73 ± 7 a | 60 ± 20 a | 40 ± 20 a | 73 ± 7 a | 47 ± 7 a | 33 ± 18 a | 27 ± 18 a | 13 ± 7 a |
| | *P* value Irrig | 0.731 | 0.598 | 0.494 | 0.521 | 0.849 | 0.240 | 0.221 | 0.799 |
| Years Comb. | 100% | 60 ± 14 a | 57 ± 16 a | 33 ± 11 a | 67 ± 11 a | 40 ± 14 a | 43 ± 15 a | 3 ± 3 a | 23 ± 10 a |
| | 60% | 83 ± 6 a | 47 ± 13 a | 43 ± 10 a | 63 ± 13 a | 51 ± 8 a | 23 ± 10 a | 23 ± 10 a | 23 ± 10 a |
| | *P* value Irrig | 0.306 | 0.618 | 0.526 | 0.629 | 0.697 | 0.244 | 0.075 | 1.000 |

[a] Values in a column followed by the same letter are not significantly different according to Dunnett's Test ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[b] Total decline is the sum of early and advanced decline incidence.

[c] Plants were said to have advanced decline when all branches were symptomatic (turgor loss and/or necrotic leaves) or were dead.

**Table 2.** Area Under the Disease Progress Curve (AUDPC) values based on advanced vine decline incidence in each cultivar comparing irrigation treatments in the inoculated field (years separated)[ab].

| | HM3887[b] | | SVTM9016[b] | | N6428[b] | | H5608[b] | |
|---|---|---|---|---|---|---|---|---|
| Irrig (% ET) | 2021 | 2022 | 2021 | 2022 | 2021 | 2022 | 2021 | 2022 |
| 100% | 2.2 ± 0.6 a | 2.8 ± 0.7 a | 0.5 ± 0.5 a | 2.7 ± 1.5 a | 0.9 ± 1.2 a | 4.0 ± 0.6 a | 1.3 ± 0.5 a | 4.0 ± 0.9 a |
| 60% | 2.1 ± 0.4 a | 2.6 ± 0.3 a | 1.7 ± 1.0 a | 3.7 ± 0.4 a | 0.4 ± 1.0 a | 3.7 ± 0.4 a | -0.4 ± 1.3 a | 4.4 ± 0.1 a |
| *P* value Irrig | 0.853 | 0.615 | 0.550 | 0.199[c] | 0.504 | 0.350 | 0.092[c] | 0.091 |

[a] AUDPC curves were calculated using incidence data collected at three time points between DI onset and harvest.

[b] Values in a column followed by the same letter are not significantly different according to Dunnett's test ($P = 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3).

[c] Values were calculated using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524 (n = 3 per year).

**Table 3.** Any stem rot incidence as a proportion of plants evaluated comparing irrigation treatments in the fumigated and inoculated treatments (years separated and combined).

| | | HM3887[a] | | | SVTM9016[a] | | | N6428[ab] | | H5608[a] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Path | Irrig (% ET) | 2021 | 2022 | Years Comb. | 2021 | 2022 | Years Comb. | 2021 | 2022 | 2021 | 2022 | Years Comb. |
| Fum | 100% | 0±0 a | 0±0 a | 0±0 a | 27±13 a | 7±7 a | 17±8 a | 53±7 a | 13±7 a | 20±12 a | 13±13 a | 17±8 a |
| | 60% | 33±18 b | 7±7 a | 20±10 b | 7±7 a | 13±13 a | 10±7 a | 20±0 a | 7±7 a | 27±7 a | 20±12 a | 23±6 a |
| Inoc | 100% | 87±7 c | 100±0 b | 93±4 c | 87±7 b | 93±7 b | 90±4 b | 67±7 b | 93±7 b | 87±13 b | 93±7 b | 90±7 b |
| | 60% | 100±0 d | 100±0 b | 100±0 d | 93±7 b | 80±20 b | 87±10 b | 87±7 b | 80±12 b | 100±0 b | 87±7 b | 93±4 b |
| *P* value Pathogen | | < 0.001 | < 0.0001 | < 0.0001 | 0.001 | 0.002 | < 0.001 | 0.002 | 0.001 | 0.001 | 0.002 | < 0.001 |
| *P* value Irrigation | | 0.024 | 0.356 | 0.017 | 0.690 | 0.880 | 0.688 | 0.781 | 0.297 | 0.268 | 1.000 | 0.426 |
| *P* value Path x Irrig | | 0.469 | 0.356 | 0.341 | 0.242 | 0.632 | 0.651 | 0.012 | 0.833 | 0.822 | 0.441 | 0.622 |

[a] Values in a column followed by the same letter are not significantly different according to Dunnett's test ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[b] Years could not be combined due to a Year x Irrigation treatment effect ($P = 0.007$).

**Table 4.** Total yield biomass comparing irrigation treatments within each cultivar in the fumigated and inoculated treatments (years separated and combined).

| | | | Cultivar[a] | | | |
|---|---|---|---|---|---|---|
| Pathogen | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| Fumigated | 2021 | 100% | 155,907 ± 14,399 a | 177,866 ± 11,876 a | 124,067 ± 24,746 a | 132,850 ± 18,470 a |
| | | 60% | 128,459 ± 18,141 a | 104,304 ± 15,253 a | 136,144 ± 21,876 a | 109,794 ± 3,959 a |
| | | *P* value Irrig | 0.212 | 0.063 | 0.053 | 0.275[b] |
| | 2022 | 100% | 121,871 ± 3,294 a | 101,010 ± 30,208 a | 122,969 ± 12,077 a | 122,969 ± 5,810 b |
| | | 60% | 97,716 ± 12,944 a | 108,696 ± 8,715 a | 119,675 ± 6,113 a | 77,954 ± 8,575 a |
| | | *P* value Irrig | 0.072[b] | 0.513[b] | 0.762 | 0.012 |
| | Years Comb. | 100% | 138,889 ± 10,078 a | 139,438 ± 22,496 a | 123,518 ± 12,317 a | 127,910 ± 8,937 b |
| | | 60% | 113,087 ± 12,107 a | 106,500 ± 7,917 a | 127,910 ± 10,805 a | 93,874 ± 8,278 a |
| | | *P* value Irrig | 0.107 | 0.205 | 0.697 | 0.019 |
| Inoculated | 2021 | 100% | 40,624 ± 14,524 a | 103,206 ± 32,736 b | 60,386 ± 22,041 a | 60,386 ± 20,861 a |
| | | 60% | 37,330 ± 16,174 a | 62,582 ± 23,752 b | 73,562 ± 34,089 a | 57,093 ± 27,448 a |
| | | *P* value Irrig | 0.730 | 0.154 | 0.672 | 0.885 |
| | 2022 | 100% | 19,763 ± 5,032 b | 38,428 ± 6,113 a | 34,036 ± 8,575 a | 28,546 ± 4,392 a |
| | | 60% | 9,881 ± 3,294 a | 71,369 ± 17,974 a | 30,742 ± 9,759 a | 32,938 ± 16,578 a |
| | | *P* value Irrig | 0.035 | 0.225 | 0.824[b] | 0.653[b] |
| | Years Comb. | 100% | 30,193 ± 8,307 a | 70,817 ± 20,775 a | 47,211 ± 12,107 a | 44,466 ± 11,899 a |
| | | 60% | 23,605 ± 9,600 a | 66,974 ± 13,465 a | 52,152 ± 18,524 a | 45,015 ± 15,324 a |
| | | *P* value Irrig | 0.557 | 0.867 | 0.806 | 0.627[b] |

[a] Values in a column followed by the same letter are not significantly different according to Dunnett's Test ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[b] *P* values were calculated using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524 (n = 3 per year).

**Table 5.** Total yield differences between the fumigated and inoculated treatments within each cultivar comparing irrigation treatments (years separated and combined).

| Cultivar | Year | Irrig (% ET) | Yield Diff (%) (Fum – Inoc)[a] | *P* value Irrig |
|---|---|---|---|---|
| HM3887 | 2021 | 100% | -72 ± 11 a | 0.608 |
| | | 60% | -69 ± 13 a | |
| | 2022 | 100% | -84 ± 4 a | 0.039 |
| | | 60% | -89 ± 5 b | |
| | Years Comb. | 100% | -78 ± 6 a | 0.883 |
| | | 60% | -79 ± 8 a | |
| SVTM9016 | 2021 | 100% ET | -40 ± 20 a | 0.825[b] |
| | | 60% ET | -40 ± 23 a | |
| | 2022 | 100% ET | -58 ± 9 a | 0.275[b] |
| | | 60% ET | -31 ± 20 a | |
| | Combined | 100% ET | -49 ± 10 a | 0.295 |
| | | 60% ET | -35 ± 14 a | |
| N6428 | 2021 | 100% ET | -40 ± 27 a | 0.812 |
| | | 60% ET | -35 ± 39 a | |
| | 2022 | 100% ET | -72 ± 7 a | 0.894 |
| | | 60% ET | -74 ± 9 a | |
| | Combined | 100% ET | -56 ± 14 a | 0.873[b] |
| | | 60% ET | -54 ± 20 a | |
| H5608 | 2021 | 100% ET | -52 ± 20 a | 0.754 |
| | | 60% ET | -48 ± 24 a | |
| | 2022 | 100% ET | -76 ± 4 a | 0.416 |
| | | 60% ET | -58 ± 21 a | |
| | Combined | 100% ET | -64 ± 11 a | 0.749[b] |
| | | 60% ET | -53 ± 14 a | |

[a] Values in a column followed by the same letter are not significantly different according to Dunnett's Test ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[b] *P* values were calculated using Kruskal-Wallis for nonparametric data with RStudio v. 2023.06.1+524 (n = 3 per year).

**Table 6.** The percent of red marketable fruit comparing irrigation treatments within each cultivar in the fumigated and inoculated treatments (years separated and combined)[ab].

| | | | Cultivar[c] | | | |
|---|---|---|---|---|---|---|
| Pathogen | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| Fumigated | 2021 | 100% | 84 ± 3 a | 87 ± 1 a | 86 ± 1 a | 89 ± 2 a |
| | | 60% | 85 ± 3 a | 81 ± 2 a | 86 ± 3 a | 85 ± 3 a |
| | | *P* value Irrig | 0.923 | 0.051 | 0.827[d] | 0.335 |
| | 2022 | 100% | 89 ± 0 a | 54 ± 9 b | 89 ± 3 a | 88 ± 5 b |
| | | 60% | 87 ± 2 a | 79 ± 2 b | 90 ± 2 a | 79 ± 1 a |
| | | *P* value Irrig | 0.260 | 0.513[d] | 0.885 | 0.013 |
| | Years Comb. | 100% | 90 ± 3 a | 77 ± 7 a | 89 ± 2 a | 93 ± 2 b |
| | | 60% | 89 ± 2 a | 81 ± 1 a | 90 ± 2 a | 86 ± 2 a |
| | | *P* value Irrig | 0.822 | 0.337[d] | 0.875 | 0.020 |
| Pathogen | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| Inoculated | 2021 | 100% | 43 ± 6 a | 69 ± 16 a | 53 ± 8 a | 59 ± 8 a |
| | | 60% | 41 ± 0 a | 49 ± 6 a | 62 ± 12 a | 52 ± 20 a |
| | | *P* value Irrig | 0.513[d] | 0.513[d] | 0.275[d] | 0.685 |
| | 2022 | 100% | 72 ± 6 a | 76 ± 7 a | 69 ± 3 a | 77 ± 4 a |
| | | 60% | 64 ± 0 a | 72 ± 13 a | 65 ± 5 a | 75 ± 9 a |
| | | *P* value Irrig | 0.513[d] | 0.827[d] | 0.222 | 0.918 |
| | Years Comb. | 100% | 57 ± 8 a | 72 ± 8 a | 61 ± 5 a | 68 ± 6 a |
| | | 60% | 52 ± 5 a | 60 ± 8 a | 63 ± 6 a | 63 ± 11 a |
| | | *P* value Irrig | 1.000[d] | 0.513[d] | 0.705 | 0.754 |

[a] A representative subset of total fruit harvested in the field was collected from each plot and sorted into five categories: red marketable (red/pink fruit), green (all green), sunburned, blossom end rot (BER), and rot (any combination of rot or L/U).

[b] Percentages were calculated by dividing the mass of fruit in each category by the total fruit yield.

[c] Values in a column followed by the same letter are not significantly different according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[d] *P* values were calculated using Kruskal-Wallis for non-parametric data with RStudio v. 2023.06.1+524.

**Table 7.** Sunburned fruit as a percentage of the total yield comparing irrigation treatments within each cultivar in the fumigated and inoculated treatments (years separated and combined)[ab].

| | | | Cultivar[c] | | | |
|---|---|---|---|---|---|---|
| Pathogen | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| Fumigated | 2021 | 100% | 0.8 ± 0.8 a | 0.0 ± 0.2 a | 0.0 ± 0.1 a | 2.0 ± 2.0 a |
| | | 60% | 0.0 ± 0.0 a | 1.0 ± 0.3 a | 1.0 ± 0.1 a | 0.0 ± 0.2 a |
| | | *P* value Irrig | 0.317[d] | 0.472 | 0.046[d] | 0.246[d] |
| | 2022 | 100% | 1.4 ± 0.6 a | 4.0 ± 1.3 a | 1.0 ± 1.1 a | 1.0 ± 0.8 a |
| | | 60% | 3.1 ± 0.7 a | 6.0 ± 1.7 a | 1.0 ± 0.1 a | 5.0 ± 3.3 a |
| | | *P* value Irrig | 0.197 | 0.141 | 0.513[d] | 0.408 |
| | Years Comb. | 100% | 1.1 ± 0.5 a | 1.0 ± 0.4 a | 0.7 ± 0.3 a | 1.8 ± 0.7 a |
| | | 60% | 1.9 ± 0.8 a | 3.3 ± 1.3 a | 0.8 ± 0.3 a | 2.6 ± 1.1 a |
| | | *P* value Irrig | 0.868[d] | 0.200 | 0.053[d] | 0.912 |
| Pathogen | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| Inoculated | 2021 | 100% | 17.2 ± 3.4 a | 7.5 ± 6.1 a | 3.2 ± 1.3 a | 10.3 ± 4.1 a |
| | | 60% | 19.9 ± 2.7 a | 12.6 ± 7.9 a | 2.8 ± 2.1 a | 13.6 ± 9.1 a |
| | | *P* value Irrig | 0.055[d] | 0.522[d] | 0.689 | 0.936 |
| | 2022 | 100% | 15.3 ± 2.8 a | 14.2 ± 6.9 a | 12.1 ± 3.2 a | 15.1 ± 4.1 a |
| | | 60% | 26 ± 3.1 b | 17.3 ± 12.3 a | 12.8 ± 2.5 a | 17.9 ± 7.2 a |
| | | *P* value Irrig | 0.050[d] | 0.954 | 0.954 | 0.858 |
| | Years Comb. | 100% | 16.2 ± 1.0 a | 10.9 ± 4.4 a | 6.2 ± 2.5 a | 12.7 ± 2.8 a |
| | | 60% | 22.9 ± 2.3 a | 16.2 ± 6.6 a | 6.6 ± 2.7 a | 15.7 ± 5.3 a |
| | | *P* value Irrig | 0.066[d] | 0.522[d] | 0.882 | 0.947 |

[a] A representative subset of total fruit harvested in the field was collected from each plot and sorted into five categories: red marketable (red/pink fruit), green (all green), sunburned, blossom end rot (BER), and rot (any combination of rot or L/U).

[b] Percentages were calculated by dividing the mass of fruit in each category by the total fruit yield.

[c] Values in a column followed by the same letter are not significantly different according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[d] *P* values were calculated using Kruskal-Wallis for non-parametric data with RStudio v. 2023.06.1+524.

**Table 8.** Damaged fruit as a percentage of the total yield comparing irrigation treatments within each cultivar in the fumigated and inoculated treatments (years separated and combined)[ab].

| | | | Cultivar[c] | | | |
|---|---|---|---|---|---|---|
| Pathogen | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| Fumigated | 2021 | 100% | 11.9 ± 2.3 a | 3.5 ± 0.2 a | 2.8 ± 0.9 b | 5.3 ± 2.7 a |
| | | 60% | 13.0 ± 3.5 a | 3.4 ± 1.7 a | 2.0 ± 0.6 a | 8.3 ± 1.2 a |
| | | *P* value Irrig | 0.929 | 0.513[d] | 0.020 | 0.275[d] |
| | 2022 | 100% | 1.2 ± 1.4 b | 0.2 ± 1.0 a | 0.2 ± 1.7 a | 0.1 ± 5.2 a |
| | | 60% | 0.2 ± 1.7 a | 0.7 ± 0.5 a | 0.7 ± 1.1 a | 0.3 ± 1.1 a |
| | | *P* value Irrig | 0.046[d] | 0.527 | 0.228 | 0.150 |
| | Years Comb. | 100% | 6.5 ± 2.6 a | 1.9 ± 0.8 a | 1.5 ± 0.7 a | 2.7 ± 1.7 a |
| | | 60% | 6.4 ± 3.2 a | 2.0 ± 1.0 a | 1.3 ± 0.5 a | 4.3 ± 1.9 a |
| | | *P* value Irrig | 0.521[d] | 0.905 | 0.872[d] | 0.199[d] |
| Pathogen | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| Inoculated | 2021 | 100% | 37.2 ± 2.2 a | 27.9 ± 5.6 a | 10.1 ± 10.3 a | 22.1 ± 1.3 a |
| | | 60% | 36.7 ± 1.3 a | 23.3 ± 8.1 a | 29.5 ± 8.3 a | 26.0 ± 9.1 a |
| | | *P* value Irrig | 0.827[d] | 0.127[d] | 0.783 | 0.513[d] |
| | 2022 | 100% | 29.6 ± 1.9 a | 12.6 ± 4.6 a | 16.1 ± 1.6 a | 10.7 ± 5.3 a |
| | | 60% | 22.0 ± 6.6 a | 16.6 ± 7.5 a | 15.8 ± 6.8 a | 20.5 ± 5.9 a |
| | | *P* value Irrig | 0.513[d] | 0.827[d] | 0.513[d] | 0.339 |
| | Years Comb. | 100% | 33.4 ± 2.1 a | 13.1 ± 3.5 a | 20.2 ± 5.8 a | 16.4 ± 3.5 a |
| | | 60% | 29.3 ± 4.4 a | 22.6 ± 5.8 a | 20.0 ± 5.0 a | 23.3 ± 5.0 a |
| | | *P* value Irrig | 0.873[d] | 0.294 | 0.936 | 0.522[d] |

[a] A representative subset of total fruit harvested in the field was collected from each plot and sorted into five categories: red marketable (red/pink fruit), green (all green), sunburned, blossom end rot (BER), and rot (any combination of rot or L/U).

[b] Percentages were calculated by dividing the mass of fruit in each category by the total fruit yield.

[c] Values in a column followed by the same letter are not significantly different according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[d] *P* values were calculated using Kruskal-Wallis for non-parametric data with RStudio v. 2023.06.1+524.

**Table 9.** Hue (red color in degrees) of individual cultivars comparing irrigation treatments in the fumigated and inoculated treatments (years separated and combined)[ab].

| | | | Cultivar[c] | | | |
|---|---|---|---|---|---|---|
| Pathogen | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| Fumigated | 2021 | 100% | 20.8 ± 0.4 a | 20.7 ± 0.3 a | 20.7 ± 0.3 a | 19.8 ± 0.2 a |
| | | 60% | 20.8 ± 0.4 a | 21.0 ± 0.5 a | 20.3 ± 0.3 a | 20.2 ± 0.2 a |
| | | *P* value Irrig | 1.000[d] | 0.529 | 0.456[d] | 0.293 |
| | 2022 | 100% | 21.2 ± 0.2 a | 22.5 ± 0.3 a | 22.3 ± 0.3 a | 21.5 ± 0.3 a |
| | | 60% | 21.3 ± 0.2 a | 22.3 ± 0.4 a | 22.0 ± 0.3 a | 21.2 ± 0.2 a |
| | | *P* value Irrig | 0.451[d] | 0.667 | 0.529 | 0.184 |
| | Years Comb. | 100% | 21.0 ± 0.2 a | 21.6 ± 0.5 a | 21.5 ± 0.4 a | 20.7 ± 0.4 a |
| | | 60% | 21.1 ± 0.2 a | 21.7 ± 0.4 a | 21.2 ± 0.4 a | 20.7 ± 0.2 a |
| | | *P* value Irrig | 0.665[d] | 0.936[d] | 0.594 | 1.000 |
| Inoculated | Year | Irrig (% ET) | HM3887 | SVTM9016[e] | N6428 | H5608 |
| | 2021 | 100% | 21.8 ± 0.2 a | 21.2 ± 0.2 a | 21.7 ± 0.3 a | 20.8 ± 0.4 a |
| | | 60% | 21.5 ± 0.0 a | 21.8 ± 0.2 a | 21.7 ± 0.3 a | 21.0 ± 0.8 a |
| | | *P* value Irrig | 0.114[d] | 0.068[d] | 1.000[d] | 0.658[d] |
| | 2022 | 100% | 22.7 ± 0.6 a | 24.2 ± 0.3 a | 23.3 ± 0.4 a | 21.8 ± 0.2 a |
| | | 60% | 23.3 ± 0.4 a | 22.8 ± 0.7 a | 24.0 ± 0.3 a | 22.7 ± 0.9 a |
| | | *P* value Irrig | 0.466 | 0.099[d] | 0.261[d] | 0.507[d] |
| | Years Comb. | 100% | 22.3 ± 0.3 a | NA | 22.5 ± 0.4 a | 21.3 ± 0.3 a |
| | | 60% | 22.4 ± 0.5 a | NA | 22.8 ± 0.6 a | 21.8 ± 0.6 a |
| | | *P* value Irrig | 0.934[d] | NA | 0.682[d] | 0.502 |

[a] A representative subset of total fruit harvested in the field was collected from each plot and sorted into five categories: red marketable (red/pink fruit), green (all green), sunburned, blossom end rot (BER), and rot (any combination of rot or L/U).

[b] Percentages were calculated by dividing the mass of fruit in each category by the total fruit yield.

[c] Values in a column followed by the same letter are not significantly different according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[d] *P* values were calculated using Kruskal-Wallis for non-parametric data with RStudio v. 2023.06.1+524 .

[e] Years could not be combined due to a Year x Irrigation treatment effect.

**Table 10.** Brix (soluble solids in degrees) of all cultivars comparing irrigation treatments in the fumigated and inoculated treatments (years separated and combined)[ab].

| | | | Cultivar[c] | | | |
|---|---|---|---|---|---|---|
| Pathogen | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| Fumigated | 2021 | 100% | 5.93 ± 0.24 a | 5.13 ± 0.24 a | 5.37 ± 0.30 a | 5.27 ± 0.13 a |
| | | 60% | 6.03 ± 0.15 a | 5.53 ± 0.17 a | 5.50 ± 0.21 a | 5.50 ± 0.15 a |
| | | *P* value Irrig | 0.756 | 0.147 | 0.270 | 0.487[d] |
| | 2022 | 100% | 5.97 ± 0.28 a | 5.77 ± 0.55 a | 5.17 ± 0.30 a | 5.07 ± 0.09 a |
| | | 60% | 6.77 ± 0.37 a | 5.77 ± 0.22 a | 5.50 ± 0.36 a | 5.53 ± 0.26 a |
| | | *P* value Irrig | 0.120 | 0.827[d] | 0.549 | 0.184[d] |
| | Years Comb. | 100% | 5.95 ± 0.17 a | 5.45 ± 0.30 a | 5.27 ± 0.19 a | 5.17 ± 0.08 a |
| | | 60% | 6.40 ± 0.24 a | 5.65 ± 0.13 a | 5.50 ± 0.19 a | 5.52 ± 0.14 b |
| | | *P* value Irrig | 0.145[d] | 0.470[d] | 0.469[d] | 0.018 |
| Inoculated | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| | 2021 | 100% | 5.80 ± 0.17 a | 5.20 ± 0.15 a | 5.47 ± 0.38 a | 5.23 ± 0.45 a |
| | | 60% | 5.80 ± 0.21 a | 5.37 ± 0.20 a | 5.23 ± 0.24 a | 5.20 ± 0.26 a |
| | | *P* value Irrig | 1.000 | 0.199 | 0.606 | 0.827[d] |
| | 2022 | 100% | 6.70 ± 0.53 a | 5.90 ± 0.12 a | 5.93 ± 0.09 a | 5.67 ± 0.22 a |
| | | 60% | 6.43 ± 0.18 a | 5.57 ± 0.15 a | 6.13 ± 0.19 a | 5.67 ± 0.52 a |
| | | *P* value Irrig | 0.513[d] | 0.214 | 0.376[d] | 1.000 |
| | Years Comb. | 100% | 6.25 ± 0.32 a | 5.55 ± 0.18 a | 5.70 ± 0.20 a | 5.45 ± 0.24 a |
| | | 60% | 6.12 ± 0.19 a | 5.47 ± 0.12 a | 5.68 ± 0.24 a | 5.43 ± 0.28 a |
| | | *P* value Irrig | 0.720 | 0.709 | 0.958 | 0.965 |

[a] A representative subset of total fruit harvested in the field was collected from each plot and sorted into five categories: red marketable (red/pink fruit), green (all green), sunburned, blossom end rot (BER), and rot (any combination of rot or L/U).

[b] Percentages were calculated by dividing the mass of fruit in each category by the total fruit yield.

[c] Values in a column followed by the same letter are not significantly different according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[d] *P* values were calculated using Kruskal-Wallis for non-parametric data with RStudio v. 2023.06.1+524.

**Table 11.** Acidity (pH) of all cultivars comparing irrigation treatments in the fumigated and inoculated treatments (years separated and combined)[ab].

| | | | Cultivar[c] | | | |
|---|---|---|---|---|---|---|
| Pathogen | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| Fumigated | 2021 | 100% | 4.42 ± 0.02 a | 4.37 ± 0.01 a | 4.48 ± 0.03 a | 4.46 ± 0.01 a |
| | | 60% | 4.46 ± 0.03 a | 4.40 ± 0.02 a | 4.50 ± 0.04 a | 4.47 ± 0.05 a |
| | | *P* value Irrig | 0.268[d] | 0.184[d] | 0.724 | 0.827[d] |
| | 2022 | 100% | 4.55 ± 0.01 a | 4.44 ± 0.02 a | 4.54 ± 0.03 a | 4.55 ± 0.02 a |
| | | 60% | 4.52 ± 0.03 a | 4.46 ± 0.00 a | 4.50 ± 0.01 a | 4.60 ± 0.03 a |
| | | *P* value Irrig | 0.513[d] | 0.369[d] | 0.376[d] | 0.275[d] |
| | Years Comb. | 100% | 4.49 ± 0.03 a | 4.41 ± 0.02 a | 4.51 ± 0.02 a | 4.51 ± 0.02 a |
| | | 60% | 4.49 ± 0.02 a | 4.43 ± 0.02 a | 4.50 ± 0.02 a | 4.54 ± 0.04 a |
| | | *P* value Irrig | 0.936[d] | 0.260[d] | 0.669 | 0.510 |
| Inoculated | Year | Irrig (% ET) | HM3887 | SVTM9016 | N6428 | H5608 |
| | 2021 | 100% | 4.59 ± 0.01 a | 4.44 ± 0.05 a | 4.51 ± 0.00 a | 4.55 ± 0.04 a |
| | | 60% | 4.55 ± 0.02 a | 4.50 ± 0.04 a | 4.56 ± 0.05 a | 4.59 ± 0.08 a |
| | | *P* value Irrig | 0.259 | 0.102 | 0.507[d] | 0.533 |
| | 2022 | 100% | 4.63 ± 0.06 a | 4.48 ± 0.05 a | 4.54 ± 0.02 a | 4.66 ± 0.01 a |
| | | 60% | 4.69 ± 0.01 a | 4.40 ± 0.06 a | 4.58 ± 0.05 a | 4.66 ± 0.08 a |
| | | *P* value Irrig | 0.513[d] | 0.410 | 0.565 | 0.513[d] |
| | Years Comb. | 100% | 4.61 ± 0.03 a | 4.46 ± 0.03 a | 4.53 ± 0.01 a | 4.61 ± 0.03 a |
| | | 60% | 4.62 ± 0.03 a | 4.45 ± 0.04 a | 4.57 ± 0.03 a | 4.63 ± 0.06 a |
| | | *P* value Irrig | 0.826 | 0.748[d] | 0.334[d] | 0.721 |

[a] A representative subset of total fruit harvested in the field was collected from each plot and sorted into five categories: red marketable (red/pink fruit), green (all green), sunburned, blossom end rot (BER), and rot (any combination of rot or L/U).

[b] Percentages were calculated by dividing the mass of fruit in each category by the total fruit yield.

[c] Values in a column followed by the same letter are not significantly different according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[d] *P* values were calculated using Kruskal-Wallis for non-parametric data with RStudio v. 2023.06.1+524.

**Table 12.** Vine decline (total vine decline and advanced decline) incidence at harvest as a proportion of plants with symptoms in all four cultivars in the inoculated treatment (years separated and combined)[a].

| | | Advanced Decline (%)[bc] | | | Total Decline (%)[bd] | | |
|---|---|---|---|---|---|---|---|
| Cultivar | Irrig (% ET) | 2021 | 2022 | Years Comb. | 2021 | 2022 | Years Comb. |
| HM3887 | 100% | 33 ± 13 a | 47 ± 27 b | 40 ± 14 b | 67 ± 18 a | 53 ± 24 a | 60 ± 14 a |
| | 60% | 55 ± 16 a | 47 ± 7 b | 51 ± 8 b | 93 ± 7 a | 73 ± 7 a | 83 ± 6 a |
| SVTM9016 | 100% | 40 ± 31 a | 47 ± 13 b | 43 ± 15 b | 40 ± 31 a | 73 ± 7 a | 57 ± 16 a |
| | 60% | 13 ± 7 a | 33 ± 18 b | 23 ± 10 b | 33 ± 18 a | 60 ± 20 a | 47 ± 13 a |
| N6428 | 100% | 7 ± 7 a | 0 ± 0 a | 3 ± 3 a | 20 ± 12 a | 47 ± 18 a | 33 ± 11 a |
| | 60% | 20 ± 12 a | 27 ± 18 a | 23 ± 10 a | 47 ± 7 a | 40 ± 29 a | 43 ± 10 a |
| H5608 | 100% | 27 ± 18 a | 20 ± 12 ab | 23 ± 10 ab | 53 ± 18 a | 80 ± 12 a | 67 ± 11 a |
| | 60% | 33 ± 18 a | 13 ± 7 ab | 23 ± 10 ab | 53 ± 27 a | 73 ± 7 a | 63 ± 13 a |
| *P* value Irrigation | | 0.815 | 0.899 | 0.768 | 0.522 | 0.581 | 0.855 |
| *P* value Cultivar | | 0.377 | 0.050 | 0.008 | 0.098 | 0.233 | 0.038 |
| *P* value Irrig x Cult | | 0.593 | 0.388 | 0.192 | 0.660 | 0.874 | 0.596 |

[a] There was no vine decline in the fumigated field.

[b] Values in a column followed by the same letter are not significantly different according to Tukey's HSD (*P* = 0.05). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 each year).

[c] Plants were said to have advanced decline when all branches were symptomatic (turgor loss and/or necrotic leaves) or were dead.

[d] Total decline is the sum of early and advanced decline incidence.

**Table 13.** Advanced decline Area Under the Disease Progress Curve (AUDPC) based on advanced decline incidence comparing cultivars and irrigation treatments in the inoculated treatment in 2021 and 2022.

| | | Adv Decl AUDPC[ab] | |
|---|---|---|---|
| Irrigation | Cultivar | 2021 | 2022 |
| 100% ET | HM3887 | 2.2 ± 0.4 a | 2.8 ± 0.5 a |
| | SVTM9016 | 2.1 ± 0.3 a | 2.6 ± 0.2 a |
| | N6428 | 1.7 ± 0.5 a | 2.8 ± 0.5 a |
| | H5608 | 2.2 ± 0.5 a | 3.2 ± 0.7 a |
| 60% ET | HM3887 | 1.7 ± 0.6 a | 3.2 ± 0.6 a |
| | SVTM9016 | 2.2 ± 0.6 a | 3.9 ± 0.3 a |
| | N6428 | 1.8 ± 0.2 a | 2.9 ± 0.2 a |
| | H5608 | 1.8 ± 0.3 a | 3.5 ± 0.3 a |
| *P* value Irrigation | | 0.334 | 0.204 |
| *P* value Cultivar | | 0.934 | 0.221 |
| *P* value Irrig x Cult | | 0.890 | 0.694 |

[a] AUDPC curves were calculated using incidence data collected at three time points between DI onset and harvest.

[b] Values in a column followed by the same letter are not significantly different according to Tukey's HSD (*P* = 0.05). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3).

**Table 14.** "Any stem rot" at harvest as a proportion of plants with symptoms comparing cultivars and irrigation treatments in the inoculated treatment[ab].

| Cultivar | Irrig (% ET) | 2021[c] | 2022[c] |
|---|---|---|---|
| HM3887 | 100% | 87 ± 7 a | 100 ± 0 a |
| | 60% | 100 ± 0 b | 100 ± 0 a |
| SVTM9016 | 100% | 87 ± 7 a | 93 ± 7 a |
| | 60% | 93 ± 7 b | 80 ± 20 a |
| N6428 | 100% | 67 ± 7 a | 93 ± 7 a |
| | 60% | 87 ± 7 b | 80 ± 12 a |
| H5608 | 100% | 87 ± 13 a | 93 ± 7 a |
| | 60% | 100 ± 0 b | 87 ± 7 a |
| *P* value Irrigation | | 0.024 | 0.256 |
| *P* value Cultivar | | 0.102 | 0.337 |
| *P* value Irrig x Cult | | 0.936 | 0.904 |

[a] Any stem rot incidence was quantified as the percent of five randomly selected plants per treatment with rot.

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

[c] Values in a column followed by the same letter are not significantly different according to Dunnett's Test (*P* = 0.05). The ± is the standard error of the mean.

**Table 15.** Total yield biomass comparing cultivars and irrigation treatments in the inoculated treatment (years separated and combined)[ab].

| Year | Irrig | Cultivar | Yield Biomass (kg/ha)[c] |
|---|---|---|---|
| 2021 | 100% | HM3887 | 40,624 ± 14,524 a |
| | | SVTM9016 | 103,206 ± 32,736 b |
| | | N6428 | 60,386 ± 22,041 a |
| | 60% | H5608 | 60,386 ± 20,861 a |
| | | HM3887 | 37,330 ± 16,174 a |
| | | SVTM9016 | 62,582 ± 23,752 b |
| | | N6428 | 73,562 ± 34,089 a |
| | | H5608 | 57,093 ± 27,448 a |
| *P* value Irrigation | | | 0.324 |
| *P* value Cultivar | | | 0.017 |
| *P* value Irrigation x Cultivar | | | 0.181 |
| 2022 | 100% | HM3887 | 19,763 ± 5,032 a |
| | | SVTM9016 | 38,428 ± 6,113 a |
| | | N6428 | 34,036 ± 8,575 a |
| | 60% | H5608 | 28,546 ± 4,392 a |
| | | HM3887 | 9,881 ± 3,294 a |
| | | SVTM9016 | 71,369 ± 17,974 a |
| | | N6428 | 30,742 ± 9,759 a |
| | | H5608 | 32,938 ± 16,578 a |
| *P* value Irrigation | | | 0.399 |
| *P* value Cultivar | | | 0.010 |
| *P* value Irrigation x Cultivar | | | 0.186 |
| Years Comb. | 100% | HM3887 | 30,193 ± 8,307 a |
| | | SVTM9016 | 70,817 ± 20,775 a |
| | | N6428 | 47,211 ± 12,107 a |
| | 60% | H5608 | 44,466 ± 11,899 a |
| | | HM3887 | 23,605 ± 9,600 a |
| | | SVTM9016 | 66,974 ± 13,465 a |
| | | N6428 | 52,152 ± 18,524 a |
| | | H5608 | 45,015 ± 15,324 a |
| *P* value Irrigation | | | 0.887 |
| *P* value Cultivar | | | 0.014 |
| *P* value Irrigation x Cultivar | | | 0.967 |

[a] Total fruit yields (kg/ha) were extrapolated from fruit harvested in the easternmost monitoring plots (4.6 m x 1.5 m) within each row.

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524.

[c] Mean values followed by the same letter are not significantly different according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean.

**Table 16.** Total yield differences between the fumigated and inoculated treatments comparing irrigation and cultivar treatments (years separated and combined).

| Irrig (% ET) | Cultivar | 2021 | 2022 | Years Comb. |
|---|---|---|---|---|
| 100% | HM3887 | -72 ± 11 a | -84 ± 4 a | -78 ± 6 a |
| | SVTM9016 | -40 ± 20 a | -58 ± 9 a | -49 ± 10 a |
| | N6428 | -40 ± 27 a | -72 ± 7 a | -56 ± 14 a |
| | H5608 | -52 ± 20 a | -76 ± 4 a | -64 ± 11 a |
| 60% | HM3887 | -69 ± 13 a | -89 ± 5 a | -79 ± 8 a |
| | SVTM9016 | -40 ± 23 a | -31 ± 20 a | -35 ± 14 a |
| | N6428 | -35 ± 39 a | -74 ± 9 a | -54 ± 20 a |
| | H5608 | -48 ± 24 a | -58 ± 21 a | -53 ± 14 a |
| *P* value Irrigation | | 0.708 | 0.201 | 0.386 |
| *P* value Cultivar | | 0.056 | 0.008 | 0.012 |
| *P* value Irrig x Cult | | 0.997 | 0.368 | 0.872 |

**Table 17.** Red marketable fruit as a percentage of the total yield biomass of all cultivars comparing irrigation in the inoculated treatment (years separated and combined)[ab].

| Irrig (% ET) | Cultivar | 2021[c] | 2022[c] | Years Comb.[c] |
|---|---|---|---|---|
| 100% ET | HM3887 | 43 ± 6 a | 72 ± 6 a | 57 ± 8 a |
| | SVTM9016 | 69 ± 16 a | 76 ± 7 a | 72 ± 8 a |
| | N6428 | 53 ± 8 a | 69 ± 3 a | 61 ± 5 a |
| | H5608 | 59 ± 8 a | 77 ± 4 a | 68 ± 6 a |
| 60% ET | HM3887 | 41 ± 0 a | 64 ± 0 a | 52 ± 5 a |
| | SVTM9016 | 49 ± 6 a | 72 ± 13 a | 60 ± 8 a |
| | N6428 | 62 ± 12 a | 65 ± 5 a | 63 ± 6 a |
| | H5608 | 52 ± 20 a | 75 ± 9 a | 63 ± 11 a |
| *P* value Irrigation | | 0.470 | 0.376 | 0.341 |
| *P* value Cultivar | | 0.254 | 0.372 | 0.269 |
| *P* value Irrig x Cult | | 0.432 | 0.960 | 0.739 |

[a] The percent red marketable fruit was calculated as a proportion of total fruit yields harvested in the easternmost monitoring plots (4.6 m x 1.5 m) within each row.

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524.

[c] Mean values followed by the same letter are not significantly different according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean.

**Table 18.** Sunburned fruit as a percentage of the total yield biomass of all cultivars comparing irrigation in the inoculated treatment (years separated and combined)[ab].

| Irrigation | Cultivar | 2021[c] | 2022[c] | Years Comb.[c] |
|---|---|---|---|---|
| 100% ET | HM3887 | 17.2 ± 3.4 a | 15.3 ± 2.8 a | 16.2 ± 1 a |
| | SVTM9016 | 7.5 ± 6.1 a | 14.2 ± 6.9 a | 10.9 ± 4.4 a |
| | N6428 | 3.2 ± 1.3 a | 12.1 ± 3.2 a | 6.2 ± 2.5 a |
| | H5608 | 10.3 ± 4.1 a | 15.1 ± 4.1 a | 12.7 ± 2.8 a |
| 60% ET | HM3887 | 19.9 ± 2.7 a | 26 ± 3.1 a | 22.9 ± 2.3 a |
| | SVTM9016 | 12.6 ± 7.9 a | 17.3 ± 12.3 a | 16.2 ± 6.6 a |
| | N6428 | 2.8 ± 2.1 a | 12.8 ± 2.5 a | 6.6 ± 2.7 a |
| | H5608 | 13.6 ± 9.1 a | 17.9 ± 7.2 a | 15.7 ± 5.3 a |
| *P* value Irrigation | | 0.700 | 0.454 | 0.428 |
| *P* value Cultivar | | 0.012 | 0.597 | 0.015 |
| *P* value Irrig x Cult | | 0.803 | 0.870 | 0.833 |

[a] The percent sunburned fruit was calculated as a proportion of total fruit yields harvested in the easternmost monitoring plots (4.6 m x 1.5 m) within each row.

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524.

[c] When there was a significant effect of Cultivar, Tukey's HSD was used to determine significant differences ($P < 0.05$). When there was a significant effect of Irrigation, Dunnett's Test was used to determine significant differences ($P < 0.05$). Values followed by the same letter are not significantly different. The ± is the standard error of the mean.

**Table 19.** Damaged fruit as a percentage of the total yield biomass of all cultivars comparing irrigation in the inoculated treatment[a].

| Irrigation | Cultivar | 2021[b] | 2022[b] | Years Comb.[b] |
|---|---|---|---|---|
| 100% ET | HM3887 | 37 ± 0 a | 30 ± 0 a | 33 ± 2 a |
| | SVTM9016 | 10 ± 6 a | 16 ± 5 a | 13 ± 3 b |
| | N6428 | 28 ± 10 a | 13 ± 2 a | 20 ± 6 ab |
| | H5608 | 22 ± 1 a | 11 ± 5 a | 16 ± 4 ab |
| 60% ET | HM3887 | 37 ± 0 a | 22 ± 6 a | 29 ± 4 a |
| | SVTM9016 | 29 ± 8 a | 16 ± 8 a | 23 ± 6 b |
| | N6428 | 23 ± 8 a | 17 ± 7 a | 20 ± 5 ab |
| | H5608 | 26 ± 9 a | 21 ± 6 a | 23 ± 5 ab |
| *P* value Irrigation | | 0.343 | 0.797 | 0.403 |
| *P* value Cultivar | | 0.119 | 0.271 | 0.031 |
| *P* value Irrig x Cult | | 0.291 | 0.488 | 0.500 |

[a] The percent damaged fruit was calculated as a proportion of total fruit yields harvested in the easternmost monitoring plots (4.6 m x 1.5 m) within each row.

[b] Mean values followed by the same letter are not significantly different according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

**Table 20.** Hue (red color in degrees) of all cultivars comparing irrigation treatments in the inoculated treatment (years separate and combined)[a].

| Irrig (% ET) | Cultivar | 2021[b] | 2022[b] | Years Comb.[b] |
|---|---|---|---|---|
| 100% | HM3887 | 21.8 ± 0.2 a | 22.7 ± 0.6 ab | 22.3 ± 0.3 a |
| | SVTM9016 | 21.2 ± 0.2 a | 24.2 ± 0.3 b | 22.7 ± 0.7 a |
| | N6428 | 21.7 ± 0.3 a | 23.3 ± 0.4 ab | 22.5 ± 0.4 a |
| | H5608 | 20.8 ± 0.4 a | 21.8 ± 0.2 a | 21.3 ± 0.3 a |
| 60% | HM3887 | 21.5 ± 0.0 a | 23.3 ± 0.4 ab | 22.4 ± 0.5 a |
| | SVTM9016 | 21.8 ± 0.2 a | 22.8 ± 0.7 b | 22.3 ± 0.4 a |
| | N6428 | 21.7 ± 0.3 a | 24.0 ± 0.3 ab | 22.8 ± 0.6 a |
| | H5608 | 21.0 ± 0.8 a | 22.7 ± 0.9 a | 21.8 ± 0.6 a |
| *P* value Irrigation | | 0.587 | 0.543 | 0.634 |
| *P* value Cultivar | | 0.102 | 0.040 | 0.147 |
| *P* value Irrig x Cult | | 0.486 | 0.114 | 0.848 |

[a] Approximately 0.5 kg of harvested fruit that had been categorized as "red marketable" per treatment was taken to the Processing Tomato Advisory Board (PTAB) (Davis, CA) for analysis. Lower values signify redder fruit.

[b] Values in a column followed by the same letter are not significantly different according to least square means significant difference ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

**Table 21.** Brix (soluble solids in degrees) of all cultivars comparing irrigation treatments in the inoculated treatments in 2021, 2022, and years combined[a].

| Irrig (% ET) | Cultivar | 2021[b] | 2022[b] | Years Comb.[b] |
|---|---|---|---|---|
| 100% | HM3887 | 5.8 ± 0.2 a | 6.7 ± 0.5 a | 6.3 ± 0.3 a |
| | SVTM9016 | 5.2 ± 0.2 a | 5.9 ± 0.1 a | 5.6 ± 0.2 a |
| | N6428 | 5.5 ± 0.4 a | 5.9 ± 0.1 a | 5.7 ± 0.2 a |
| | H5608 | 5.2 ± 0.4 a | 5.7 ± 0.2 a | 5.5 ± 0.2 a |
| 60% | HM3887 | 5.8 ± 0.2 a | 6.4 ± 0.2 a | 6.1 ± 0.2 a |
| | SVTM9016 | 5.4 ± 0.2 a | 5.6 ± 0.1 a | 5.5 ± 0.1 a |
| | N6428 | 5.2 ± 0.2 a | 6.1 ± 0.2 a | 5.7 ± 0.2 a |
| | H5608 | 5.2 ± 0.3 a | 5.7 ± 0.5 a | 5.4 ± 0.3 a |
| *P* value Irrigation | | 0.853 | 0.642 | 0.699 |
| *P* value Cultivar | | 0.031 | 0.035 | 0.009 |
| *P* value Irrig x Cult | | 0.767 | 0.795 | 0.992 |

[a] Approximately 0.5 kg of harvested fruit that had been categorized as "red marketable" per treatment was taken to the Processing Tomato Advisory Board (PTAB) (Davis, CA) for analysis. Lower values signify redder fruit.

[b] Values in a column followed by the same letter are not significantly different according to least square means significant difference ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

**Table 22.** Acidity (pH) of all cultivars comparing irrigation treatments in the inoculated treatment (years separate and combined)[a].

| Irrig (% ET) | Cultivar | 2021[b] | 2022[b] | Years Comb.[b] |
|---|---|---|---|---|
| 100% | HM3887 | 4.59 ± 0.01 b | 4.63 ± 0.06 a | 4.61 ± 0.03 b |
| | SVTM9016 | 4.44 ± 0.06 a | 4.48 ± 0.05 a | 4.46 ± 0.03 a |
| | N6428 | 4.51 ± 0.01 ab | 4.54 ± 0.02 a | 4.53 ± 0.01 ab |
| | H5608 | 4.55 ± 0.04 b | 4.66 ± 0.01 a | 4.61 ± 0.03 b |
| 60% | HM3887 | 4.69 ± 0.02 b | 4.69 ± 0.01 a | 4.62 ± 0.03 b |
| | SVTM9016 | 4.50 ± 0.04 a | 4.40 ± 0.06 a | 4.45 ± 0.04 a |
| | N6428 | 4.56 ± 0.05 ab | 4.58 ± 0.05 a | 4.57 ± 0.03 ab |
| | H5608 | 4.59 ± 0.08 b | 4.66 ± 0.08 a | 4.63 ± 0.06 b |
| *P* value Irrigation | | 0.246 | 0.892 | 0.517 |
| *P* value Cultivar | | 0.019 | 0.002 | < 0.001 |
| *P* value Irrig x Cult | | 0.379 | 0.530 | 0.872 |

[a] Approximately 0.5 kg of harvested fruit that had been categorized as "red marketable" per treatment was taken to the Processing Tomato Advisory Board (PTAB) (Davis, CA) for analysis. Lower values signify redder fruit.

[b] Values in a column followed by the same letter are not significantly different according to least square means significant difference ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

**Table 23.** Water stress based on stem water potential in each cultivar associated with irrigation treatment at 3 and 6 weeks post DI onset in 2021 and 2 and 7 weeks post DI onset in 2022[a].

| | | | Cultivar[b] | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | HM3887 | | SVTM9016 | | N6428 | | H5608 | |
| Year | WPI[c] | Irrig (% ET) | SWP (bar) | *P* value | SWP (bar) | *P* value | SWP (bar) | *P* value | SWP (bar) | *P* value |
| 2021 | 3 | 100% ET | -8.3 ± 0.2 a | < 0.001 | -8.8 ± 0.4 a | 0.042 | -12.3 ± 0.9 b | 0.031 | -12.6 ± 0.2 b | 0.001 |
| | | 60% ET | -12.2 ± 0.6 b | | -10.9 ± 0.6 b | | -9.3 ± 0.3 a | | -9.8 ± 0.3 a | |
| | 6 | 100% ET | -12.0 ± 1.0 a | 0.059 | -12.0 ± 1.0 a | 0.298 | -13.6 ± 0.7 a | 0.367 | -12.5 ± 0.3 a | 0.528 |
| | | 60% ET | -12.9 ± 1.0 a | | -14.4 ± 1.4 a | | -12.4 ± 0.9 a | | -12.1 ± 0.5 a | |
| 2022 | 2 | 100% ET | -10.8 ± 0.2 a | 0.038 | -11.1 ± 0.1 a | 0.798 | -10.2 ± 0.2 a | 0.287 | -9.6 ± 0.4 a | 0.348 |
| | | 60% ET | -12.1 ± 0.4 b | | -11.3 ± 1.0 a | | -11.1 ± 0.7 a | | -7.4 ± 1.9 a | |
| | 7 | 100% ET | -13.1 ± 0.1 a | 0.011 | -13.7 ± 0.8 a | 0.440 | -11.1 ± 0.3 a | 0.072 | -12.6 ± 0.7 a | 0.029 |
| | | 60% ET | -15.6 ± 0.3 b | | -14.6 ± 0.1 a | | -12.4 ± 0.4 a | | -15.3 ± 0.4 b | |

[a] Midday stem water potential was measured using a pressure bomb (Model 615, PMS Instrument Co., Albany, OR).

[b] Values in a column followed by the same letter are not significantly different according to according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear model with RStudio v. 2023.06.1+524.

[c] Weeks post DI-onset

**Table 24.** Fruit with blossom end rot (BER) at harvest as a percentage of the total yield biomass of all cultivars comparing irrigation in the fumigated treatment (years separated)[ab].

| Irrigation | Cultivar | 2021[c] | 2022[c] |
|---|---|---|---|
| 100% ET | HM3887 | 1 ± 0 a | 1 ± 0 a |
| | SVTM9016 | 8 ± 1 b | 29 ± 10 b |
| | N6428 | 7 ± 3 b | 5 ± 3 a |
| | H5608 | 3 ± 2 ab | 3 ± 1 a |
| 60% ET | HM3887 | 1 ± 0 a | 2 ± 1 a |
| | SVTM9016 | 13 ± 1 b | 11 ± 2 b |
| | N6428 | 9 ± 4 b | 5 ± 1 a |
| | H5608 | 5 ± 2 ab | 7 ± 2 a |
| *P* value Irrigation | | 0.050 | 0.893 |
| *P* value Cultivar | | < 0.001 | < 0.001 |
| *P* value Irrig x Cult | | 0.714 | 0.046 |

[a] The percentage of fruit with blossom end rot (BER) was calculated as a proportion of total fruit yields harvested in the easternmost monitoring plots (4.6 m x 1.5 m) within each row.

[b] Years could not be combined due to a year x irrigation x cultivar effect ($P = 0.040$).

[c] Mean values followed by the same letter are not significantly different according to Tukey's HSD ($P < 0.05$). The ± is the standard error of the mean. Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524 (n = 3 per year).

**Supplemental Tables**

**Supplemental Table 1.** Noteworthy dates in the 2021 and 2022 field seasons.

| Action | 2021 | 2022 |
|---|---|---|
| Transplant | 4/20/21 | 4/13/22 |
| DI starts | 7/7/21 | 6/30/22 |
| SWP[z] measure 1 | 7/16/21 | 6/27/22 |
| SWP measure 2 | 7/26/21 | 7/21/22 |
| Cut water | 8/4/21 | 7/28/22 |
| SWP measure 3 | 8/16/21 | 8/23/22 |
| Harvest | 9/1/21 | 8/25/22 |
| Total days without water[y] | 28 | 28 |
| Season length[x] | 134 | 134 |

[z] SWP = Stem water potential

[y] Total days without water is the number of days between harvest and when water was cut.

[x] Season length was calculated as the number of days between transplant and harvest.

**Supplemental Table 2.** Soil nutrients in the inoculated and fumigated treatments at each time point in 2021 and 2022[ab].

| Year | Pathogen | Time Point | N (mg/kg) | P (mg/kg) | K (mg/kg) | Zn (mg/kg) | Ca (mg/kg) | Mg (mg/kg) | Na (mg/kg) |
|---|---|---|---|---|---|---|---|---|---|
| 2021 | Inoc | 1 | 36.3 | 23.3 | 333 | NA | NA | NA | NA |
| | | 2 | 34.9 | 15.7 | 338.5 | NA | NA | NA | NA |
| | | 3 | 53.1 | 15.8 | 389.3 | NA | NA | NA | NA |
| | | 4 | 71.3 | 15.8 | 440 | NA | NA | NA | NA |
| | Fum | 1 | 15.8 | 29.3 | 362 | NA | NA | NA | NA |
| | | 2 | 14.9 | 23.1 | 340.5 | NA | NA | NA | NA |
| | | 3 | 16.4 | 28.3 | 328.8 | NA | NA | NA | NA |
| | | 4 | 18 | 33.5 | 317 | NA | NA | NA | NA |
| 2022 | Inoc | 1 | 41 | 32.2 | 403 | NA | NA | NA | NA |
| | | 2 | 20 | 20.2 | 332 | 0.9 | 1670 | 1690 | 25.9 |
| | | 3 | 38 | 30.6 | 365 | 0.8 | 1650 | 1760 | 26.2 |
| | Fum | 1 | 46 | 32.8 | 390 | 0.9 | NA | NA | NA |
| | | 2 | 26 | 37.8 | 441 | 1.1 | 1540 | 1510 | 27.5 |
| | | 3 | 21 | 27.9 | 412 | 0.9 | 1460 | 1580 | 28.6 |

[a] To collect samples, the top layer of organic matter was removed then a 2.5 cm diameter soil corer was used to collect the top 15 cm of soil from 10 locations in a diagonal transect across each field in a NE to SW direction.

[b] Collection time points were 5/5/21, 6/17/21, 8/3/21, 4/5/22, 7/7/22, and 8/24/22.

**Supplemental Table 3.** Leaf nutrients N, P, K, and Ca as a percentage of leaf material in all four cultivars in the fumigated and inoculated treatments in 2021 and 2022.

| Year | Time Point | Pathogen | Cultivar | Irrigation (% ET) | Nitrogen (%) | Phosphorus (%) | Potassium (%) | Calcium (%) |
|---|---|---|---|---|---|---|---|---|
| 2021 | 1 | Fum | H5608 | 100% | 2.441 | 0.185 | 0.88 | 2.553 |
| 2021 | 1 | Fum | H5608 | 60% | 2.117 | 0.143 | 0.69 | 2.795 |
| 2021 | 1 | Fum | HM3887 | 100% | 1.582 | 0.172 | 0.78 | 3.038 |
| 2021 | 1 | Fum | HM3887 | 60% | 2.164 | 0.146 | 0.74 | 3.31 |
| 2021 | 1 | Fum | N6428 | 100% | 2.303 | 0.159 | 0.92 | 2.533 |
| 2021 | 1 | Fum | N6428 | 60% | 2.763 | 0.158 | 0.83 | 2.444 |
| 2021 | 1 | Fum | SVTM9016 | 100% | 2.289 | 0.169 | 1.15 | 2.731 |
| 2021 | 1 | Fum | SVTM9016 | 60% | 2.389 | 0.193 | 1.14 | 2.796 |
| 2021 | 1 | Inoc | H5608 | 100% | 3.023 | 0.227 | 0.87 | 2.24 |
| 2021 | 1 | Inoc | H5608 | 60% | 3.395 | 0.219 | 0.82 | 2.874 |
| 2021 | 1 | Inoc | HM3887 | 100% | 3 | 0.211 | 0.97 | 2.524 |
| 2021 | 1 | Inoc | HM3887 | 60% | 2.992 | 0.21 | 0.89 | 2.772 |
| 2021 | 1 | Inoc | N6428 | 100% | 3.147 | 0.197 | 0.95 | 2.513 |
| 2021 | 1 | Inoc | N6428 | 60% | 2.936 | 0.206 | 0.75 | 2.592 |
| 2021 | 1 | Inoc | SVTM9016 | 100% | 2.955 | 0.229 | 1 | 2.483 |
| 2021 | 1 | Inoc | SVTM9016 | 60% | 2.832 | 0.195 | 0.82 | 2.43 |
| 2021 | 2 | Fum | H5608 | 100% | 1.746 | 0.158 | 0.51 | 3.844 |
| 2021 | 2 | Fum | H5608 | 60% | 1.615 | 0.123 | 0.51 | 3.928 |
| 2021 | 2 | Fum | HM3887 | 100% | 1.493 | 0.159 | 0.44 | 4.825 |
| 2021 | 2 | Fum | HM3887 | 60% | 1.553 | 0.139 | 0.42 | 4.547 |
| 2021 | 2 | Fum | N6428 | 100% | 1.891 | 0.15 | 0.6 | 3.686 |
| 2021 | 2 | Fum | N6428 | 60% | 1.811 | 0.155 | 0.58 | 4.215 |
| 2021 | 2 | Fum | SVTM9016 | 100% | 1.885 | 0.176 | 0.87 | 3.427 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 2021 | 2 | Fum | SVTM9016 | 60% | 1.87 | 0.172 | 0.75 | 3.544 |
| 2021 | 2 | Inoc | H5608 | 100% | 3.177 | 0.265 | 1.23 | 2.646 |
| 2021 | 2 | Inoc | H5608 | 60% | 2.95 | 0.243 | 0.95 | 2.952 |
| 2021 | 2 | Inoc | HM3887 | 100% | 3.238 | 0.21 | 1.25 | 2.613 |
| 2021 | 2 | Inoc | HM3887 | 60% | 3.258 | 0.228 | 1.2 | 2.499 |
| 2021 | 2 | Inoc | N6428 | 100% | 2.235 | 0.194 | 0.68 | 3.204 |
| 2021 | 2 | Inoc | N6428 | 60% | 2.86 | 0.225 | 0.91 | 3.156 |
| 2021 | 2 | Inoc | SVTM9016 | 100% | 2.684 | 0.266 | 1.06 | 3.012 |
| 2021 | 2 | Inoc | SVTM9016 | 60% | 2.874 | 0.23 | 1.02 | 2.88 |
| 2022 | 1 | Fum | H5608 | 100% | 4.508 | 0.354 | 2.22 | 1.869 |
| 2022 | 1 | Fum | H5608 | 60% | 4.949 | 0.365 | 2.06 | 1.467 |
| 2022 | 1 | Fum | HM3887 | 100% | 4.735 | 0.394 | 2.22 | 1.483 |
| 2022 | 1 | Fum | HM3887 | 60% | 4.588 | 0.355 | 2.1 | 1.069 |
| 2022 | 1 | Fum | N6428 | 100% | 4.806 | 0.369 | 2.11 | 1.457 |
| 2022 | 1 | Fum | N6428 | 60% | 5.089 | 0.391 | 2.1 | 1.47 |
| 2022 | 1 | Fum | SVTM9016 | 100% | 4.79 | 0.333 | 1.87 | 1.156 |
| 2022 | 1 | Fum | SVTM9016 | 60% | 4.91 | 0.403 | 2.4 | 1.33 |
| 2022 | 1 | Inoc | H5608 | 100% | 4.634 | 0.316 | 1.69 | 1.312 |
| 2022 | 1 | Inoc | H5608 | 60% | 5.358 | 0.361 | 1.91 | 1.239 |
| 2022 | 1 | Inoc | HM3887 | 100% | 4.282 | 0.288 | 1.77 | 1.135 |
| 2022 | 1 | Inoc | HM3887 | 60% | 4.471 | 0.304 | 1.74 | 1.165 |
| 2022 | 1 | Inoc | N6428 | 100% | 5.07 | 0.361 | 1.96 | 1.093 |
| 2022 | 1 | Inoc | N6428 | 60% | 5.139 | 0.338 | 1.72 | 1.091 |
| 2022 | 1 | Inoc | SVTM9016 | 100% | 4.906 | 0.345 | 1.85 | 1.162 |
| 2022 | 1 | Inoc | SVTM9016 | 60% | 5.077 | 0.318 | 1.76 | 0.964 |
| 2022 | 2 | Fum | H5608 | 100% | 2.383 | 0.189 | 0.45 | 4.431 |
| 2022 | 2 | Fum | H5608 | 60% | 2.789 | 0.191 | 0.52 | 4.37 |
| 2022 | 2 | Fum | HM3887 | 100% | 2.852 | 0.222 | 0.82 | 4.005 |
| 2022 | 2 | Fum | HM3887 | 60% | 2.363 | 0.193 | 0.93 | 3.139 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 2022 | 2 | Fum | N6428 | 100% | 2.534 | 0.215 | 0.73 | 4.163 |
| 2022 | 2 | Fum | N6428 | 60% | 2.913 | 0.215 | 0.55 | 4.662 |
| 2022 | 2 | Fum | SVTM9016 | 100% | 3.009 | 0.2 | 0.76 | 3.383 |
| 2022 | 2 | Fum | SVTM9016 | 60% | 2.75 | 0.194 | 0.69 | 4.012 |
| 2022 | 2 | Inoc | H5608 | 100% | 4.893 | 0.354 | 1.63 | 2.716 |
| 2022 | 2 | Inoc | H5608 | 60% | 4.51 | 0.294 | 1.31 | 2.636 |
| 2022 | 2 | Inoc | HM3887 | 100% | 4.718 | 0.309 | 1.73 | 2.504 |
| 2022 | 2 | Inoc | HM3887 | 60% | 3.838 | 0.263 | 1.26 | 2.977 |
| 2022 | 2 | Inoc | N6428 | 100% | 4.783 | 0.328 | 1.34 | 2.385 |
| 2022 | 2 | Inoc | N6428 | 60% | 3.667 | 0.251 | 0.84 | 3.461 |
| 2022 | 2 | Inoc | SVTM9016 | 100% | 4.784 | 0.304 | 1.37 | 2.31 |
| 2022 | 2 | Inoc | SVTM9016 | 60% | 4.618 | 0.284 | 1.29 | 2.288 |

**Supplemental Table 4.** Number of plant samples collected, and molecular identification of *Fusarium* isolates from the four cultivars in both irrigation treatments in the fumigated field in 2021 and 2022[ab].

| Year | Irrig (% ET) | Cultivar | No. Plant samples | Foxy[c] (unclass)[d] | Forl[c] (tentative)[e] | *F. noneumartii*[d] |
|---|---|---|---|---|---|---|
| 2021 | 100% | HM3887 | 7 | 2 (29%) | 0 | 0 |
| | | SVTM9016 | 5 | 0 | 3 (60%) | 0 |
| | | N6428 | 7 | 3 (43%) | 2 (14%) | 0 |
| | | H5608 | 5 | 0 | 2 (40%) | 0 |
| | 60% | HM3887 | 5 | 1 (20%) | 1 (20%) | 0 |
| | | SVTM9016 | 5 | 0 | 0 | 0 |
| | | N6428 | 5 | 0 | 1 (20%) | 0 |
| | | H5608 | 5 | 0 | 1 (20%) | 0 |
| 2022 | 100% | HM3887 | 5 | 8 (160%) | NA | 1 (20%) |
| | | SVTM9016 | 5 | 2 (40%) | NA | 0 |
| | | N6428 | 5 | 0 | NA | 0 |
| | | H5608 | 5 | 4 (80%) | NA | 0 |
| | 60% | HM3887 | 5 | 3 (60%) | NA | 0 |
| | | SVTM9016 | 5 | 2 (40%) | NA | 0 |
| | | N6428 | 5 | 3 (60%) | NA | 0 |
| | | H5608 | 5 | 4 (80%) | NA | 0 |

[a] Fungal isolations were conducted only plants with stem discoloration and/or rot.

[b] Numbers in parentheses represent the isolates identified to that species (>98% ID) as a percentage of symptomatic plants collected in that treatment

[c] Foxy = *Fusarium oxysporum*; Forl = *Fusarium oxysporum* f. sp. *radicis-lycopersici* (Fusarium crown and root rot pathogen).

[d] Molecular identification of species was conducted by amplifying either the 1-alpha (TEF) or the internal transcribed sequence (ITS) genes. The resulting sequences were used for species identification based on NCBI BLAST or Fusarium Mycobank (https://fusarium.mycobank.org/page/Pairwise%20alignment).

[e] Determined using SIX PCR.

**Supplemental Table 5.** Number of plant samples collected and molecular identification from the four cultivars in both irrigation treatments in the inoculated field in 2021[ab].

| Irrig (% ET) | Cultivar | # Plant samples | Foxy (unclass)[c] | Forl (tentative)[d] | F. noneumartii[c] |
|---|---|---|---|---|---|
| 100% | HM3887 | 5 | 0 | 0 | 1 (20%) |
| | SVTM9016 | 5 | 1 (20%) | 0 | 1 (20%) |
| | N6428 | 5 | 2 (40%) | 2 (40%) | 3 (60%) |
| | H5608 | 5 | 1 (20%) | 1 (20%) | 1 (20% |
| 60% | HM3887 | 5 | 0 | 0 | 0 |
| | SVTM9016 | 5 | 1 (20%) | 2 (40%) | 3 (60%) |
| | N6428 | 5 | 0 | 0 | 1 (20%) |
| | H5608 | 5 | 0 | 0 | 0 |

[a] Fungal isolations were conducted only plants with stem discoloration and/or rot.

[b] Numbers in parentheses represent the isolates identified to that species (>98% ID) as a percentage of symptomatic plants collected in that treatment

[c] Molecular identification of species was conducted by amplifying either the 1-alpha (TEF) or the internal transcribed sequence (ITS) genes. The resulting sequences were used for species identification based on either NCBI BLAST or the Fusarium Mycobank Database (https://fusarium.mycobank.org/page/Pairwise%20alignment).

[d] *In planta* phenotyping trials were not conducted for these isolates.

**Supplemental Table 6.** Total yield biomass comparing cultivars and irrigation treatments in the fumigated treatment (years separated and combined)[ab].

| Year | Irrig | Cultivar | Yield Biomass (kg/ha)[c] |
|---|---|---|---|
| 2021[c] | 100% | HM3887 | 155,907 ± 14,399 a |
| | | SVTM9016 | 177,866 ± 11,876 a |
| | | N6428 | 124,067 ± 24,746 a |
| | 60% | H5608 | 132,850 ± 18,470 a |
| | | HM3887 | 128,459 ± 18,141 b |
| | | SVTM9016 | 104,304 ± 15,253 b |
| | | N6428 | 136,144 ± 21,876 b |
| | | H5608 | 109,794 ± 3,959 b |
| *P* value Irrigation | | | 0.035[d] |
| *P* value Cultivar | | | 0.526 |
| *P* value Irrigation x Cultivar | | | 0.105 |
| 2022[c] | 100% | HM3887 | 121,871 ± 3,294 a |
| | | SVTM9016 | 101,010 ± 30,208 a |
| | | N6428 | 122,969 ± 12,077 a |
| | 60% | H5608 | 122,969 ± 5,810 a |
| | | HM3887 | 97,716 ± 12,944 a |
| | | SVTM9016 | 108,696 ± 8,715 a |
| | | N6428 | 119,675 ± 6,113 a |
| | | H5608 | 77,954 ± 8,575 a |
| *P* value Irrigation | | | 0.076 |
| *P* value Cultivar | | | 0.370 |
| *P* value Irrigation x Cultivar | | | 0.176 |
| Years Comb. | 100% | HM3887 | 138,889 ± 10,078 b |
| | | SVTM9016 | 139,438 ± 22,496 b |
| | | N6428 | 123,518 ± 12,317 b |
| | 60% | H5608 | 127,910 ± 8,937 b |
| | | HM3887 | 113,087 ± 12,107 a |
| | | SVTM9016 | 106,500 ± 7,917 a |
| | | N6428 | 127,910 ± 10,805 a |
| | | H5608 | 93,874 ± 8,278 a |
| *P* value Irrigation | | | 0.011 |
| *P* value Cultivar | | | 0.526 |
| *P* value Irrigation x Cultivar | | | 0.321 |

[a] Total fruit yields (kg/ha) were extrapolated from fruit harvested in the easternmost monitoring plots (4.6 m x 1.5 m) within each row.

[b] Variables were analyzed using a linear mixed effect model with RStudio v. 2023.06.1+524.

[c] Mean values followed by the same letter are not significantly different according to Dunnett's Test ($P < 0.05$). The ± is the standard error of the mean.

[d] *P* values were calculated using Kruskal-Wallis for non-parametric data with RStudio v. 2023.06.1+524.

**Chapter 3: Characterizing shifts in processing tomato root fungal communities under deficit irrigation and effects of soil management practices**

## 1. Introduction

California agriculture faces challenges with increasingly severe cyclic droughts. Due to a lack of summer rain, warm season crops such as processing tomatoes are irrigated with stored surface water released as snowpack over the summer. Problematically, the period between 2000 and 2017 was the driest 18-year period over 100 years (Bureau of Reclamation, 2020) and snowpack was only 56% of the statewide average as of April 1, 2020, compared to previous years (CA Department of Water Resources, 2020). Surface water is allocated out to growers by state regulators; in 2014 and 2015, allocations to California producers dipped as low as 0%, resulting in less available land for food production, and increased water costs and use of poor-quality water which can increase soil salinity (Szabolcs, 1994). These water scarcity challenges are motivating many California growers to reduce irrigation inputs.

One way to do this is called “deficit irrigation” (DI), which consists of reducing irrigation to the point where it no longer meets the optimum (100%) evapotranspiration (ET) requirements of the crop. Not all crops are amenable to DI, but the practice can work well for tomatoes (Khapte et al., 2019), which are among the top 10 commodities grown in California (CDFA, 2023). Tomato growers can reduce irrigation to approximately 80% ET around fruit reddening without yield impacts; some further reduce inputs to 60% ET around four weeks before harvest (*pers comm*, Tom Turini). In addition to reducing water inputs, the practice can also increase color and soluble solids in fruit (Lu et al., 2019; Zegbe-Domínguez et al., 2003).

Previous studies indicate that in the presence of plant pathogens, DI can increase disease risk across a range of crops and growing conditions (Del Castillo Múnera et al., 2019a, 2019b; Swett, 2020) as has been found when plants are water stressed (Parsons and Munkvold, 2010; Ragazzi et al., 1995). Studies in CA processing tomato described in Chapter 1 provide some of the first evidence for disease enhancement in this cropping system. In this study, we observed a 1.5-fold increase in stem rot in 2020, and stem rot increases from year 1 to 2 were significantly greater under DI (Chapter 1). Known diseases, including Fusarium crown and root rot (*F. oxysporum* f. sp. *radicis lycopersici*, Forl) and Fusarium stem rot and vine decline (*F. noneumartii*, FRD) were diagnosed in 40% of diseased plants. However, etiology of stem and root rot disease in the remaining 60% of affected plants was not determined and may indicate enhancement of previous undescribed (likely opportunistic) pathogens, or pathogens that are difficult to detect using culture-based approaches. A better understanding of whether other stem rot/decline diseases are enhanced by DI can provide a broader framework in which to effectively manage plant health under water scarcity.

Previous studies have documented the potential for DI and other environmental stressors to favor facultative pathogens or enable organismal shifts from a biotrophic or saprotrophic to a necrotrophic state. For example, in rhizosphere microbial community studies in greenhouse grown poinsettia the authors observed increased abundance of facultative pathogens under lower irrigation inputs (Del Castillo Múnera et al., 2022). This is also a common phenomenon in oaks (*Quercus* spp.) such as with *Armillaria* species causing root disease (Intini, 1991; Luisi et al., 1991) and *Hypoxylon* species causing bole cankers (Vannini, 1991; Fenn et al., 1991). This could explain the fact that we were able to isolate a range of

*Fusarium* species from symptomatic plant tissue, however only 43% of those were known tomato pathogens. It is possible that the other *Fusarium* species we isolated are facultative or even novel tomato pathogens.

An additional possible explanation for increased disease under DI is the direct or indirect effects of reduced soil moisture on the beneficial root microbial community. Reduced soil moisture can directly affect the root microbiome via diminished access to water-soluble nutritive compounds, placing osmotic stress on beneficial microbes (Schimel, 2018). In a greenhouse study with poinsettia, Del Castillo Múnera et al. (2022) reported a 98% reduction in the abundance of the fungal parasite *Clonostachys rosea* under reduced irrigation. Indirect effects can occur because of physiological changes in the plant resulting from water stress that influence microbial communities. For example, closing stomata is a strategy to reduce water loss via respiration, but it also limits photosynthesis. Limited photosynthesis influences root exudates important for chemotaxis, root entry, and root colonization (Berendsen et al., 2012; Raaijmakers et al., 2008; Rahman et al., 2021) which can in turn influence root colonization of beneficials.

Previous studies suggest that one way to mitigate the impacts of DI is through the use of soil amendments and/or cover cropping (Agbna et al., 2017; Hirich et al., 2014; Qin and Leskovar, 2018; Qin and Leskovar, 2020). In Chapter 1, the addition of composted poultry manure decreased the incidence of vine decline and fruit damage under DI, but it is unclear why. One possible explanation is that the compost suppressed pathogens by encouraging antagonistic microbes. This hypothesis is supported by studies where Fusarium wilt in cucumber (*Cucumis sativas*) (Qiu et al., 2012) and plant parasitic nematodes in maize and bean

(Atandi et al., 2017) were suppressed under organic culture. Several studies have shown that incorporation of compost increased soil microbial diversity, which may include beneficials. For example, in a long-term study with rice (*Oryzae sativa*) and corn (*Zea mays*) the authors observed higher microbial populations in organic (incorporation of commercial hog dung compost and peat) versus conventional systems (Chang et al., 2014). Should increases in soil microbial diversity with organic amendments correlate with an increase in abundance/diversity of beneficials, this could in turn suppress pathogens or favor beneficials. Cover crops can also indirectly influence plant-pathogen interactions. There is no shortage of literature demonstrating the positive effects of cover cropping on soil microbial biomass, activity, community structure, and function (e.g., Finney et al., 2017; Martínez-García et al., 2018). Cover crops have also been shown to increase soil microbial diversity, resulting in pathogen inhibition; for example, high microbial biomass and activity was associated with suppression of *Pythium* growth in soil (van Os and van Ginkel, 2001). Thus, it stands to reason that cover crops can influence plant-pathogen interactions via increasing soil microbial diversity and activity. Studies are needed to determine whether the use of organic amendments and/or cover cropping under reduced irrigation inputs could prevent disease via facultative pathogen suppression and/or favoring beneficials.

To better understand whether there is a microbial basis for outcomes observed in Chapter 1, and microbial roles in the interplay between soil amendment and DI, the objectives of this study were to 1) explore fungal communities associated with DI-enhanced stem rot using culture-dependent methods (under standard synthetic fertilizer nutrient management), 2) evaluate the abilities of putative facultative Fusarium pathogens dominant in the ecosystem to

cause disease in tomato; 3) evaluate whole rhizosphere fungal community changes under grower standard and extreme DI, and 4) compare the effects of synthetic fertilizer, compost, and cover crop-based soil management methods on fungal root microbial communities under DI.

## 2. Methods

### *2.1 Overview of studies*

Overall, this work encompasses two different field studies comparing the effects of deficit irrigation and soil amendments on disease development in processing tomatoes. In the first study we examined the effects of deficit irrigation (DI) levels representative of what growers currently use. We used the second study as an opportunity to examine the effects of DI levels that were more extreme with soil fertility management practices established for 25 years. Field trials took place in at the Russell Ranch Sustainable Agriculture Facility in Yolo County (38.54'N, -121.87'W), a region where approximately 15% of CA tomatoes are grown (USDA NASS, 2023). This area typically experiences hot dry summers and cooler wet winters. The experimental plots spanned two soil types: Rincon silty clay loam and Yolo silt loam. Irrigation setup was the same for both studies; all rows were irrigated using one subsurface drip irrigation line buried at approximately 25 cm depth along the middle of each bed. Emitters were spaced every 30 cm. Irrigation treatments were based on evapotranspirative (ET) needs of the plants as measured by an onsite Tule system (Oakland, CA), which monitors actual ET in the field ($ET_a$) along with the volume of irrigation applied.

### *2.2 Experimental design and treatment application – "Grower Model DI"*

The field used for this trial had previously been rangeland planted to perennial grasses until the 1990s. Since then, it has been planted to a corn-tomato rotation. The trial was arranged in a split plot RCBD; irrigation treatment was the main plot, in which the field (14 ha) was divided into two plots; each plot was assigned an irrigation treatment (100% or 60% potential crop ET, corresponding to "Well-Watered" (WW) and "Deficit" (DI) treatments, respectively) (Fig. 2). Within each irrigation treatment there were two soil amendment treatments: "Synthetic" (no compost control + 205 kg N/ha through drip) and "Synthetic & Compost" (poultry manure compost at approximately 4500 kg/ha + 205 kg N/ha through drip). Each amendment was allocated to three rows within each of the three blocks. Rows were approximately 185 m long and 1.5 m wide. Heinz tomato seedlings (H1662) were planted 0.3 m apart. For the purposes of this study, observations were conducted in the southernmost row of the three rows within each treatment in each block.

Irrigation levels were selected based on what processing tomato growers in Fresno use (*pers comm,* Tom Turini) and previous studies done by the Gaudin Lab at UC Davis (*unpublished*). Specifically, plants in both irrigation treatments received enough water to replace 100% of their evapotranspirative (ET) needs until approximately 47 days preharvest in Year 1 and 63 days preharvest in Year 2. At this point the two irrigation treatments diverged; rows in the "Optimum" side of the field continued to receive 100% of the irrigation hours recommended by Tule while rows in the "Deficit" side received only 60% of the Tule recommended irrigation hours (Fig. 2). Irrigation was stopped completely 10 days preharvest in both years. In this study, soil moisture sensors (TEROS10, METER Group) were used in the second year to confirm that the deficit irrigation treatment resulted in reduced soil moisture.

One sensor was buried approximately 30 cm deep halfway between the drip line and edge of the bed in two blocks per irrigation field for a total of four sensors (Fig. 2). Sensors measured soil moisture in 15-minute increments between June 16 and Sep 2.

*2.3 Experimental design and treatment application – "Extreme DI" Experiment*

This study took place in 2018 as part of the Century Experiment, a 25 year-long field trial examining the ecological impacts of different farm management practices located in Winters, CA. This study was arranged in a split-split plot design. Soil management method was the main plot with two treatments: Organic (OMT) and Conventional (CMT). The Organic treatment consisted of a (*Solanum lycopersicum* L.)/corn (*Zea mays*) rotation with a winter cover crop (mix of legumes and grass incorporated before compost application and planting) and composted poultry manure (404 Mg N/ha + 4.5 Mg/ha incorporated before planting). The Conventional treatment was in a two-year tomato/corn rotation (no winter cover crop) with mineral fertilizer (205 kg N/ha incorporated before planting) (Fig. 1).

Irrigation was the sub plot with two treatments: 100% ET and 25% ET (severe DI). Plants were irrigated to replace 100% of their evapotranspiration (ET) rates for eight weeks after transplanting, at which point irrigation was reduced to 25% ET or kept at 100% ET until water was cut completely two weeks before harvest. Seedlings (variety: H8504) were transplanted on May 1 in single rows on a 1.5 m wide raised bed; planting density was 21,000 plants/ha.

*2.4 Culture-dependent characterization of fungal communities associated with late season decline*

In studies detailed in Chapter 1, we found that in the Grower Model study stem rot incidence was greater under DI. Of the diseased plants analyzed in Chapter 1, only 40% were

diagnosed with known pathogens, indicating that other stem rot pathogens may be present and are influenced by DI. To explore this community more fully, we conducted a culture-based analysis of the full suite of species present and evaluated pathogenicity of commonly recovered species not known to be pathogens. Diseased plants were also diagnosed in the Extreme DI study, although disease incidence and severity data were not collected. This analysis helped provide a context dataset for culture independent analysis, by indicating which species might be pathogens in the system.

A subset of plants with vine decline and stem rot was collected between DI onset and harvest from each treatment in both studies (Supp. Tables 1 and 2). To diagnose stem/root rot diseases, healthy-diseased margins in stem tissue were excised and surface disinfested by rinsing with tap water then 0.1% Tween (Sigma Aldrich, St. Louis, MO), dipping in 70% ethanol for 30s then 20% bleach (Clorox, Oakland, CA) for 2 min. Tissue (1 cm segments) was then either placed on growth media for fungal isolations or incubated (24°C, 46% RH, 12:12 L:D for 10 days) for Southern blight evaluations. Broad fungal diagnosis was conducted using the general growth medium 1/10 potato dextrose agar (1/10 PDA + tet) (3.9 g potato dextrose, 16.1 g agar, 1 L distilled water) amended with 0.3 g tetracycline in 10 cm diameter Petri dishes. For Fusarium disease diagnosis, tissue was placed on Fusarium selective media (FSM) (15 g Bactone Peptone, 1 g $KH_2PO_4$ monobasic, 0.5 g $MgSO_4 – 7H_2O$, 20 g agar, 0.6 g PCNB (Terraclor 75%), 0.1 g ampicillin, 0.3 g streptomycin sulfate, and 1 L deionized water). Plates were sealed with parafilm and incubated (24°C, 46% RH, 12:12 L:D for 3-7 days).

Dominant emerging fungi were sub-cultured to 1/10 PDA and 0.6% KCl agar (6g KCl, 14 g agar, 1 L distilled water) (Fusarium only) and grown for 3-7 days (24°C, 46% RH, 12:12 L:D) then

grouped based on colony morphological characteristics (Leslie and Sommerell, 2008). Subcultures were identified to genus based on spore morphology and ontogeny when possible. Fusarium isolates were further identified to species complex. Isolates with longer monophialids were identified as members of the *F. solani* species complex (FSSC) and isolates with short monophialids were identified as *F. oxysporum.* DNA from a subset of isolates representing each morphological group or species complex (≥ 3/group) was extracted using PrepMan Ultra (Thermo Fisher Scientific, Waltham, MA). The internal transcribed spacer (ITS) gene forward primer ITS1 (5´-TCCGTAGGTGAACCTGCGG- 3) and reverse primer ITS4 (5´-TCCGTAGGTGAACCTGCGG- 3') were amplified as described in Liu et al. (1999). TEF analysis was conducted for *Fusarium* spp. using the translation elongation factor 1-alpha (TEF) gene forward primer EF1 (5' – ATGGGTAAGGA(A/G)GACAAGAC – 3') and reverse primer EF2 (5' – GGA(G/A)GTACCAGT(G/C)ATCATGTT – 3') (O'Donnell et al., 1998). Amplified PCR products were cleaned using ExoSAP-IT (Thermo Fisher Scientific, Waltham, MA) and Sanger sequenced using the ITS4 reverse primer (Quintara Bio, Hayward, CA). Resulting sequences were identified using NCBI BLAST (https://blast.ncbi.nlm.nih.gov). Tef sequence analysis was conducted using Mycobank (https://www.mycobank.org) and the Fusarium ID library (http://www.fusariumdb.org). The identity of *F. oxysporum* isolates as *F. oxysporum* f. sp. *lycopersici* (Fol) was evaluated in only the Grower Model DI study isolates using the SIX 3 gene region forward primer (5' – CCAGCCAGAAGGCCAGTTT – 3') and reverse primer (5'-GGCAATTAACCACTCTGCC-3') (van Der Does et al., 2008).

*Fusarium oxysporum* isolates that did not have the amplified SIX3 region were not Fol, indicating identity as either non-pathogenic strains or the crown and root rot pathogen *F.*

*oxysporum* f. sp. *radicis lycopersici* (Forl). There were 23 and 43 *F. oxysporum* isolates that did not have the amplified SIX3 region in 2019 and 2020, respectively; 19 and 17 isolates from 2019 and 2020, respectively, were further evaluated for formae speciales ID in Forl phenotyping trials using cultivars with and without the FR gene that conveys resistance to Forl (Fazio et al., 1999) and the I3 gene conveying resistance to Fol race 3 (McGrath and Maltby, 1988). Because SIX3 false negatives can occur (Wang et al., 2023), we included several isolates with and without resistance to Fol race 3. For these assays, we selected N6428 (no FR but resistant to Fusarium wilt race 3), HM4909 (FR but not resistant to Fusarium wilt race 3), and Brandywine (no FR or Fusarium wilt R). Known isolates of both pathogens, Fol race 3 (CS3) and Forl (CS141), were used as positive controls and non-inoculated plants served as negative controls.

For each isolate, three plants were inoculated per cultivar for a total of nine plants per isolate. Cultivars were grouped together, and isolate x plant replicates were randomized within each cultivar. Seeds were surface disinfested with 70% ethanol for 10 min, 50% sodium hypochlorite for 10 min, then rinsed with sterile water. Disinfested seeds were sown in 3.8L pots filled with pre-moistened UC Mix (Davis, CA). Pots were watered to saturation and at post-emergence were placed on a drip irrigation system with a photoperiod of 12 h per day. Spore suspensions of each isolate were made by scraping mycelium on the surface of 10 7-day old PDA plates that were flooded with approximately 5 mL 0.5% KCl. The resulting liquid was filtered through two layers of sterile cheesecloth. Suspensions were diluted to $1 \times 10^5$ spores/mL by adding 700 mL 0.1% water agar. When plants were three weeks old, 50 mL of this suspension was poured onto the substrate around the base of the plant. For negative controls, 0.1% water agar without spores was used. Plants were maintained in the greenhouse at 18-

32°C 12:12 L:D with standard irrigation and drip fertilizer as needed. They were monitored until symptoms were observed in plants inoculated with the positive controls at 80-90 days after inoculation. Isolates were identified as Forl if they caused stem rot in non-FR plants but not in the FR plants. Isolates were identified as Fol race 3 if they caused wilt and vascular discoloration only in plants without race 3 resistance. Isolates were identified as non-pathogens of tomato if we did not observe stem rot in non-FR plants or wilt and vascular discoloration/crown rot in non-Fol plants. The incidence of dominant pathogens was quantified by treatment across years. This was calculated by dividing the number of collected plants with each disease per treatment across years by the total number of samples collected in that treatment across years.

*2.4 Root collection and preparation for culture independent-based characterization of rhizosphere fungal communities*

For both studies, plants were randomly selected and represented a mix of healthy and declining individuals. In the Grower Model DI study study, ten plants from each experimental row were excavated for a total of 120 plants at harvest. All lateral roots were collected from the lower 5 cm portion of each plant's root system and into sterile 50 mL tubes. In the Extreme DI study, lateral roots were collected from five plants in each treatment. In total we analyzed 57 lateral root samples from both years of the Grower Model DI study, and 38 lateral root samples from the Extreme DI study for amplicon sequencing (Supp. Table 3).

All roots were first washed by rinsing with tap water, agitating with 0.1% Tween (Sigma Aldrich, St. Louis, MO) for 3 hours at 150 rpm and rinsing with DI water. To disinfest the root surfaces, roots were then soaked in 20% bleach for 4 min, and rinsed with sterile DI water twice to remove residual bleach. Caps were sanitized in 20% bleach for 4 min, rinsed with sterile DI

water and allowed to air dry. Tubes were covered with a Kim wipe (Kimberly-Clark Corporation, Irving, TX) and lyophilized at -50°C for 72h. Sanitized caps were replaced onto tubes, which were stored at room temperature before grinding and DNA extraction.

*2.5 DNA extraction and amplicon sequencing*

Approximately 100 mg of surface disinfested and lyophilized root tissue was homogenized by grinding with liquid nitrogen before DNA extraction with a Quick-DNA Fecal/Soil Microbe MiniPrep Kit (Zymo Research, Irvine, CA) according to the manufacturer's instructions for fecal samples. Resulting DNA concentrations were measured using a Qubit 1X dsDNA High sensitivity (HS) assay kit (Invitrogen, Waltham, MA) as per the manufacturer's instructions; sample concentrations were diluted to 5 ng/uL. The fungal internal transcribed spacer unit 1 (ITS1) was targeted using the primer pair ITS1F (Gardes and Bruns, 1993) and ITS2 (White et al., 1990).

A two-step PCR was performed using 10 ng of DNA as template. All amplifications were performed on a BioRad C100 Touch (Hercules, CA) and an Applied Biosystems SimpliAmp (Waltham, MA). The first PCR step reaction consisted of 1U DreamTaq Green master mix (Thermofisher, Waltham, MA), 0.25 μM primers with Nextera adapters, 0.4 μg/μL BSA (ThermoFisher), and 2 uL (10 ng) DNA in a 20 μL reaction volume. Reactions were randomized and performed in triplicate. Amplification was done with initial denaturation at 94°C for 2 min; followed by 35 cycles of 94°C for 2 min, 55°C for 30 s, 72°C for 30 s; and a final extension at 72°C for 5 min. During the second PCR step, Nextera barcodes were added in 5 cycles. The second PCR step reaction consisted of 0.8U DreamTaq Green master mix, 0.20 μM primers with Nextera adapters, 0.32 μg/μL BSA, and 2 μL product from the first step in a 25 μL reaction

volume. Once again, reactions were randomized and performed in triplicate using the same temperature and time settings except there were only five extension cycles. Products from the second amplification step were imaged on a 1% agarose gel then pooled together and submitted to the UC Davis DNA Technologies Core facility for clean-up and sequencing on an Illumina MiSeq via 250-bp paired-end runs.

*2.6 Sequencing processing and statistical analyses*

The demultiplexed sequences were quality checked using FastQC (version 0.12.0) (Andrews, 2010). Primers were removed from the amplicons using cutadapt (version 4.4) (Martin, 2011). The sequences were further trimmed to remove 45 and 30 bases from the ITS1 and ITS2 ends, respectively. To generate amplicon sequencing variants (ASVs) from the preprocessed reads, dada2 (version 1.26) was used (Callahan et al., 2016). Prior to ASV inference, the reads were filtered, trimmed, and merged, using a BAND_SIZE of 32. The merged sequences were then checked for chimera and taxonomically classified. Taxonomy was assigned to the ASVs using the UNITE database (Abarenkov et al., 2010) and against the NCBI nucleotide collection (nr/nt) using BLAST (Altschul et al., 1990) to remove plant and other nonfungal sequences. After processing, libraries from samples with < 100 sequences were removed. Across both studies, 9,734,598 sequences making up 784 taxa were obtained. The sequences were imported into R via phyloseq and normalized to 7,430 reads.

Data were then filtered to remove ASVs abundant in the negative controls and not the samples. For comparisons, 100% ET was set as the control against the 25% ET (Extreme DI) and 60% ET (Grower Model DI) treatments while “Conventional” was set as the control in the soil against the “Organic” treatment. The relative ASV abundance was estimated by dividing the

absolute ASV abundance by the total number of sequences per sample. $\alpha$-Diversity of the communities, defined by irrigation and soil amendment (Extreme DI), and irrigation, soil amendment, and year (Grower Model DI), was estimated by ASV richness and the Shannon and Simpson indices (phyloseq package) (McMurdie and Holmes, 2013).

*2.7 Pathogenicity trials previously uncharacterized* Fusarium *species associated with DI-enhanced field symptoms*

In this study several *Fusarium* species not known to be pathogens were commonly recovered from symptomatic plant tissue. To evaluate their potential as opportunistic pathogens, these isolates were subjected to pathogenicity trials. This resulted in pathogenicity trials with one isolate each of *F. acuminatum* (RR20-22B)*, F. brachygibbosum* (CS560)*,* and *F. redolens* (CS568)*. Fusarium noneumartii* isolate CS109 was included as a positive control. Non-inoculated controls were also included as environmental checks.

Heinz tomato (HM8504) seeds were surface disinfested with 70% ethanol for 10 min, 50% sodium hypochlorite for 10 min, then rinsed with sterile water. Disinfested seeds were sown in 3.8L pots filled with pre-moistened UC Mix (Davis, CA). Pots were watered to saturation and post-emergence were placed on a drip irrigation system with a photoperiod of 12 h per day. At six weeks post planting, seedlings were inoculated with either a spore suspension (*F. acuminatum* and *F. redolens*) or via plug inoculation (*F. brachygibbosum*) when spores were not produced in culture.

To plug inoculate, seedling stems were wounded with a sterile probe approximately 1 cm above the substrate line. Agar plugs (5mm) were taken from the 7–10-day-old isolates of *F. brachygibbosum* (isolate CS560) or *F. noneumartii* (isolate CS109) grown on 1/10 PDA and

placed, colonized surface down, onto the wounded surfaces and sealed with Parafilm (Bemis Co. Inc., Neenah, WI). Sterile agar plugs were placed on wounds to serve as the negative controls in five plants. Three days later, Parafilm and agar plugs were removed. Plants were monitored for 12 weeks, and the length of any external stem lesions was measured. The wound plug pathogenicity assay was repeated twice for all isolates except CS560.

Fore spore suspension inoculation, suspensions were made by scraping mycelia on the surface of 10 7-day old PDA plates that were flooded with approximately 5 mL 0.5% KCl. The resulting liquid was filtered through two layers of sterile cheesecloth. Suspensions were diluted to approximately 1 x $10^5$ spores/mL by adding 700 mL 0.1% water agar. Stems of 3-5 plants per isolate were each wounded with a sterile probe just below the soil line, enough to penetrate the epidermis (approximately 1mm). Respective spore suspensions (50 mL) were then poured onto the substrate around the base of the plant. For negative controls, 0.1% sterile water agar was applied to the base of five wounded and five non-wounded plants. Plants were monitored for 9-11 weeks, and the length of external stem lesions was recorded. Plants were also given a disease ranking based on percent canopy decline (0 = healthy; 1 = 1-20%; 2 = 21-40%; 3 = 41-60%; 4 = 61-80%; 5 = 81-100%). The spore suspension pathogenicity assays were conducted twice. A third trial was conducted with a subset of the isolates (*F. acuminatum*) and *F. noneumartii* isolate CS573 was included as a positive control; only internal stem lesions were measured in this trial.

*2.8 Statistical analyses*

All analyses were performed using RStudio v. 2023.06.1+524 (Rstudio Team, 2023). Samples from the “Extreme DI” study were analyzed separately from the “Grower Model DI”

study. For the latter, data from each year were analyzed separately. Statistical analyses of $\alpha$-diversity were performed using a linear model with irrigation, soil amendment, and year ("Grower Model DI" study only) as fixed variables. $\beta$-Diversity was estimated by calculating the Bray-Curtis distances (vegan package) (Oksanen et al., 2019). To determine whether irrigation, soil amendment, or year ("Grower Model DI" study only) significantly altered community composition, we performed two- and three-factor permutational multivariate analysis of variance (PERMANOVA) using the adonis function (vegan package) (Oksanen et al., 2019). Non-metric multidimensional scaling (NMDS), Principal coordinate analysis plots (PCoA), and heat maps were generated using the phyloseq and ggplot2 packages (Fiske and Chandler, 2011). Differential abundance of ASVs among irrigation and soil amendment treatments was estimated with DESeq2.

## 3. Results

### *3.1 Fungal communities associated with DI-enhanced stem rot*

Using culture-dependent methods, we recovered a total of 12 fungal species/Foxy strains across both irrigation treatments (in the synthetic fertilizer treatment) (Fig. 3). In both years, more species were detected under 60% ET (9 species on average) than 100% ET (7 species on average). *Fusarium* was the predominant genus identified across treatments in both years, making up approximately 96% and 91% of the genera identified across years in the 100% ET and 60% ET treatments, respectively (Fig. 3). *Fusarium oxysporum* was the predominant species identified, making up 75% and 73% of the *Fusarium* isolates identified across years in the 100% ET and 60% ET treatments, respectively. Forl was identified in both treatments across

both years. *Fusarium solani* (4 isolates) was identified in both irrigation treatments but was found only in 2019. *Fusarium noneumartii* was only found under 60% ET in 2019 (2 isolates). *Fusarium brachygibbosum, F. redolens*, and *F. acuminatum* were all isolated in both years and both irrigation treatments (1-2 isolates/species). Beyond the *Fusarium* species, *Setophoma terrestris, Pleosporales* spp., *Pyrenochaeta lycopersici* (the cause of corky root), and *Alternaria alternata* isolates were also identified (~8% of total isolates identified).

*3.2 Characterizing the pathogenicity of* Fusarium *species found in the Grower Model DI study*

One *F. brachygibbosum* isolate recovered from tissue with stem rot resulted in significantly longer external stem lesions than the non-inoculated controls ($P < 0.001$) (Table 2). Inoculation with one *F. acuminatum* isolate recovered from tissue with stem rot produced external lesions, the lengths were not significantly different from the non-inoculated controls (Table 2). Inoculation with the *F. redolens* isolate did not result in external stem lesions. In the third spore suspension trial with the *F. acuminatum* isolate, plants developed longer internal stem lesions than the non-inoculated – wounded control plants, similar to the *F. noneumartii* positive control (CS573) ($P < 0.001$) (Table 3). Canopy decline ratings were slightly higher in plants inoculated with the *F. acuminatum* and *F. redolens* isolates but were not significantly different than the non-inoculated controls (Table 4).

*3.3 Effects of grower-modeled deficit irrigation on processing tomato root fungal communities*

Using amplicon sequencing, we identified ASVs belonging to 66 fungal species across irrigation treatments. In 2019 we identified 80 and 34 ASVs in the 100% ET and 60% ET treatments, respectively. In 2020 we identified 67 and 62 ASVs in these same treatments. Combining years, there were 109 and 75 ASVs in the 100% ET and 60% ET treatments,

respectively. *Pseudopyrenochaeta lycopersici* (syn. *Pyrenochaeta lycopersici*) was the predominant species, making up 69% and 54% of the ASVs across years in the 100% ET and 60% ET treatments, respectively (Fig. 4). *Verticillium dahliae* was the second most predominant species, making up 13% and 20% of the ASVs across years in the 100% ET and 60% ET treatments, respectively. *Fusarium* species together made up the third most predominant group representing 9% and 15% of the ASVs across years in the 100% ET and 60% ET treatments, respectively. Because ITS is not a reliable region for *Fusarium* species ID, identification was made at the species complex level. Species complexes with known tomato pathogens (*Fusarium solani* species complex and *F. oxysporum*) made up approximately 9% and 16% of the *Fusarium* ASVs across years in the 100% ET and 60% ET treatments, respectively. Based on $\alpha$-diversity analyses, irrigation did not influence the number of ASVs ($P = 0.754$) (Fig. 5). Irrigation also did not influence the Shannon or Simpson diversity indices ($P > 0.05$).

*3.4 Effects of extreme deficit irrigation on processing tomato stem rot and root fungal communities*

Stem rot-associated species. In analyzing pathogens present in stem/root rot tissue, using culture-dependent methods, we isolated and identified four fungal taxa (*Fusarium oxysporum*, *F. solani,* an unknown *Fusarium* spp., and *Microascus* spp.) isolated from symptomatic plants across both irrigation treatments in the Conventional treatment (*in planta* phenotyping was not conducted for these isolates thus we did not identify isolates as Forl or non-pathogenic strains) (Fig. 6). *Fusarium* was the predominant genus, making up 80% and 100% of the identified isolates in the 100% ET and 25% ET treatments, respectively. The only other taxon identified was *Microascus* spp., which made up 20% of the identified isolates in the 100% ET treatment.

Root-associated community. Using amplicon sequencing, we identified ASVs belonging to 66 fungal species with 41 ASVs in the 100% ET treatment and 46 ASVs in the 25% ET treatment. *Pseudopyrenochaeta lycopersici* (51%) was the most abundant species in both irrigation treatments (Fig. 7). Approximately 13% of ASVs were in the *Fusarium* genus, (*F. oxysporum, F. solani,* and *F. equiseti* species complexes) across years in both irrigation treatments. Pathogenic species (*F. oxysporum* and FSSC) made up approximately 76% and 82% of the *Fusarium* ASVs across years in the 100% ET and 25% ET irrigation treatments, respectively. Based on $\alpha$-diversity analyses, irrigation did not influence fungal diversity ($P = 0.874$) (Fig. 8) or the Shannon or Simpson diversity indices ($P > 0.05$).

*3.5 Examining the effects of soil management method on fungal root communities under grower-modeled deficit irrigation*

Stem rot-associated species. Using culture-dependent methods, we identified 13 and 7 species in the Synthetic and Compost treatments, in stem rot tissue respectively, across years (Fig. 9). Forl was identified across all sampled treatments in both years. *Fusarium solani* and *F. noneumartii* were consistently identified only in the 60% ET treatment in both years; in 2020, both species were only present in the Compost treatment. *Glomerella acutata* was also identified only in the 60% ET – Compost treatment. Additionally, under DI, *Pyrenochaeta lycopersici* (corky root) was only detected in the Synthetic (and not Compost) treatment in 2019.

Root-associated communities. Using amplicon sequencing, we identified ASVs in roots belonging to 137 fungal species across the irrigation x soil management treatments. Across both irrigation treatments, there was a total of 115 ASVs in the Synthetic treatment and 69

ASVs in the Compost treatment. Based on $\alpha$-diversity analyses there was no effect of soil management on fungal community diversity ($P$ = 0.807). The Shannon and Simpson indices also did not reveal differences between soil management treatments ($P$ > 0.05) (Fig. 10). The structure of fungal communities colonizing roots did not differ depending on soil amendment, as evident in the PCoA (Fig. 11). Axis 1 accounted for 50.9% of the variability while Axis 2 accounted for 18.3% of the variability. According to the PERMANOVA test (not shown), there was an effect of irrigation in 2019 (adonis $P$ = 0.014) on fungal community structure, but there was no effect of soil amendment that year (adonis $P$ = 0.354) and there was no effect of irrigation (adonis $P$ = 0.544) or soil amendment (adonis $P$ = 0.341) in 2020.

Pathogen community effects. *Pseudopyrenocaeta lycopersici* was the predominant taxa in all treatments except for the Compost – 60% ET treatment in 2019, in which *Verticillium dahliae* was the predominant taxa (approximately 62%) (Fig. 12). There was no effect of irrigation or soil amendment treatment on either pathogen ($P$ = 0.754 and $P$ = 0.807 for irrigation and amendment, respectively). The proportion of ASVs belonging to *Fusarium* species (*F. oxysporum, F. solani, F. acuminatum, F. falciforme, F. equiseti,* and *F. verticillioides*) ranged from approximately 5-19% across the soil management and irrigation treatments in both years. The putative pathogenic ASVs in the *F. solani* and *F. oxysporum* species complexes increased under DI in both soil management treatments in both years.

Non-pathogen community effects. Based on differential abundance of sequence variants analyses, the abundance of one ASV corresponding to *Alternaria* decreased under DI by a 7.3 $\log_2$ fold-change ($P$ < 0.0001) across both soil amendments in 2019 (Table 5). In 2020, the abundance of one ASV corresponding to *Clonostachys* significantly increased under DI by a 23.4

$log_2$ fold-change ($P < 0.0001$). We did not observe significantly different taxa between the soil management treatments in 2019, but in 2020 the abundance of an ASV corresponding to *Fusarium* significantly increased under the organic treatment compared to the conventional treatment by a 4.9 $log_2$ fold-change ($P < 0.001$).

*3.6 Examining the effects of soil management on fungal communities under extreme deficit irrigation*

Stem rot-associated communities. In the Extreme DI study, using culture-dependent methods we isolated and identified 6 total species/strains with 4 species found under the Conventional treatment and 5 species under the Organic treatment (Fig. 13). While the number of species in the Conventional treatment under 100% ET and 25% ET were similar (3 and 2, respectively), they were slightly higher under DI in the Organic treatment (3 and 5 species, respectively). *Fusarium* species were still the predominant group, making up 60% of the total species identified. Although we did not observe a difference in the number of species identified under the 100% ET - Organic treatment compared with the 100% ET - Conventional treatment, the species shifted from *Fusarium* spp. and *Microascus* spp. to *F. oxysporum* and *Clonostachys* spp. *Fusarium solani* was the only species consistently isolated across treatments.

Fungal root communities. Using amplicon sequencing, across irrigation treatments, we identified ASVs belonging to 164 fungal species across the irrigation x soil management treatments (84 and 120 ASVs in the 100% ET and 25% ET in the Organic treatment, respectively, and 66 and 147 ASVs in the Conventional and Organic treatments, respectively). Although an uncultured fungus ASV predominated the Organic treatment, *Alternaria* spp. was the second most common taxa identified under 100% ET (approximately 17% of ASVs) and

*Pseudopyrenochaeta lycopersici* was the second most common taxa under 25% ET (approximately 8%) (Fig. 14). The proportion of ASVs that belonged to *Fusarium* species (*F. oxysporum, F. solani, F. acuminatum, F. falciforme, F. equiseti, F. trincinctum, F. lateritium*) decreased in the Organic treatment with approximately 17% and 4% of ASVs in the 100% ET and 25% ET treatments, respectively (both species complexes combined).

Based on $\alpha$-diversity analyses, there was greater fungal diversity in the Organic treatment ($P = 0.003$) (Fig. 15), however there was no effect of soil management on diversity based on the Shannon or Simpson indices ($P > 0.05$). The structure of fungal communities colonizing roots clearly differed depending on the soil amendment, as illustrated by nonmetric multidimensional scaling analyses (NMDS) (Fig. 16). The soil amendment parameter was responsible for 15% of the variability of the communities between root samples according to the PERMANOVA test, while the irrigation treatment explained 1% of the variability (not shown). There was a significant effect of soil management (adonis $P = 0.002$) on the fungal community structure, but not irrigation treatment (adonis $P = 0.962$).

Based on differential abundance of sequence variants analyses, the abundance of nine taxa shifted between the soil amendment treatments but no taxa shifts were observed between the irrigation treatments (Table 6). Across both irrigation treatments, the abundance of *Pseudopyrenochaeta lycopersici* (corky root pathogen) increased by a 3.0 $\log_2$ fold-change ($P < 0.0001$) in the Conventional treatment compared with the Organic treatment. Under the Conventional treatment, the abundance of *Alternaria* decreased by an 8.9 $\log_2$ fold-change compared with the Organic treatment ($P < 0.0001$). Also under the Conventional treatment, Dactylonectria (associated with black foot disease of grapevine) decreased by a -4.7 $\log_2$ fold-

change (*P* = 0.021) and the abundance of ASVs corresponding to four saprotrophic/endophytic fungal genera (*Aspergillus, Cladosporium, Mortierella,* and *Mucor*) decreased compared with the Organic treatment. *Ceratobasidium* was the only ASV identified that increased (6.0 $\log_2$ fold-change, *P* = 0.012) in the Conventional treatment.

**4. Discussion and conclusion**

We evaluated the effects of a two-year sequential application of grower-modeled deficit irrigation (DI – 60% ET) under synthetic fertilizer on stem rot and root-associated fungal communities. Across years, we recovered 7 and 9 species under 100% ET and 60% ET, respectively, from stem rot (in both years, more species were detected under DI). Using amplicon sequencing, across years, we identified 109 and 75 ASVs in the roots in 100% ET and 60% ET treatments, respectively. The effect of DI on the number of ASVs decreased over time; we observed a 57% reduction under DI in 2019 and a 7% reduction under DI in 2020.

In evaluating pathogen shifts, *Fusarium* species including the crown and root rot pathogen (*Fusarium oxysporum* f. sp. *radicis-lycopersici* - Forl) and the stem rot and vine decline pathogen (*F. noneumartii* - FN) were the most common species identified in stem rot, which was significantly higher under DI (see Chapter 1). The corky root pathogen (*Pseudopyrenochaeta lycopersici*) and wilt pathogen (*Verticillium dahliae*) were the most common species identified in roots using amplicon sequencing. The corky root pathogen was detected under DI (in 2019), whereas *V. dahliae* was recovered in both treatments with no difference in abundance. The recovery of *P. lycopersici* and *F. noneumartii* only under DI in 2019 and the increased recovery frequency of *F. oxysporum* under DI in 2020 using culture-

dependent methods could explain the increased field symptoms we observed under DI in Chapter 1.

Evaluating the effects of soil amendment – DI interactions in the two-year sequential application of grower-modeled DI. We identified 13 and 7 species present in stem rot in the Synthetic and Compost treatments, respectively. Forl was consistently recovered from all stem rot in sampled treatments in both years. *Fusarium solani* and *F. noneumartii* were consistently identified only in the 60% ET treatment in both years, indicating a DI-enhancing effect; in 2020, both species were present only in the Compost treatment, indicating that compost may also enhance microbial activity. Using culture-independent methods, across years we identified 115 and 69 ASVs in the roots in the Synthetic and Compost treatments, respectively. The number of ASVs in roots were consistently reduced by ~40% under Compost in both years, but there was no detectable effect of irrigation.

*Fusarium* species including Forl and FN were the predominant species diagnosed in stem rot tissue using culture-dependent methods, however *P. lycopersici* and *V. dahliae* were the most predominant species identified using amplicon sequencing. This is likely because the latter species is slow-growing and easily outcompeted by Fusarium in culture. With culture-dependent work, creating pure cultures requires isolating colonies early before they coalesce on growth media, making it so that slower-growing saprobes like these can be missed. *Verticillium dahliae* can be challenging to isolate from plant tissue as it grows slowly and its characteristic whorl structures can be obscured by other faster-growing fungi in the plant tissue. *Fusarium* species are not as challenging to isolate from plant tissue, particularly with the use of Fusarium selective media, which explains the high isolation frequency of this genus.

We observed decreased abundance of *V. dahliae* under DI in both soil amendment treatments in 2020. These results could help explain the decreased decline incidence we observed in the DI – Compost treatment compared to the DI – Synthetic treatment that year (Chapter 1). Interestingly, in the Grower Model DI study both methods revealed increased abundance of *Fusarium* spp. in the Compost treatment in 2020, indicating that compost may facilitate *Fusarium* spp. infection (see Ch. 1).

Examining the effects of beneficials, amplicon sequencing alone revealed increased abundance of *Clonostachys* under DI in 2020. Because *Clonostachys* is a diverse genus made up of saprobes, endophytes, pathogens, and mycoparasites we cannot infer why this increase occurred without species level information, however the genus contains *C. rosea*, which is a known mycoparasite (Nygren et al., 2018) and has been shown to promote tomato root growth (Han et al., 2022).

There were several instances in the Grower Model DI study where other *Fusarium* spp. (*F. acuminatum*, *F. brachygibbosum,* and *F. redolens*) were isolated from symptomatic plant tissue. Pathogenicity trials with these isolates confirmed the non-pathogen status of *F. redolens*, but also suggest that *F. brachygibbosum* and *F. acuminatum* may be weakly pathogenic. Previous studies of *F. brachygibbosum* suggest that this pathogen can cause wilt symptoms in tomato (Liu et al., 2022), however the work does not mention the stem lesions we observed in our pathogenicity trials. Of note, *F. brachygibossum* and *F. redolens* were isolated from plant tissue in the Grower Model DI study but were not identified with amplicon sequencing. This is most likely the result of our using translation elongation factor 1-alpha (TEF) gene primers for isolates with Fusarium-like morphology with the culture-dependent

methods whereas we used the internal transcribed spacer (ITS) region for amplicon sequencing, which are unable to accurately resolve *Fusarium* species. Additionally, with the culture-dependent method we used nucleotide alignment databases more suited to *Fusarium* identification than UNITE and NCBI.

We then evaluated the effects of extreme DI (25% ET) under conventional soil management practices using culture-dependent methods and amplicon sequencing. With the former, *Fusarium* was the predominant genus recovered from diseased stems. With amplicon sequencing, we identified 41 and 46 ASVs in the roots in 100% ET and 25% ET treatments, respectively. The corky root pathogen *P. lycopersici* was the most abundant species and the wilt pathogen *V. dahliae* was the second-most abundant species in both irrigation treatments. *Fusarium solani* made up the third-most abundant species in both irrigation treatments. There was no effect of irrigation on relative abundance. The remaining taxa in the top 20 identified with amplicon sequencing include *Acrocalymma vagnum, Aspergillus chevalieri, Botryotrichum* spp*., Ceratobasidium* spp*., Cladosporium cladosporioides, Megalocystidium leucoxanthum,* and *Trichocomaceae* spp. These taxa are saprobes and likely did not contribute to disease development or suppression.

We then evaluated the effect of a 25 year-long organic soil management practice (compost amendment + cover cropping) on the extreme DI treatment. With culture-dependent methods in the Organic treatment we observed a two-fold increase in the number of species identified under DI compared with 100% ET. *Clonostachys* and *Nectria* spp. were recovered only from the Organic treatment and the latter was recovered only under DI. *Nectria* spp. are known as saprobes on woody plants but can also be parasitic (UC IPM).

Interestingly, these genera were not among the top 20 species identified using amplicon sequencing. With this technique, we observed increased alpha diversity in the Organic treatment compared with the Conventional treatment, but no effect of DI.

Since all but two of the differentially abundant taxa observed increased in the Organic treatment and all of these taxa are likely able to be saprophytic it is possible that the compost and/or cover cropping increased root endosphere diversity, which is supported by the alpha diversity results. Decreased abundance of the tomato pathogen *Pseudopyrenochaeta lycopersici* (corky root) under organic management could be a consequence of that shift. The only other taxon that decreased in abundance in the Organic treatment was a *Ceratobasidium* species. This genus is generally made up of saprobes, but the anamorph is considered part of the *Rhizoctonia* species complex, which comprises noteworthy plant pathogens such as *R. solani* (Arakawa and Inagaki, 2014). The remaining taxa in the top 20 identified only with amplicon sequencing include *Apiotrichum porosum, Aspergillus versicolor, Cladosporium allicinum, Cladosporium cladosporioides, Mortierella alpina, Mucor racemosus, Pseudogymnoascus destructans,* and *Tremellomycetes* spp. Most of these taxa are saprobes except for *P. destructans*, which is an animal pathogen (Blehert et al., 2009).

In the Extreme DI study, we did not observe an effect of DI on fungal root communities. This result was contrary to our expectations that under the more extreme deficit irrigation level, there would be a more significant effect in the Extreme DI study. Because we did not stem water potential in the Extreme DI study, we cannot say whether plants were under water stress.

*Glomerella acutata* (teleomorph *Colletotrichum fioriniae*) was the only plant pathogen that was identified solely with culture-dependent methods, however an ASV assigned to uncultured Glomus was identified (no *Colletotrichum* species were identified). *Glomerella acutata* has been reported as a pathogen of blueberry (Talgø et al., 2007), avocado (Avila-Quezada et al., 2007), wax myrtle (Mcritchie and Leahy, 1998), and rubber (Jayasinghe et al., 1997), but has not been reported as a tomato pathogen. *Verticillium dahliae* was the only plant pathogen identified solely with amplicon sequencing.

Overall, we observed an effect of soil management on alpha and beta diversity in the 25 year-long Extreme DI study, but not in the 2 year-long Grower Model DI study, likely due to longer duration over which soil management practices were in place. It is also likely that the addition of the cover crop created a greater divergence from the conventional treatment. Potential benefits from organic amendment incorporation and cover cropping such as carbon sequestration (Diacono and Montemurro, 2011), decreased soil bulk density (Tittarelli et al., 2007), and increased microbial diversity (Hartmann et al., 2015, 2017; Qin et al., 2019) occur slowly over time. It is possible that these effects were realized to a fuller extent in the Extreme DI study. Microbial community analysis comparing the bulk soil in each field could help explain this difference.

Much of the work done on the effects of reduced irrigation or drought focuses on fungal and bacterial communities in the rhizosphere and bulk soil and studies that focus on the root endosphere report a range of results. For example, in work done with grapevine (*Vitis vinifera* L.), drought decreased fungal diversity in roots (Carbone et al., 2021), but this was not the case in a study conducted in maize (*Zea mays*) (Wang et al., 2020). We may have observed a

stronger effect of DI in our work had we examined bacterial communities, which are often less tolerant to soil moisture reductions. For example, in microbial community work with Bermudagrass (Cynodon dactylon (L.) × C. transvaalensis Burtt-Davy) (Hu et al., 2023), root bacterial community composition was more responsive to water stress than the fungal community. Use of a different cultivar or different soil management treatments may have resulted in a more apparent effect of DI; in work conducted with arbuscular mycorrhizal fungi in switchgrass *(Panicum virgatum*), the effects of drought on community composition depended on cultivar and fertilizer (Emery et al., 2022). Supporting this, in Chapter 2 we found a cultivar – irrigation interaction in regard to *F. noneumartii* disease development.

Questions regarding the effects of DI on other important non-fungal tomato pathogens still remain. Inclusion of bacterial and viral communities in future analyses could create a more holistic picture of how this water-saving practice influences tomato disease and how implementing soil amendment and cover cropping affects these interactions. Clearly, amplicon sequencing is useful due to its high throughput nature and broad level quantitative depiction of community composition that is unfeasible with culture-dependent methods. Additionally, culture-dependent methods cannot account for the large proportion of bacterial and fungal organisms that are non-culturable. However, due to the limitations of ITS for certain genera such as *Fusarium*, studies should include both culture-dependent and next generation sequencing approaches until additional analytical resources are developed. In our study, plant sampling for culture-dependent identification of species was not as extensive or evenly executed across treatments as was the root collection for amplicon sequencing. This limited our ability to make definitive statements regarding treatment effects on fungal communities with

the culture-dependent data. Future work should include even sampling across treatments. Additionally, sequence data could be used to guide culture-dependent efforts to find novel pathogens.

**Literature cited**


Abarenkov K., Nilsson R.H., Larsson K.H., Alexander I.J., Eberhardt U., Erland S., Høiland K., Kjøller R., Larsson E., Pennanen T., Sen R., Taylor A.F.S., Tedersoo L., Ursing B.M., Vrålstad T., Liimatainen K., Peintner U., and Kõljalg U. (2010). The UNITE database for molecular identification of fungi - recent updates and future perspectives. New Phytol. *186*, 281-285.

Agbna G.H.D., Dongli S., Zhipeng L., Elshaikh N.A., Guangcheng S., and Timm L.C. (2017). Effects of deficit irrigation and biochar addition on the growth, yield, and quality of tomato. Sci. Hortic. *222*, 90-101.

Altschul S.F., Gish W., Miller W., Myers E.W., and Lipman D.J. (1990). Basic local alignment search tool. J. Mol. Biol. *215*, 403-410.

Andrews S. (2010). FastQC: A quality control tool for high throughput sequence data. Online. https://www.bioinformatics.babraham.ac.uk/projects/fastqc/. Accessed 22 Nov. 2023.

Arakawa M., and Inagaki K. (2014). Molecular markers for genotyping anastomosis groups and understanding the population biology of Rhizoctonia species. J. Gen. Plant Pathol. *80*, 401-407.

Atandi J.G., Haukeland S., Kariuki G.M., Coyne D.L., Karanja E.N., Musyoka M.W., Fiaboe K.K.M., Bautze D., and Adamtey N. (2017). Organic farming provides improved management of

plant parasitic nematodes in maize and bean cropping systems. Agric. Ecosyst. Environ. *247*, 265-272.

Avila-Quezada G., Silva-Rojas H.V., and Teliz-Ortiz D. (2007). First Report of the Anamorph of *Glomerella acutata* Causing Anthracnose on Avocado Fruits in Mexico. Plant Dis. *91*, 1200.

Berendsen R.L., Pieterse C.M.J., and Bakker P.A.H.M. (2012). The rhizosphere microbiome and plant health. Trends Plant Sci. *17*, 478-486.

Blehert D.S., Hicks A.C., Behr M., Meteyer C.U., Berlowski-Zier B.M., Buckles E.L., Coleman J.T.H., Darling S.R., Gargas A., Niver R., Okoniewski J.C., Rudd R.J., and Stone W.B. (2009). Bat white-nose syndrome: An emerging fungal pathogen? Science *323*, 227.

Bodner G., Nakhforoosh A., and Kaul H.P. (2015). Management of crop water under drought: a review. Agron. Sustain. Dev. *35*, 401-442.

Bureau of Reclamation (2020). Summary of Water Supply Allocations. Online. https://www.usbr.gov/mp/cvp-water/allocations.html. Accessed 19 Nov. 2023.

CA Department of Food and Agriculture (2023). California Agricultural Production Statistics - California's Top 10 Agricultural Commodities. Online. https://www.cdfa.ca.gov/Statistics/. Accessed 19 Nov. 2023.

CA Department of Water Resources (2020). California Snow Water Content. Online. https://water.ca.gov/Programs/Flood-Management/Flood-Data/Snow-Surveys. Accessed 22 Nov. 2023.

Callahan B.J., McMurdie P.J., Rosen M.J., Han A.W., Johnson A.J.A., and Holmes S.P. (2016). DADA2: High-resolution sample inference from Illumina amplicon data. Nat. Methods

*13*, 581-583.

Carbone M.J., Alaniz S., Mondino P., Gelabert M., Eichmeier A., Tekielska D., Bujanda R., and Gramaje D. (2021). Drought influences fungal community dynamics in the grapevine rhizosphere and root microbiome. J. Fungi *7*, 686.

Del Castillo Múnera J., Belayneh B.E., Lea-Cox J.D., and Swett C.L. (2019a). Effects of set-point substrate moisture control on oomycete disease risk in containerized annual crops based on the tomato–*Phytophthora capsici* pathosystem. Phytopathology *109*, 1441-1452.

Del Castillo Múnera J., Belayneh B., Ristvey A., Koivunen E.E., Lea-Cox J., and Swett C.L. (2019b). Enabling adaptation to water scarcity: Identifying and managing root disease risks associated with reducing irrigation inputs in greenhouse crop production – A case study in poinsettia. Agric. Water Manag. *226*.

Del Castillo Múnera J., Poret-Peterson A.T., and Swett C.L. (2022). Changes in Fungal and Oomycete Community Composition Following Irrigation Reductions Aimed at Increasing Water Use Efficiency in a Containerized Nursery Crop. Phytobiomes J. *6,* 247-260.

Chang E.H., Wang C.H., Chen C.L., and Chung R.S. (2014). Effects of long-term treatments of different organic fertilizers complemented with chemical N fertilizer on the chemical and biological properties of soils. Soil Sci. Plant Nutr. *60*, 499-511.

Diacono M., and Montemurro F. (2011). Long-Term Effects of Organic Amendments on Soil Fertility. Sustain. Agric. *2*, 762-783.

van Der Does H.., Lievens B., Claes L., Houterman P.M., Cornelissen B.J., and Rep M. (2008). The presence of a virulence locus discriminates *Fusarium oxysporum* isolates causing tomato

wilt from other isolates. Environ. Microbiol. *10*, 1475-1485.

Emery S.M., Bell-Dereske L., Stahlheber K.A., and Gross K.L. (2022). Arbuscular mycorrhizal fungal community responses to drought and nitrogen fertilization in switchgrass stands. Appl. Soil Ecol. *169*, 104218.

Fazio G., Stevens M.R., and Scott J.W. (1999). Identification of RAPD markers linked to fusarium crown and root rot resistance (Frl) in tomato. Euphytica. *105,* 205-210.

Fenn P., Mason J.D., Basset E.N., Holland R.T. (1991). *Hypoxylon atropuntatum* and oak decline and mortality in the southern United States. In: *Proceedings of an International Symposium on "Oak Decline in Europe"*, *15-18 May 1990, Kornik, Poland,* Polish Academy of Sciences, Kornik, Poland, 149-158.

Finney D.M., Buyer J.S., and Kaye J.P. (2017). Living cover crops have immediate impacts on soil microbial community structure and function. J. Soil Water Conserv. *72,* 261-373.

Fiske I.J., and Chandler R.B. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. *43*, 1-23.

Gardes M., and Bruns T.D. (1993). ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. Mol. Ecol. *2*, 113-118.

Han Z., Ghanizadeh H., Zhang H., Li X., Li T., Wang Q., Liu J., and Wang A. (2022). *Clonostachys rosea* promotes root growth in tomato by secreting auxin produced through the tryptamine pathway. J. Fungi. *8*, 1166.

Hartmann M., Frey B., Mayer J., Mäder P., and Widmer F. (2015). Distinct soil microbial diversity under long-term organic and conventional farming. ISME J. *9*, 1177-1194.

Hartmann M., Brunner I., Hagedorn F., Bardgett R.D., Stierli B., Herzog C., Chen X., Zingg A.,

Graf-Pannatier E., Rigling A., and Frey B. (2017). A decade of irrigation transforms the soil microbiome of a semi-arid pine forest. Mol. Ecol. *26*, 1190-1206.

Hirich A., Choukr-Allah R., and Jacobsen S.E. (2014). Deficit irrigation and organic compost improve growth and yield of quinoa and pea. J Agron Crop Sci. *200*, 390-398.

Hu J., Cyle K.T., Miller G., and Shi W. (2023). Water deficits shape the microbiome of Bermudagrass roots to be Actinobacteria rich. FEMS Microbiol. Ecol. *99*, 1-13.

Intini M. (1991). Some common fungi on oaks in Italy. In: *Proceedings of an International Symposium on "Oak Decline in Europe"*, *15-18 May 1990, Kornik, Poland,* Polish Academy of Sciences, Kornik, Poland, 129-134.

Jayasinghe C.K., Fernando T.H.P.S., and Priyanka U.M.S. (1997). *Colletotrichum acutatum* is the main cause of Colletotrichum leaf disease of rubber in Sri Lanka. Mycopathologia *137*, 53-56.

Khapte P.S., Kumar P., Burman U., and Kumar P. (2019). Deficit irrigation in tomato: Agronomical and physio-biological implications. Sci. Hort *248*, 256-264.

Leslie J.F. and Summerell B.A. *The Fusarium laboratory manual.* John Wiley & Sons, 2008.

Liu Y.J., Whelen S., and Hall B.D. (1999). Phylogenetic relationships among ascomycetes: Evidence from an RNA polymerse II subunit. Mol. Biol. Evol. *16*, 1799-1808.

Liu J., Deng S., Chang W., and Wang H. 1990. First report of tomato wilt caused by *Fusarium brachygibbosum* in China. Plant Dis. *107*, 2844.

Lu J., Shao G., Cui J., Wang X., and Keabetswe L. (2019). Yield, fruit quality and water use efficiency of tomato for processing under regulated deficit irrigation: A meta-analysis. Agric. Water Manag. *222*, 301-312.

Luisi N., Sicoli G., and Lerario P. (1991). Occurrence of *Armillaria* species on declining oaks in southern Italy. In: *Proceedings of an International Symposium on "Oak Decline in Europe"*, *15-18 May 1990, Kornik, Poland,* Polish Academy of Sciences, Kornik, Poland, 187-193.

Martin M. (2011). Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet.Journal *17*, 10-12.

Martínez-García L.B., Korthals G., Brussaard L., Jørgensen H.B., and De Deyn G.B. (2018). Organic management and cover crop species steer soil microbial community structure and functionality along with soil organic matter properties. Agric, Ecosyst. Environ. *263,* 7-17.

McGrath D.J., and Maltby J.E. (1988). Fusarium wilt race 3 resistance in tomato. In *Research and Development Conference on Vegetables, the Market and the Producer. 247,* 107-110.

McMurdie P.J., and Holmes S. (2013). Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. PLoS One *8*.

Mcritchie J.J., and Leahy R.M. (1998). Spot Anthracnose of Wax Myrtle. Plant Pathol. Circ. Fla. Dept. Agric. Consum. Serv. Div. Plant Ind. 1-2.

Nygren K., Dubey M., Zapparata A., Iqbal M., Tzelepis G.D., Durling M.B., Jensen D.F., and Karlsson M. (2018). The mycoparasitic fungus *Clonostachys rosea* responds with both common and specific gene expression during interspecific interactions with fungal prey. Evol. Appl. *11*, 931-949.

O'Donnell K., Corby Kistler H., Cigelnik E., and Ploetz R.C. (1998). Multiple evolutionary origins of the fungus causing Panama disease of banana: Concordant evidence from nuclear

and mitochondrial gene genealogies. PNAS *95*, 2044-2049.

Oksanen A.J., Blanchet F.G., Friendly M., Kindt R., Legendre P., Mcglinn D., Minchin P.R., Hara R.B.O., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E., and Wagner H. (2019). Package ‘ vegan .’

van Os G.J. and van Ginkel J.H. (2001). Suppression of *Pythium* root rot in bulbous *Iris* in relation to biomass and activity of the soil microflora. Soil Biol. Biochem. *33,* 1447-1454.

Parsons M.W., and Munkvold G.P. (2010). Associations of planting date, drought stress, and insects with Fusarium ear rot and fumonisin B1 contamination in California maize. Food Addit. Contam. - Part A *27*, 591-607.

Posit team (2023). RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. URL http://www.posit.co/.

Qin K., Dong X., Jifon J., and Leskovar D.I. (2019). Rhizosphere microbial biomass is affected by soil type, organic and water inputs in a bell pepper system. Appl. Soil Ecol. *138*, 80-87.

Qin K., and Leskovar D.I. (2018). Lignite-derived humic substances modulate pepper and soil-biota growth under water deficit stress. J. Plant Nutr. Soil Sci. *181*, 655-663.

Qin K., and Leskovar D.I. (2020). Assessments of humic substances application and deficit irrigation in triploid watermelon. HortSci. *55*, 716-721.

Qiu M., Zhang R., Xue C., Zhang S., Li S., Zhang N., and Shen Q. (2012). Application of bio-organic fertilizer can control Fusarium wilt of cucumber plants by regulating microbial community of rhizosphere soil. Biol. Fertil. Soils *48*, 807-816.

Raaijmakers J.M., Paulitz T.C., Steinberg C., Alabouvette C., and Moënne-Loccoz Y. (2008). The rhizosphere: A playground and battlefield for soilborne pathogens and beneficial

microorganisms. Plant Soil *321*, 341-361.

Ragazzi A., Moricca S., Dellavalle I., and Mancini F. (1995). Infection of cotton by *Fusarium oxysporum* f. sp. *vasinfectum* as affected by water stress. Phytoparasitica *23*, 315-321.

Rahman N.S.N.A., Hamid N.W.A., and Nadarajah K. (2021). Effects of abiotic stress on soil microbiome. Int. J. Mol. Sci. *22*. 9036.

Schimel J.P. (2018). Life in dry soils: Effects of drought on soil microbial communities and processes. Annu. Rev. Ecol. Evol. Syst. *49*, 409-432.

Swett C.L. (2020). Managing crop diseases under water scarcity. Phytopathology *58*, 387-406.

Szabolcs I. (1994) Soils and salinisation. In Handbook of Plant and Crop Stress (ed. M. Pessarakali), pp. 3–11. Marcel Dekker, New York.

Talgø V., Aamot H.U., Strømeng G.M., Klemsdal S.S., and Stensvand A. (2007). Glomerella acutata on Highbush Blueberry (*Vaccinium corymbosum* L.) in Norway. Plant Heal. Prog. *8*, 19.

Tittarelli F., Petruzzelli G., Pezzarossa B., Civilini M., Benedetti A., and Sequi P. (2007). Quality and agronomic use of compost. In Waste Management Series, pp. 119-157.

U.S. Department of Agriculture National Agricultural Statistics Service (NASS). 2022 California Processing Tomato County Estimates. Online. https://www.nass.usda.gov. Accessed 22 Nov. 2023.

University of California Integrated Pest Management. n.d. Nectria canker – *Nectria* spp. Online. https://ipm.ucanr.edu/PMG/GARDEN/PLANTS/DISEASES/nectriacanker.html#:~:text=Nectria%20fungi%20infect%20woody%20species,if%20ever%2C%20kill%20older%20plants Accessed 22 Nov. 2023.

Vannini A. (1991). *Hypoxylon mediterraneum*: symptomatology and diffusion on Turkey oak in central Italy. In: *Proceedings of an International Symposium on "Oak Decline in Europe"*, *15-18 May 1990, Kornik, Poland,* Polish Academy of Sciences, Kornik, Poland, 159-164.

Veach A.M., Chen H., Yang Z.K., Labbe A.D., Engle N.L., Tschaplinski T.J., Schadt C.W., and Cregger M.A. (2020). Plant Hosts Modify Belowground Microbial Community Response to Extreme Drought. MSystems *5*.

Wang C., Zheng Y., Liu Z., Qian Y., Li Y., Yang L., Liu S., Liang W., and Li J. (2023). The secreted FolAsp aspartic protease facilitates the virulence of *Fusarium oxysporum* f. sp. *lycopersici*. Front. Microbiol. *14*, 1-12.

Wang P., Marsh E.L., Kruger G., Lorenz A., and Schachtman D.P. (2020). Belowground microbial communities respond to water deficit and are shaped by decades of maize hybrid breeding. Environ. Microbiol. *22*, 889-904.

White T.J., Bruns T., Lee S., and Taylor J.W. (1990). Amplification and Direct Sequencing of Fungal Ribosomal RNA Genes for Phylogenetics. In PCR Protocols: A Guide to Methods and Applications, M. Innis, D. Gelfand, J. Sninsky, and T. White, eds. (Academic Press Inc.), pp. 315-322.

Zegbe-Domínguez J.A., Behboudian M.H., Lang A., and Clothier B.E. (2003). Deficit irrigation and partial rootzone drying maintain fruit dry mass and enhance fruit quality in "Petopride" processing tomato (*Lycopersicon esculentum*, Mill.). Sci. Hortic. (Amsterdam). *98*, 505-510.

## Figures

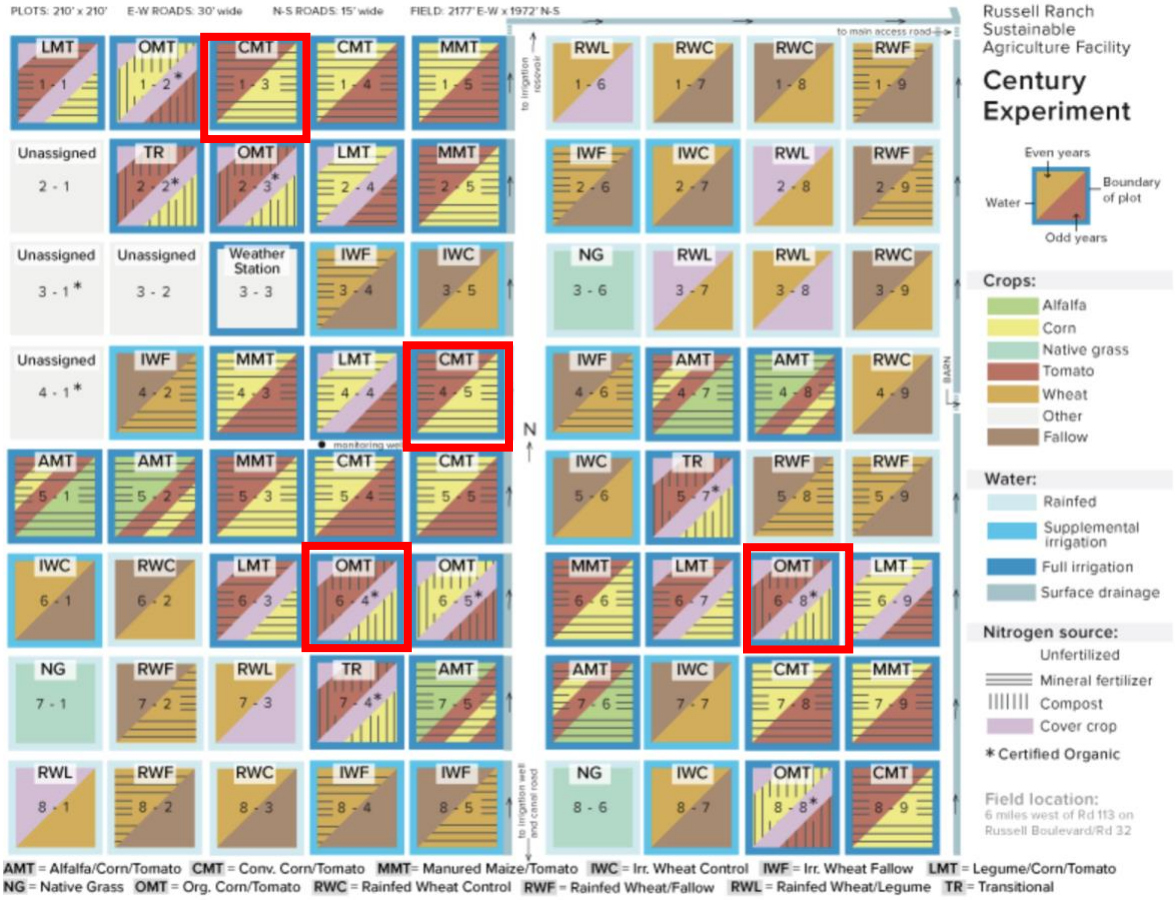



**Figure 1.** Field layout of the Russell Ranch Sustainable Agriculture Facility Century Experiment. Each square corresponds to one acre. Red squares denote the locations of our experiments in 2018. The conventional plots (CMT 1-3 and CMT 4-5) have been in a conventional corn/tomato rotation with mineral fertilizer (205 kg N/ha) since 1994 and the other two (OMT 6-4 and OMT 6-8) have been in a corn/tomato rotation since 1994 but transitioned to certified organic (winter cover crop, composted poultry manure (404 Mg N/acre), and 4.5 Mg/ha composted poultry manure) since 1999.

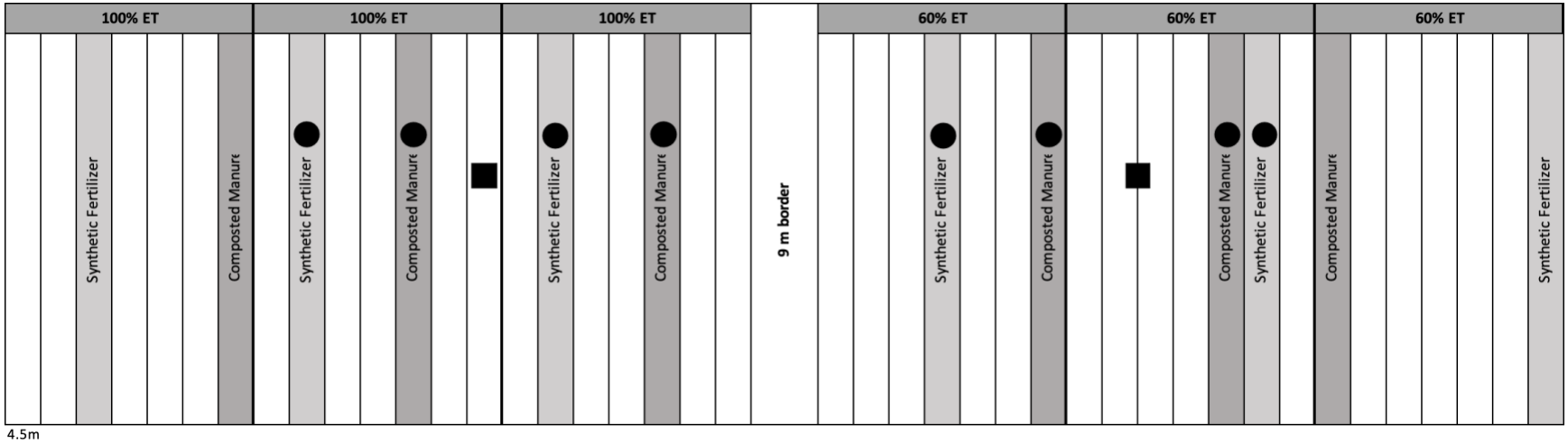



**Figure 2.** Field map representing the locations of irrigation and soil amendment treatments in the Grower Model DI study (2019-2020). The field was divided into two halves with one side corresponding to the 100% ET treatment and the other to 60% ET. An RCBD with three blocks made up of seven soil amendment treatments with varying combinations of compost type (only the two treatments used in this study are pictured) per block was set up in each half field. Each soil amendment treatment (Synthetic: 205 kg N/ha and Compost: 205 kg N/ha + 4500 kg composted poultry manure/ha) was made up of three rows. Circles represent locations of soil moisture sensors. Squares represent the locations of the soil moisture data loggers.

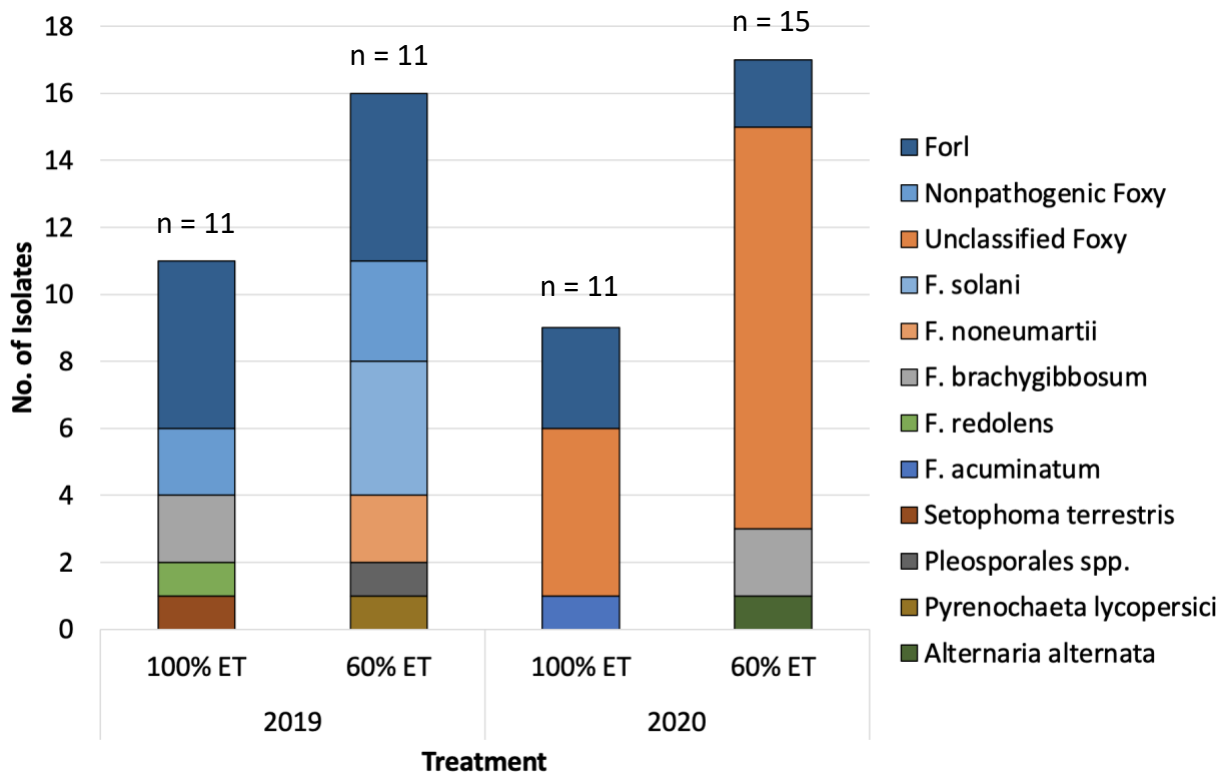



**Figure 3.** Comparing the number of species identified (>98%) in stem rot tissue between the irrigation treatments under the Synthetic treatment (205 kg N/ha) in the Grower Model DI study (2019-2020) using culture-dependent methods. Forl = *Fusarium oxysporum* f. sp. *radicis-lycopersici.* Foxy = *F. oxysporum*

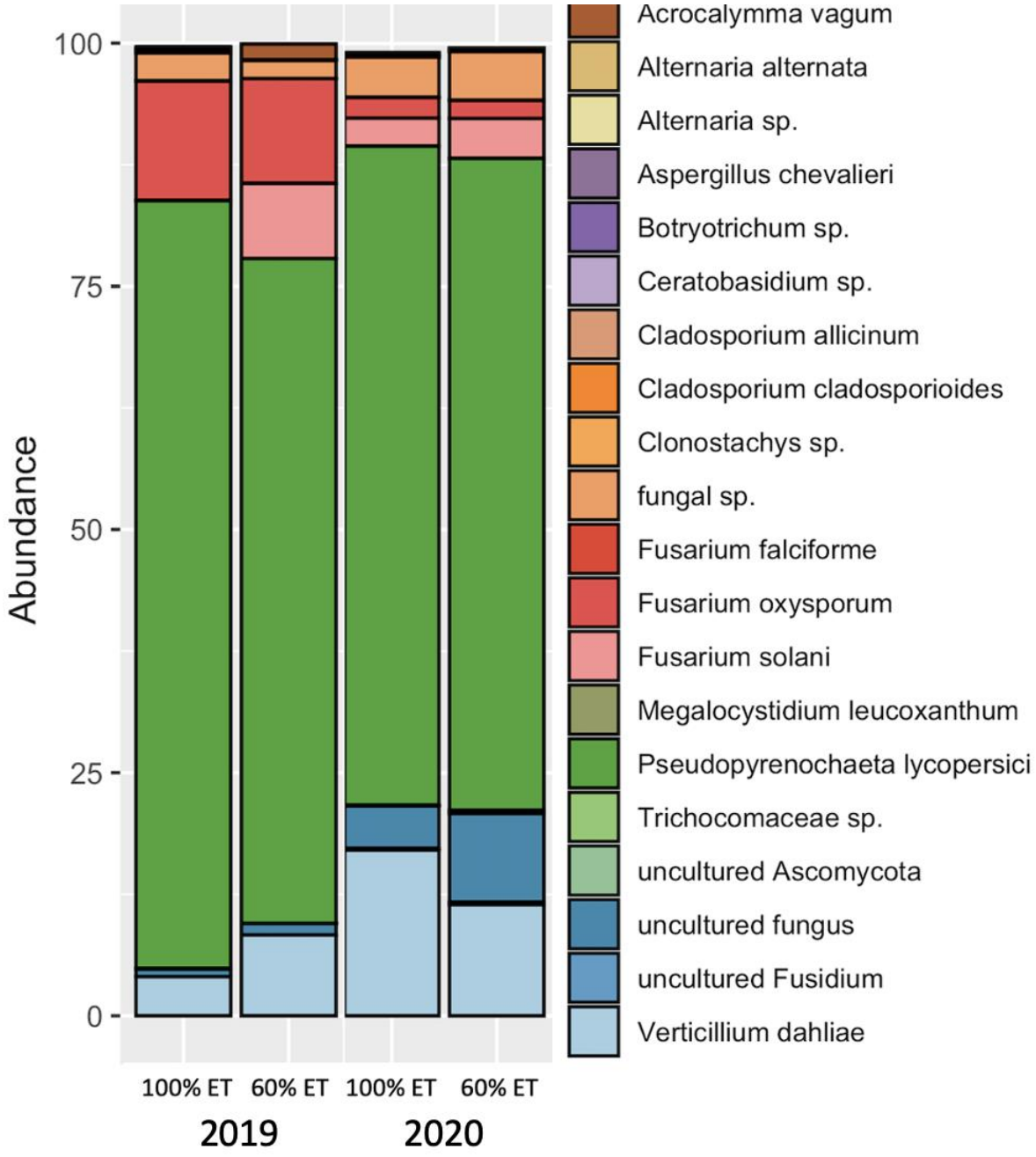



**Figure 4.** Comparing the relative abundance of the top 20 fungal species identified from tomato roots between the irrigation treatments within the Synthetic treatment (205 kg N/ha) in the Grower Model DI study (2019-2020) using amplicon sequencing.

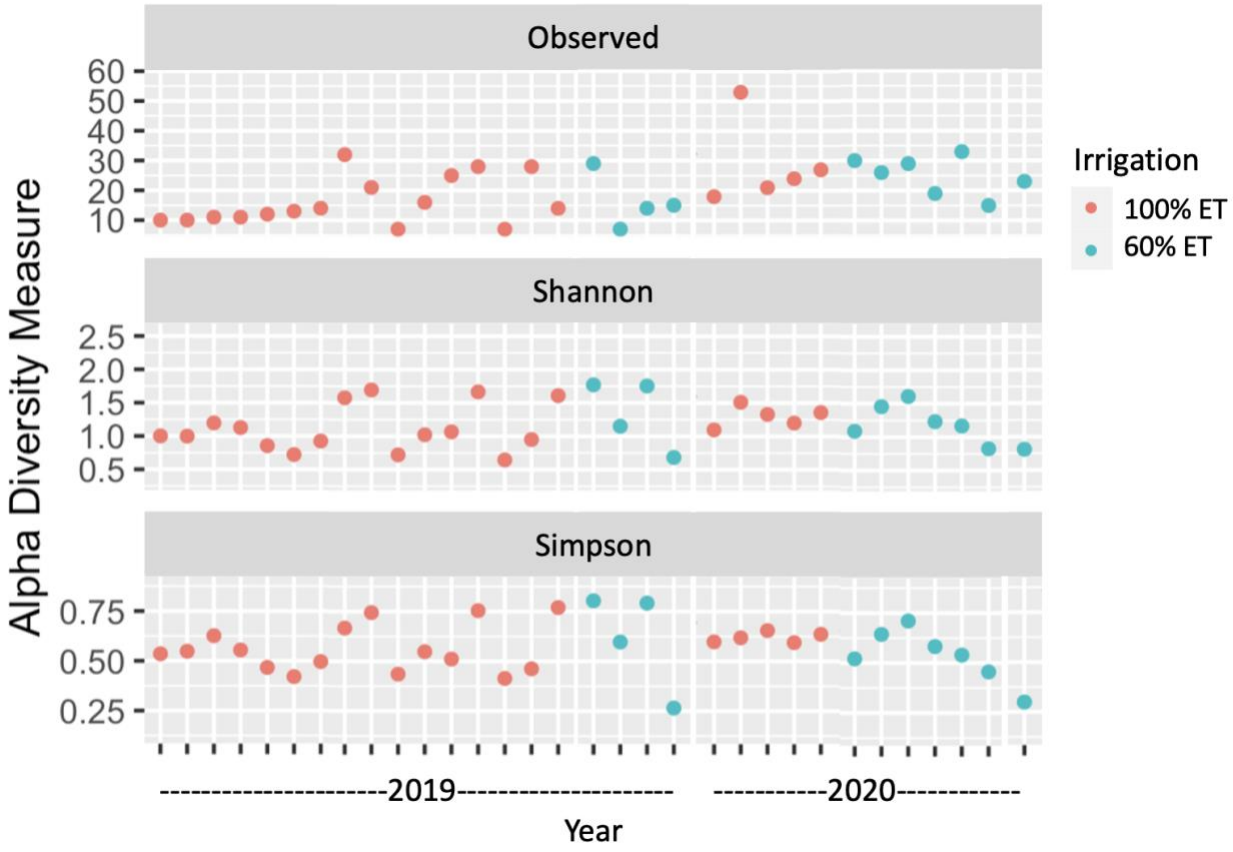



**Figure 5.** Comparing alpha diversity fungal root community measurements between the irrigation treatments under the Conventional soil management treatment (corn/tomato rotation with 205 kg N/ha) in the Grower Model DI study (2019-2020) using amplicon sequencing.

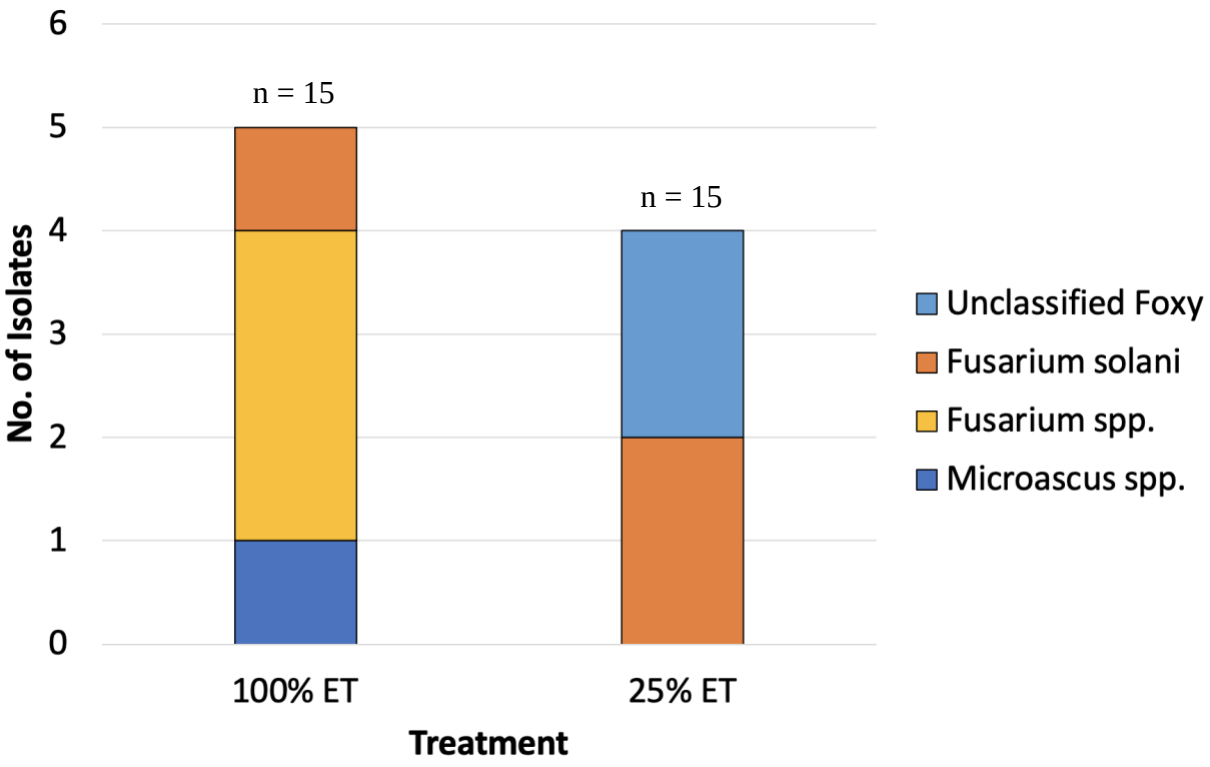



**Figure 6.** Comparing the number of stem rot-associated isolates identified to species (>98%) between the irrigation treatments under Conventional soil management (corn/tomato rotation with 205 kg N/ha) in the Extreme DI study (2018) using culture-dependent methods. Unclassified Foxy = *Fusarium oxysporum* isolates not identified to *formae speciales* (*in planta* phenotyping was not conducted for these isolates).

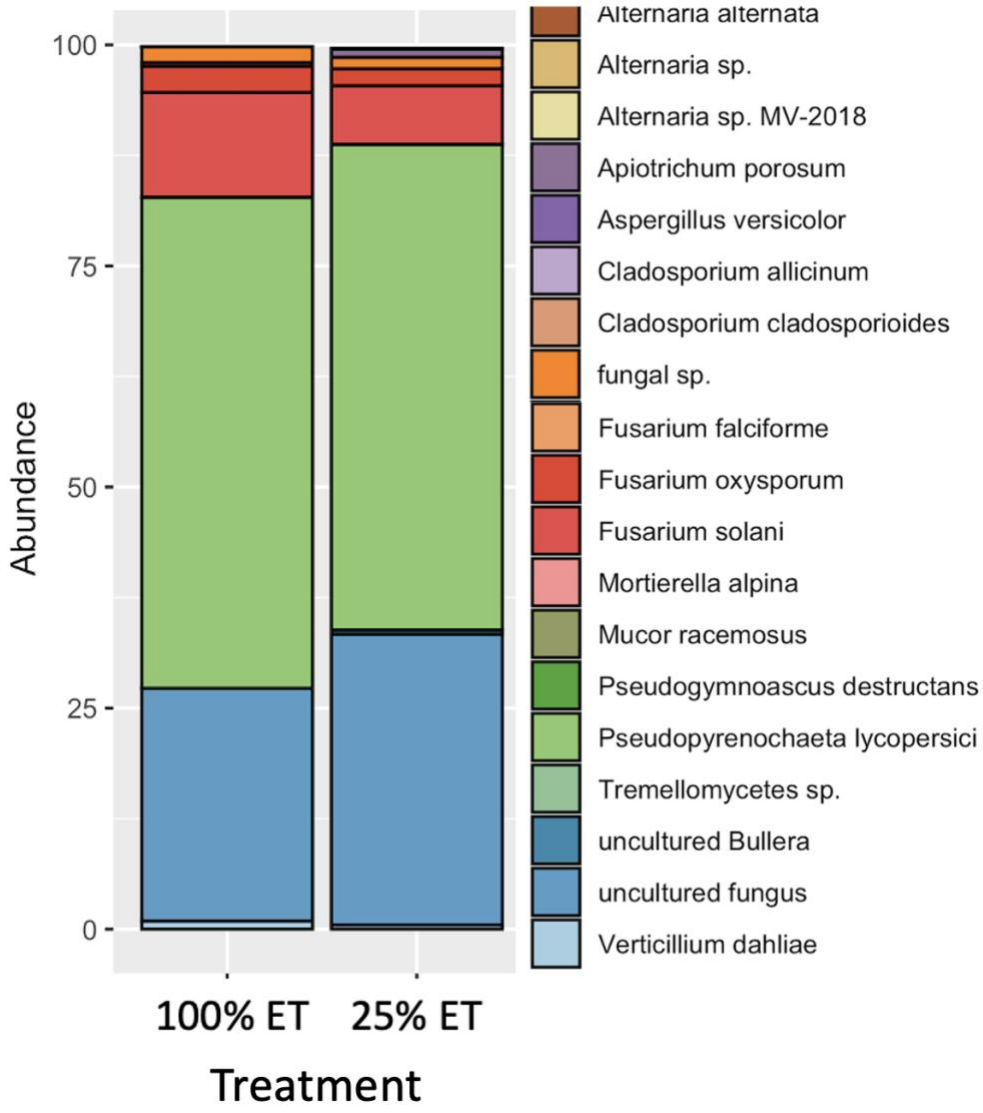



**Figure 7.** Comparing the relative abundance of the top 20 root-associated fungal species between the irrigation treatments under the Conventional soil management treatment (corn/tomato rotation with 205 kg N/ha) in the Extreme DI study (2018) using amplicon sequencing.

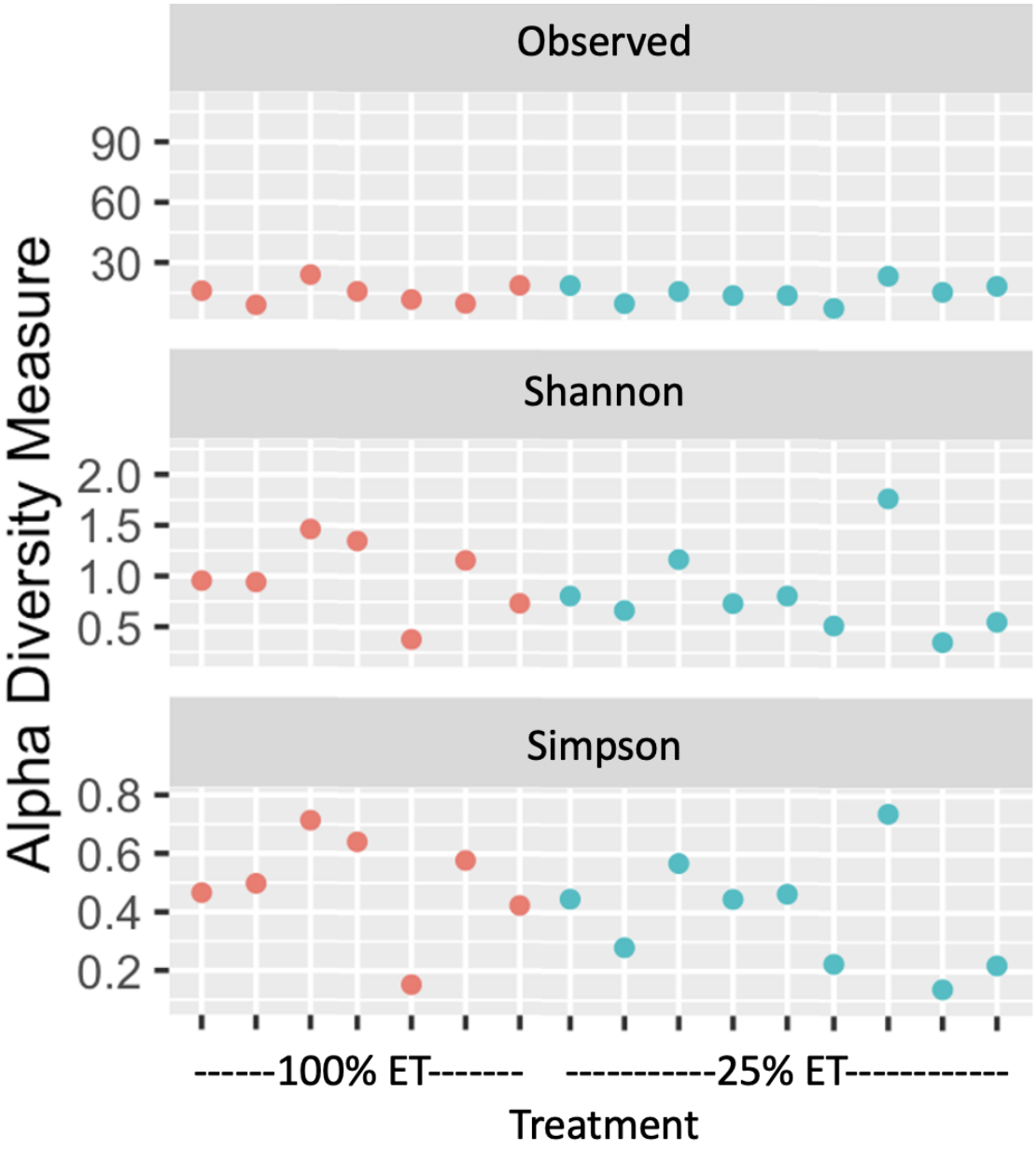



**Figure 8.** Comparing alpha diversity of root fungal communities between the irrigation treatments under the Conventional soil management treatment (corn/tomato rotation with 205 kg N/ha) in the Extreme DI study (2018) using amplicon sequencing.

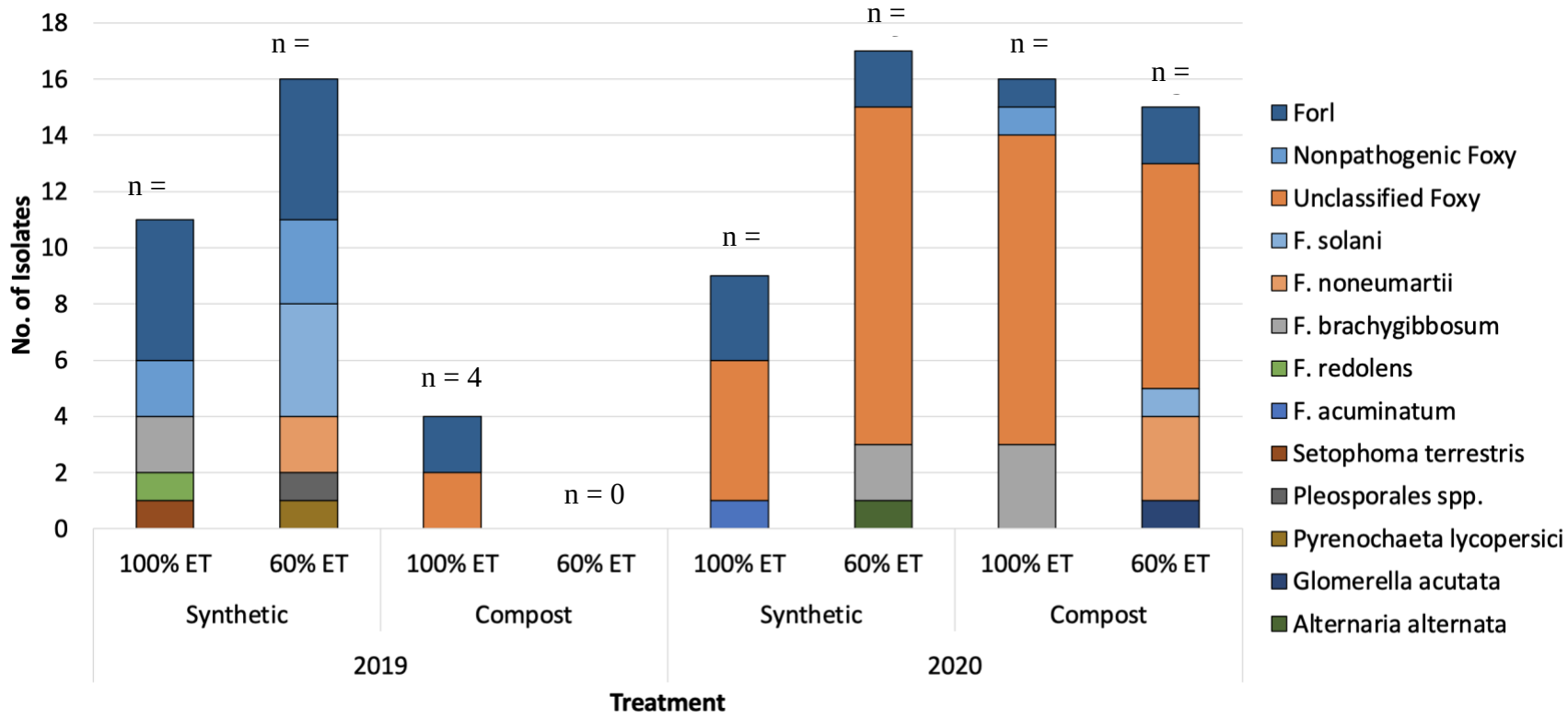



**Figure 9.** Comparing the number of stem rot-associated species identified (>98%) in stem rot tissue between the irrigation and soil amendment treatments in the Grower Model DI study (2019 and 2020) identified using culture-dependent methods. Synthetic = 205 kg N/ha; Compost = 205 kg N/ha + 4500 kg composted poultry manure/ha.

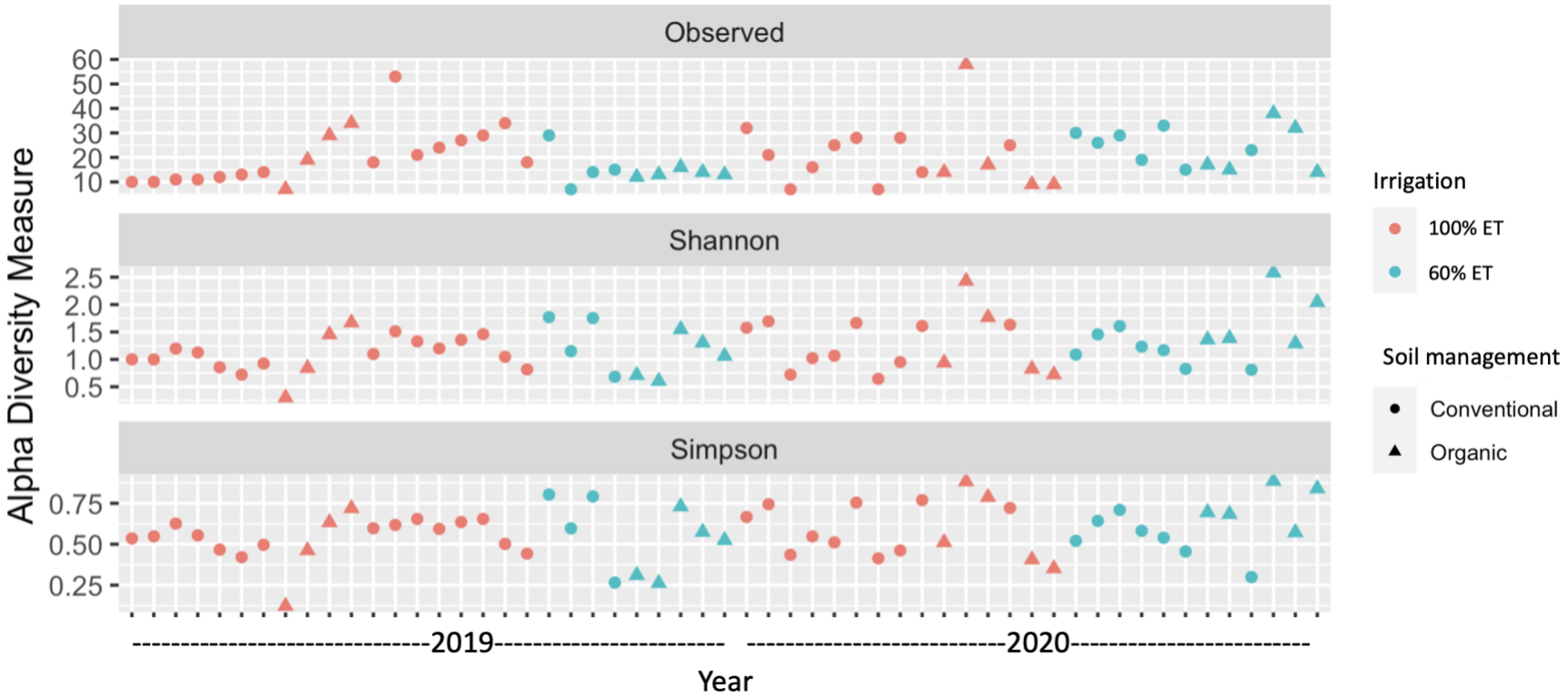



**Figure 10.** Comparing alpha diversity of root fungal communities between the irrigation and soil management treatments in the Grower Model (2019-2020) using amplicon sequencing. Pink shapes represent samples from the 100% ET irrigation treatment, blue shapes represent samples from the 25% ET irrigation treatment. Circles represent samples from the Conventional soil management treatment and triangles represent samples from the Organic soil management treatment. Conventional = corn/tomato rotation with 205 kg N/ha; Organic = corn/tomato rotation and winter cover crops with 404 Mg N/ha + 4.5 Mg/ha compost.

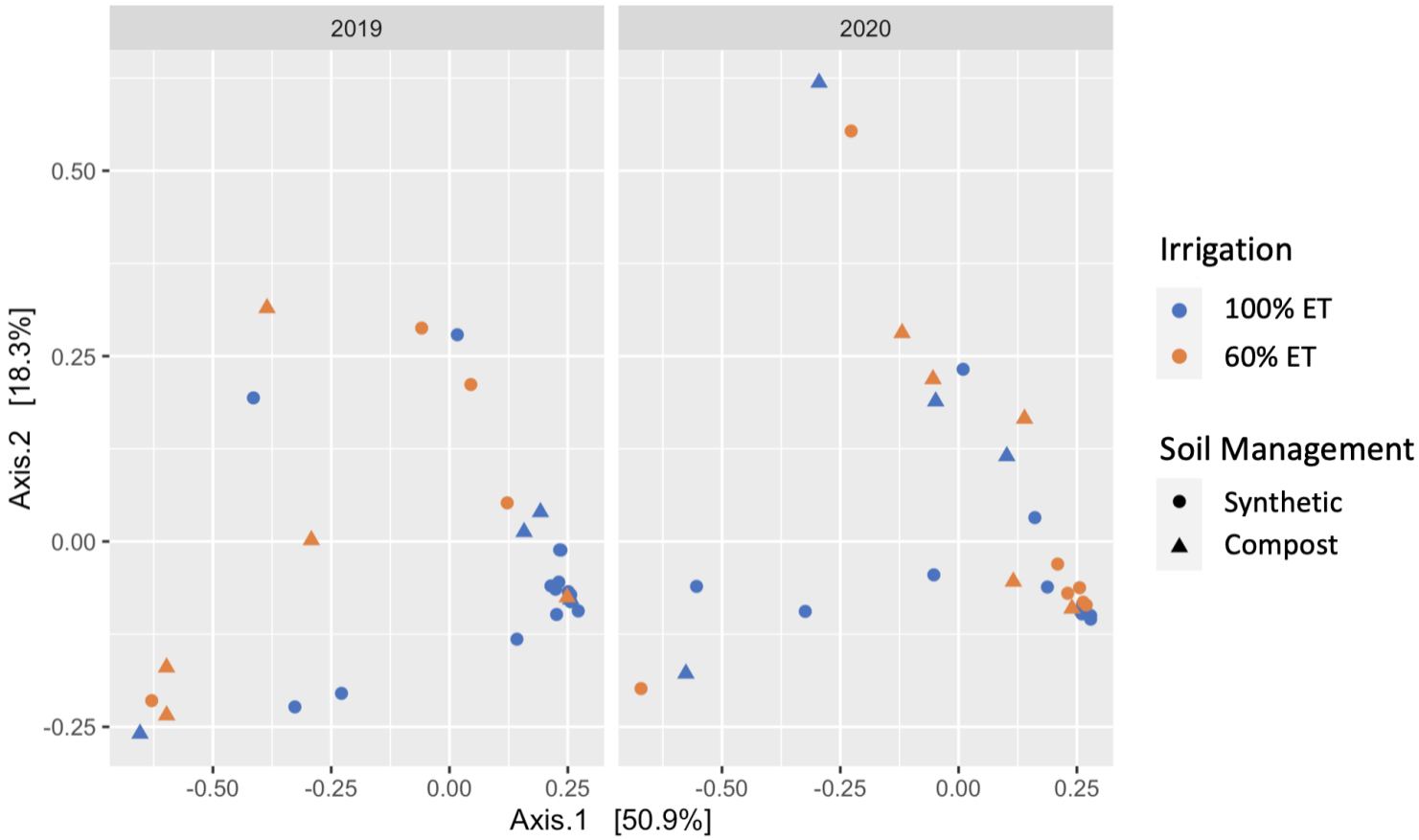



**Figure 11.** Principle component analysis (PCoA) for the Grower Model DI Study (2019-2020). Blue shapes represent samples from the 100% ET irrigation treatment, pink shapes represent samples from the 25% ET irrigation treatment. Circles represent samples from the Synthetic treatment (205 kg N/ha) and triangles represent the Compost treatment (4500 kg compost/ha and 205 kg N/ha).

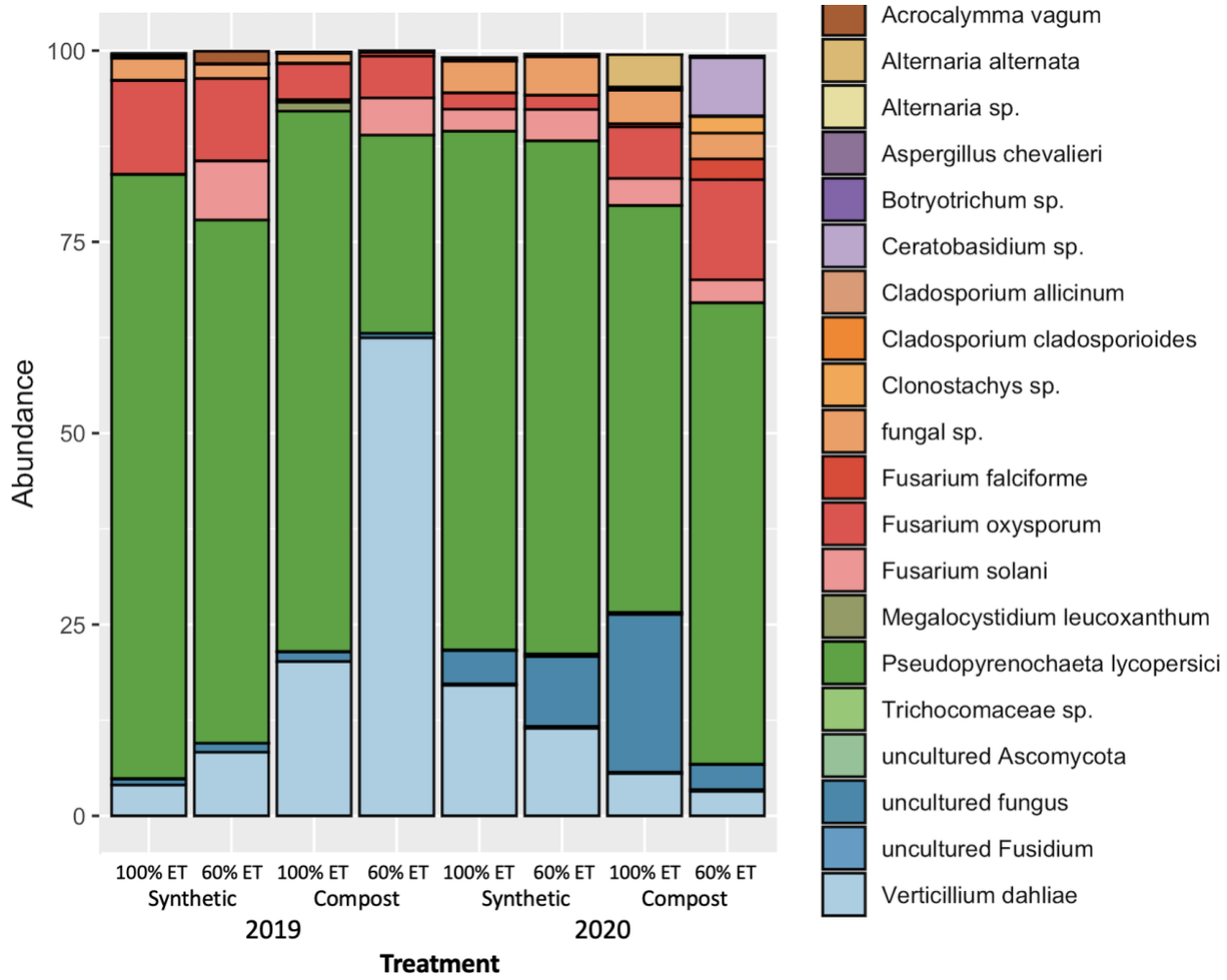



**Figure 12.** Relative abundance of the top 20 fungal species in roots across the irrigation and soil management treatments in the Grower Model study (2019 and 2020) using amplicon sequencing. Synthetic = 205 kg N/ha; Compost = 205 kg N/ha + 4500 kg composted poultry manure/ha.

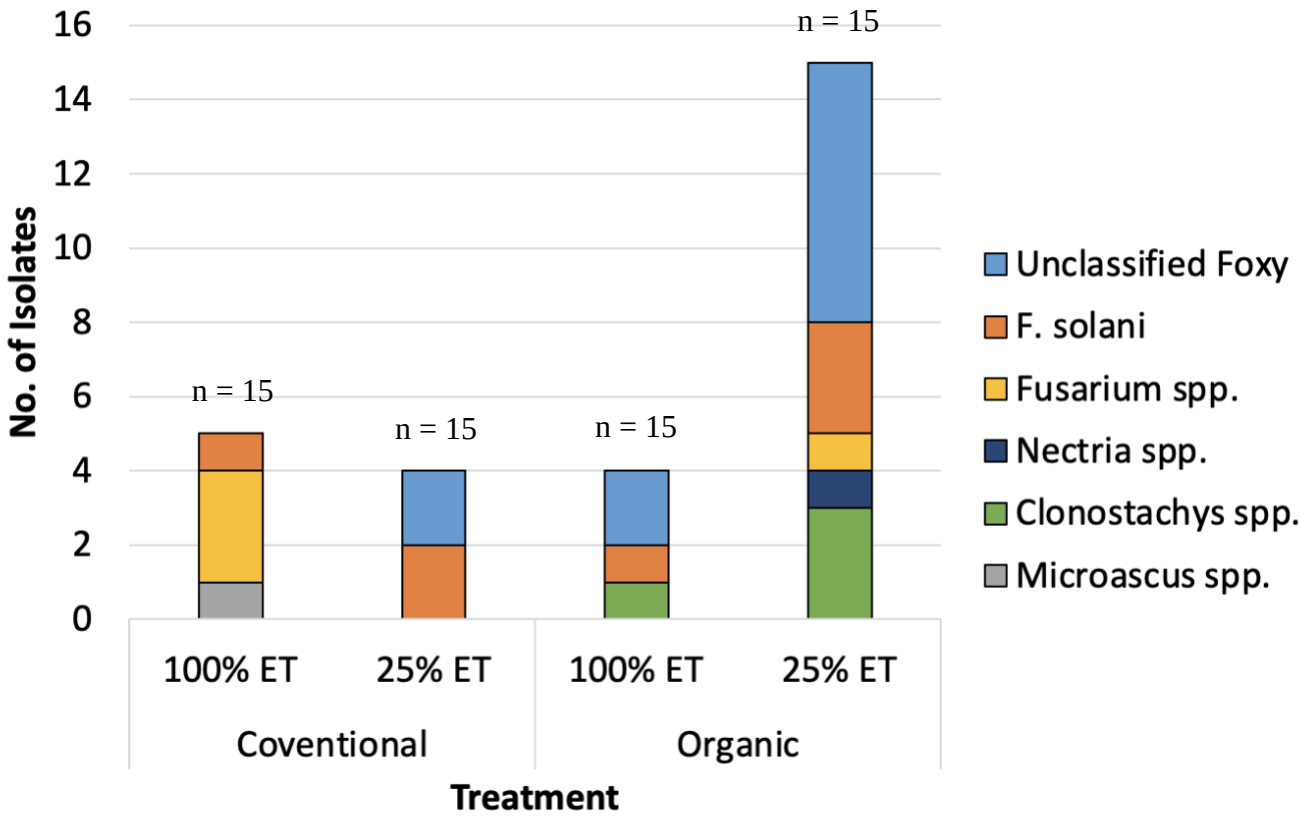



**Figure 13.** Comparing the number of species identified (>98%) in stem rot tissue between the irrigation and soil management treatments in the Extreme DI study (2018) using culture-dependent methods. Conventional = corn/tomato rotation with 205 kg N/ha; Organic = corn/tomato rotation with a winter cover crop, composted poultry manure (404 Mg N/acre), and 4.5 Mg/ha composted poultry manure).

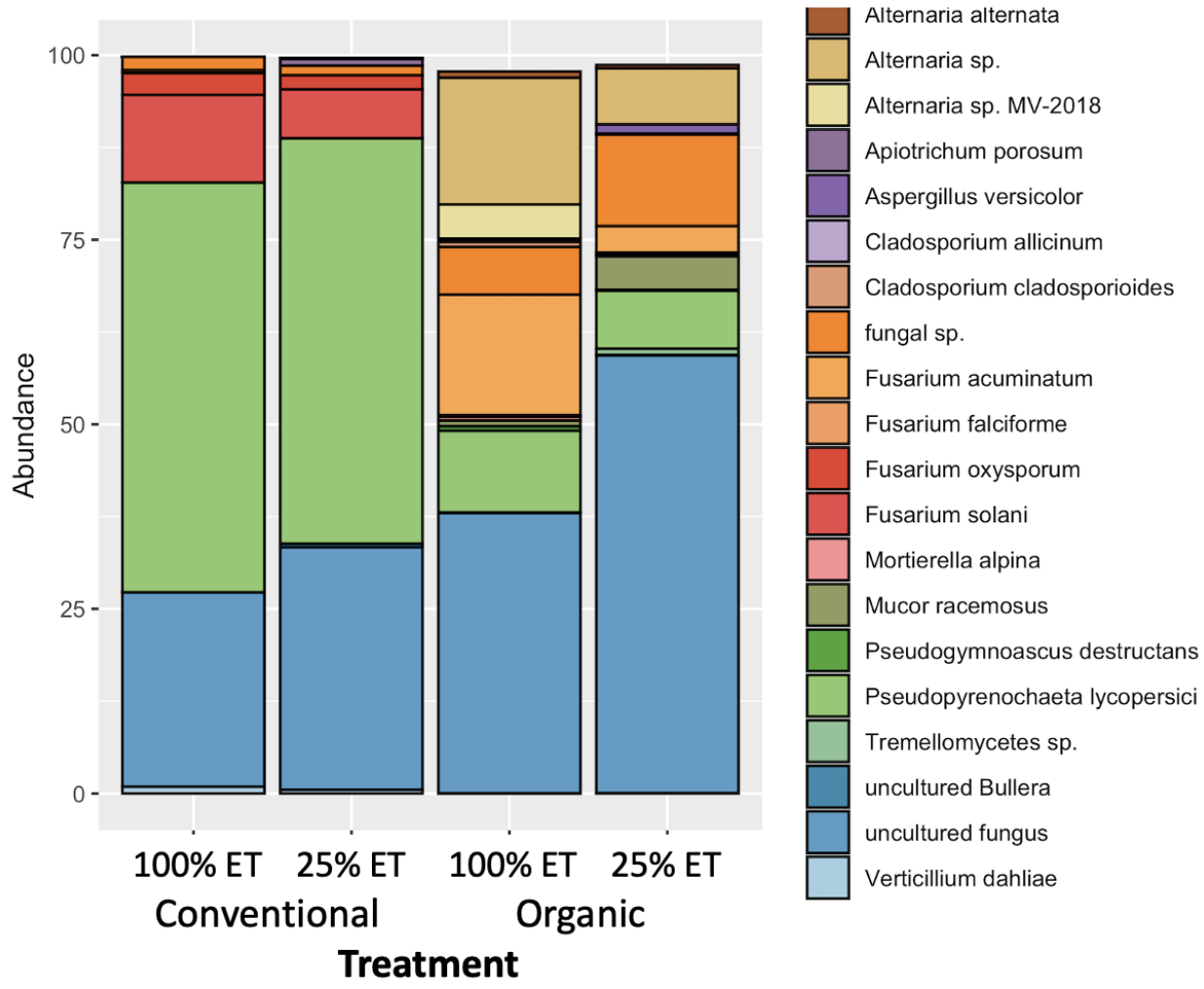



**Fig. 14.** Comparing the relative abundance of the top 20 root-associated fungal species between the irrigation and soil management treatments in the Extreme DI study (2018) using amplicon sequencing. Conventional = corn/tomato rotation with 205 kg N/ha; Organic = corn/tomato rotation with a winter cover crop, composted poultry manure (404 Mg N/acre), and 4.5 Mg/ha composted poultry manure).

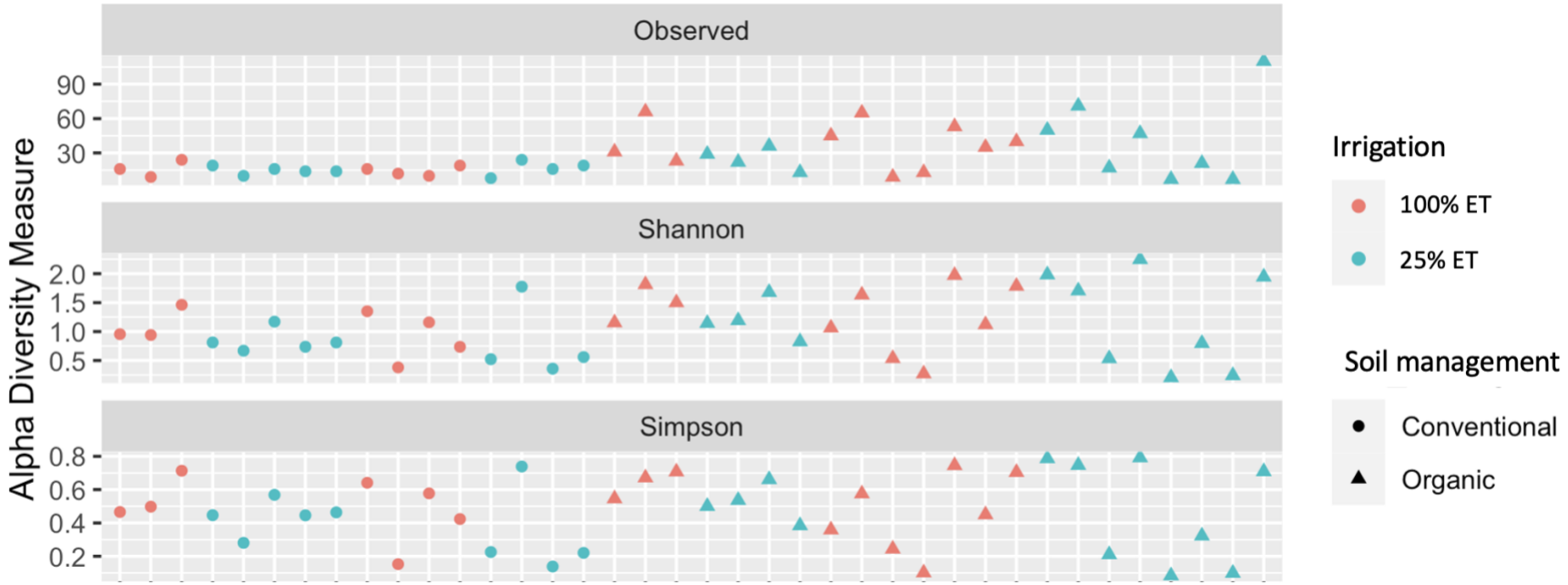



**Figure 15.** Comparing alpha diversity of root fungal communities between the irrigation and soil management treatments in the Extreme DI study (2018) using amplicon sequencing. Pink shapes represent samples from the 100% ET irrigation treatment, blue shapes represent samples from the 25% ET irrigation treatment. Circles represent samples from the Conventional soil management treatment (corn/tomato rotation with 205 kg N/ha) and triangles represent samples from the Organic soil management treatment (corn/tomato rotation with a winter cover crop, composted poultry manure (404 Mg N/acre), and 4.5 Mg/ha composted poultry manure). Alpha diversity (observed values) was significantly different between soil management treatments only ($P$ = 0.002).

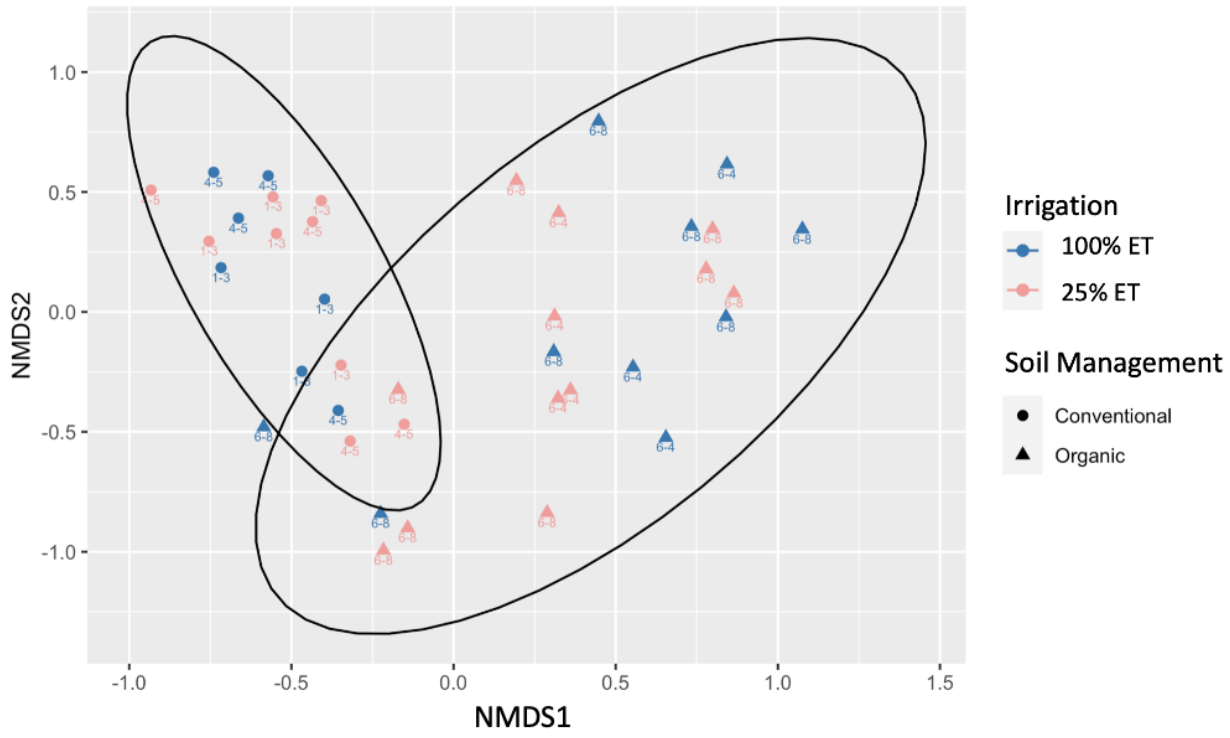



**Figure 16.** Non-metric MultiDimensional scaling (NMDS) of root fungal communities for the Extreme DI study (2018). Blue shapes represent samples from the 100% ET irrigation treatment, pink shapes represent samples from the 25% ET irrigation treatment. Circles represent samples from the Conventional soil management treatment (corn/tomato rotation with 205 kg N/ha) and triangles represent samples from the Organic soil management treatment (corn/tomato rotation with a winter cover crop, composted poultry manure (404 Mg N/acre), and 4.5 Mg/ha composted poultry manure).

.

**Tables**

**Table 1.** Recovery of *Fusarium* species from the Grower Model study from symptomatic plant tissue not previously reported as tomato pathogens averaged across 2019 and 2020[a].

| | Synthetic Only | | Synthetic & Compost | |
|---|---|---|---|---|
| Species[y] | 100% ET | 60% ET | 100% ET | 60% ET |
| *Fusarium acuminatum* | 0.5 (5%) | 0.0 | 0.0 | 0.0 |
| *Fusarium brachygibbosum* | 1.0 (9%) | 1.5 (12%) | 1.0 (10%) | 0.0 |
| *Fusarium redolens* | 0.5 (5%) | 0.0 | 0.0 | 0.0 |
| Total | 5.0 (46%) | 3.5 (27%) | 1.5 (15%) | 0 (0%) |

[a] Numbers in parentheses represent the proportion of samples the species was isolated from.

**Table 2.** External lesion lengths caused by *Fusarium* isolates recovered from symptomatic plant tissue in the Grower Model study.

| Method | Species | External Lesion (cm)[a] | *P* value Species |
|---|---|---|---|
| Agar plug | Noninoc-wound | 0.0 ± 0.0 | < 0.001 |
| | Noninoc-no wound | 0.0 ± 0.0 | |
| | *F. brachygibbosum* | 2.3 ± 0.5* | |
| | *F. noneumartii* CS109 | 3.8 ± 2.6* | |
| Spore suspension | Noninoc-wound | 0.0 ± 0.0 | < 0.0001 |
| | Noninoc-no wound | 0.0 ± 0.0 | |
| | *F. acuminatum* | 1.2 ± 0.6 | |
| | *F. redolens* | 0.0 ± 0.0 | |
| | *F. noneumartii* CS109 | 6.5 ± 1.6* | |

[a] Asterisks indicate significant differences in lesion length as determined by the Dunnett's method with the non-inoculated treatments as the control. Sample sizes were as follows: Agar plug method: n = 2-5; spore suspension method: n = 5-15.

**Table 3.** Internal lesion lengths in plants inoculated with *Fusarium* isolates recovered from symptomatic plant tissue in the Grower model study[a].

| Species | Internal Lesion (cm)[b] | *P* value Species |
|---|---|---|
| Noninoc-wound | 0.0 ± 0.0 | |
| F. noneumartii CS573 | 3.3 ± 0.3* | <0.001 |
| F. acuminatum (RR20-22B) | 3.0 ± 1.2* | |

[a] Plants were inoculated with a spore suspension 1 x $10^6$ spores/mL (n = 5).

[b] Asterisks indicate significant differences in lesion length as determined by the Dunnett's method with the non-inoculated treatments as the control.

**Table 4.** Disease ratings (0-5) for plants inoculated with *Fusarium* species isolated from symptomatic plant tissue in the Grower Model study.

| Species[x] | Disease rating[zy] |
|---|---|
| Noninoc-no wound | 0.2 ± 0.2 |
| Noninoc-wound | 0.2 ± 0.1 |
| *F. acuminatum* | 1.6 ± 0.9 |
| *F. redolens* | 0.5 ± 0.2 |
| *F. noneumartii* CS109 | 3.1 ± 0.7* |
| *P* value Species < 0.001 | |

[z] Disease ratings: 0 = healthy; 1 = 1-20% canopy decline; 2 = 21-40%; 3 = 41-60%; 4 = 61-80%; 5 = 81-100%.

[y] Asterisks indicate significant differences in lesion length as determined by the Dunnett's method with the non-inoculated treatments as the control.

[x] n = 5-13

**Table 5.** Effect of change in irrigation and soil management on taxa abundance in the Grower Model DI study (2019 and 2020).

| Year | Comparison | Genus | Known ecological function | $log_2$ FoldChange | *P* value |
|---|---|---|---|---|---|
| 2019 | 100% ET → 60% ET | *Alternaria* | Saprobe | -7.3 | 3.0E-04 |
| | Synth → Compost | None | NA | NA | NA |
| 2020 | 100% ET → 60% ET | *Clonostachys* | Saprobe, Endophyte, Epiphyte | +23.4 | 2.3E-15 |
| | Synth →. Compost | *Fusarium* | Plant pathogen | +4.9 | 1.7E-04 |

**Table 6.** Effect of organic soil management treatment on taxa abundance in the Extreme DI study (2018).

| Genus | Known ecological function | $log_2$FoldChange[a] | *P* value |
|---|---|---|---|
| *Alternaria* | Saprobe | +8.9 | 1.96E-10 |
| *Aspergillus* | Saprobe | +7.0 | 0.002 |
| *Ceratobasidium* | Saprobe | -6.0 | 0.012 |
| *Cladosporium* | Saprobe, fruit rot pathogen | +7.3 | 2.51E-07 |
| *Dactylonectria* | Plant pathogen (grapevine) | +4.7 | 0.021 |
| *Mortierella* | Saprobe | +6.9 | 3.46E-04 |
| *Mucor* | Saprobe | +6.4 | 1.19E-05 |
| *Pseudopyrenochaeta* | Plant pathogen | -3.0 | 1.53E-05 |

[a] $log_2$ fold change from the Conventional treatment to the Organic treatment.

**Supplemental Table 1.** Number of symptomatic plants collected in the Extreme DI study in 2018.

| Treatment | No. plants collected |
|---|---|
| Conventional – 100% ET | 15 |
| Organic – 100% ET | 15 |
| Conventional – 25% ET | 15 |
| Organic – 25% ET | 15 |

**Supplemental Table 2.** Number of symptomatic plants with root/stem rot diagnosed in the Grower Model DI study in each treatment in 2019 and 2020.

| Treatment | 2019 | 2020 |
|---|---|---|
| Synthetic Only – 100% ET | 11 | 11 |
| Synthetic & Compost – 100% ET | 4 | 16 |
| Synthetic Only – 60% ET | 11 | 15 |
| Synthetic & Compost – 60% ET | 0 | 13 |
| Totals | 26 | 55 |

**Supplementary Table 3.** Root samples used for amplicon sequencing from 2018, 2019, and 2020 in the Extreme DI and Grower Model DI studies.

| Study | Year | Soil Management | Irrigation (% ET) | Sample ID |
|---|---|---|---|---|
| Extreme DI | 2018 | Conventional | 100 | 6 |
| Extreme DI | 2018 | Conventional | 100 | 7 |
| Extreme DI | 2018 | Conventional | 100 | 8 |
| Extreme DI | 2018 | Conventional | 100 | 13 |
| Extreme DI | 2018 | Conventional | 100 | 14 |
| Extreme DI | 2018 | Conventional | 100 | 15 |
| Extreme DI | 2018 | Conventional | 100 | 16 |
| Extreme DI | 2018 | Conventional | 25 | 1 |
| Extreme DI | 2018 | Conventional | 25 | 2 |
| Extreme DI | 2018 | Conventional | 25 | 3 |
| Extreme DI | 2018 | Conventional | 25 | 4 |
| Extreme DI | 2018 | Conventional | 25 | 5 |
| Extreme DI | 2018 | Conventional | 25 | 9 |
| Extreme DI | 2018 | Conventional | 25 | 10 |
| Extreme DI | 2018 | Conventional | 25 | 11 |
| Extreme DI | 2018 | Conventional | 25 | 12 |
| Extreme DI | 2018 | Organic | 100 | 21 |
| Extreme DI | 2018 | Organic | 100 | 22 |
| Extreme DI | 2018 | Organic | 100 | 23 |
| Extreme DI | 2018 | Organic | 100 | 33 |
| Extreme DI | 2018 | Organic | 100 | 34 |
| Extreme DI | 2018 | Organic | 100 | 35 |
| Extreme DI | 2018 | Organic | 100 | 36 |
| Extreme DI | 2018 | Organic | 100 | 37 |
| Extreme DI | 2018 | Organic | 100 | 38 |
| Extreme DI | 2018 | Organic | 100 | 39 |
| Extreme DI | 2018 | Organic | 25 | 17 |
| Extreme DI | 2018 | Organic | 25 | 18 |
| Extreme DI | 2018 | Organic | 25 | 19 |
| Extreme DI | 2018 | Organic | 25 | 20 |
| Extreme DI | 2018 | Organic | 25 | 25 |
| Extreme DI | 2018 | Organic | 25 | 26 |
| Extreme DI | 2018 | Organic | 25 | 27 |
| Extreme DI | 2018 | Organic | 25 | 28 |
| Extreme DI | 2018 | Organic | 25 | 29 |

| | | | | |
|---|---|---|---|---|
| Extreme DI | 2018 | Organic | 25 | 30 |
| Extreme DI | 2018 | Organic | 25 | 31 |
| Extreme DI | 2018 | Organic | 25 | 32 |
| Grower Model DI | 2019 | Conventional | 100 | 48 |
| Grower Model DI | 2019 | Conventional | 100 | 49 |
| Grower Model DI | 2019 | Conventional | 100 | 55 |
| Grower Model DI | 2019 | Conventional | 100 | 56 |
| Grower Model DI | 2019 | Conventional | 100 | 60 |
| Grower Model DI | 2019 | Conventional | 100 | 61 |
| Grower Model DI | 2019 | Conventional | 100 | 63 |
| Grower Model DI | 2019 | Conventional | 100 | 64 |
| Grower Model DI | 2019 | Conventional | 100 | 65 |
| Grower Model DI | 2019 | Conventional | 100 | 66 |
| Grower Model DI | 2019 | Conventional | 100 | 105 |
| Grower Model DI | 2019 | Conventional | 100 | 106 |
| Grower Model DI | 2019 | Conventional | 100 | 107 |
| Grower Model DI | 2019 | Conventional | 100 | 108 |
| Grower Model DI | 2019 | Conventional | 100 | 109 |
| Grower Model DI | 2019 | Conventional | 60 | 70 |
| Grower Model DI | 2019 | Conventional | 60 | 72 |
| Grower Model DI | 2019 | Conventional | 60 | 73 |
| Grower Model DI | 2019 | Conventional | 60 | 74 |
| Grower Model DI | 2019 | Organic | 100 | 40 |
| Grower Model DI | 2019 | Organic | 100 | 44 |
| Grower Model DI | 2019 | Organic | 100 | 46 |
| Grower Model DI | 2019 | Organic | 100 | 47 |
| Grower Model DI | 2019 | Organic | 60 | 76 |
| Grower Model DI | 2019 | Organic | 60 | 77 |
| Grower Model DI | 2019 | Organic | 60 | 78 |
| Grower Model DI | 2019 | Organic | 60 | 79 |
| Grower Model DI | 2019 | Organic | 60 | 99 |
| Grower Model DI | 2020 | Conventional | 100 | 50 |
| Grower Model DI | 2020 | Conventional | 100 | 51 |
| Grower Model DI | 2020 | Conventional | 100 | 52 |
| Grower Model DI | 2020 | Conventional | 100 | 53 |
| Grower Model DI | 2020 | Conventional | 100 | 54 |
| Grower Model DI | 2020 | Conventional | 100 | 80 |
| Grower Model DI | 2020 | Conventional | 100 | 81 |
| Grower Model DI | 2020 | Conventional | 100 | 82 |
| Grower Model DI | 2020 | Conventional | 100 | 83 |
| Grower Model DI | 2020 | Conventional | 100 | 88 |

| | | | | |
|---|---|---|---|---|
| Grower Model DI | 2020 | Conventional | 60 | 92 |
| Grower Model DI | 2020 | Conventional | 60 | 93 |
| Grower Model DI | 2020 | Conventional | 60 | 94 |
| Grower Model DI | 2020 | Conventional | 60 | 95 |
| Grower Model DI | 2020 | Conventional | 60 | 96 |
| Grower Model DI | 2020 | Conventional | 60 | 97 |
| Grower Model DI | 2020 | Conventional | 60 | 101 |
| Grower Model DI | 2020 | Organic | 100 | 85 |
| Grower Model DI | 2020 | Organic | 100 | 86 |
| Grower Model DI | 2020 | Organic | 100 | 87 |
| Grower Model DI | 2020 | Organic | 100 | 89 |
| Grower Model DI | 2020 | Organic | 100 | 90 |
| Grower Model DI | 2020 | Organic | 60 | 98 |
| Grower Model DI | 2020 | Organic | 60 | 100 |
| Grower Model DI | 2020 | Organic | 60 | 102 |
| Grower Model DI | 2020 | Organic | 60 | 103 |
| Grower Model DI | 2020 | Organic | 60 | 104 |

## Appendix A: Evaluating deficit irrigation methods as tools for monitoring vine decline risk in processing tomatoes


### Abstract

California growers produce approximately 99 and 30% of the United States and world supply of processing tomatoes, respectively. One-third of US production occurs in Fresno County, where ongoing drought has led to dramatic decreases in water supply. To adapt, many growers use a technique known as deficit irrigation (DI), which consists of reducing water inputs to 60-80% of evapotranspirative (ET) needs around the fruit ripening stage. Previous greenhouse and field experiments suggest that DI practices can exacerbate disease caused by soil borne pathogens. However, it has not been evaluated whether the methods deployed for irrigation scheduling (based on volumetric water content (VWC) versus ET) can be used to reduce irrigation inputs while also minimizing disease risk. In a field study with two processing tomato cultivars (HM58841 and HM3887), we demonstrate increased disease risk of *Fusarium falciforme* vine decline and improved fruit quality under DI. We also show similar effects of both irrigation scheduling methods (VWC and ET) on disease risk, yield, and fruit quality. To the authors' knowledge, this study is the first to examine the effects of irrigation method on plant disease development.


### Introduction

Tomatoes are the second most consumed vegetable in the United States, second only to potatoes (USDA Economic Research Service, 2019). California growers supply

approximately 99% of US processing tomatoes (USDA NASS, 2021). In fact, tomatoes are among the top ten specialty crop commodities in the state with $1.2 billion in sales (CA Dept of Food and Agriculture, 2020). California growers planted 234,000 acres of processing tomatoes in 2020 (USDA NASS, 2021). Irrigating that acreage to replace 100% of the tomatoes' evapotranspirative (ET) needs requires, on average, 159 billion gallons of water or the equivalent of 241,000 Olympic sized swimming pools (UC IPM, 2021). Long periods of drought and increasing competition with industry and population growth means that some growers receive little to no surface water allocations for the year (Bureau of Reclamation, 2020). This kind of water scarcity is worst in Fresno County, where one third of the state's processing tomatoes are grown (USDA NASS, 2021).

One method reducing irrigation is known as deficit irrigation (DI). In processing tomato production, tomatoes are irrigated to replace 100% of the crop's ET requirements until fruit set/ripening, at which point irrigation is reduced to a replacement deficit of 60-80% ET. This method can produce desirable results of increased sugar content and enhanced fruit color (Veit-Ko hler et al., 1999; Ripoll et al., 2016) but may also increase risk for plant disease (Del Castillo Mu nera et al., 2019; Swett, 2020).

The relationship between soil moisture (volumetric water content (VWC)) and Phytophthora root rot (*Phytophthora capsici*) was studied using a sensor network irrigation system in a greenhouse setting (Del Castillo Mu nera et al., 2019). In this study it was found that decreasing soil moisture coincided with increasing root rot, whereas no such effect was observed in non-inoculated plants. In 2018, similar work was performed in a field planted to processing tomato using an ET-based system (Tule Technologies,

Davis, CA) for irrigation scheduling. This field was naturally infested with the tomato vine decline pathogen, *Fusarium falciforme,* which is a member of the *Fusarium solani* species complex that has recently been identified as a destructive pathogen of processing tomatoes in CA. It has been associated with foot and stem rot along with leaflet speckling and vine decline leading to yield losses. In this study, canopy decline, foot and crown rot were observed in significantly more DI plants than in standard irrigation plants and, most notably, *F. falciforme* was only recovered from diseased plants under DI (Beaulieu et al., in prep). These studies not only indicate that DI can increase soil borne disease risk, but also point to the potential for both VWC and ET-based systems to serve as tools for reducing irrigation with the goal of minimizing disease risk. Currently, there is little information on the relative accuracy of each system (VWC vs. ET). The objective of this study was to better understand the risk that DI poses for *F. falciforme* vine decline in processing tomato and assess the relative applications of VWC versus ET in predicting disease risk.

**Methods**

Irrigation treatments. In the experimental field, subsurface drip was placed in the center of each 91-cm bed approximately 20 cm below the soil line with 30 cm emitter spacing. Four irrigation treatments based on two irrigation scheduling parameters were used: ET and VWC. The ET treatment consisted of irrigation based on recommendations (hours per week) made by Tule Technology based on a measurement unit placed in a nearby uninoculated field; and in the VWC treatments, irrigation was turned on when soil moisture dropped below set thresholds (45% to irrigate to OPT and 35% for DI). Within

each irrigation scheduling parameter of ET and VWC, there were two sublevels: optimum (OPT) and DI. The OPT treatment consisted of irrigation based on the recommended number of hours; and in the DI treatment, beds were irrigated for 60% of the OPT recommended hours. Thus, there were four total irrigation treatments: ET-OPT, ET-DI, VWC-OPT, and VWC-DI (Fig. 1). Soil moisture was also monitored in real time using TEROS10 sensors (METER Group, Inc., Pullman, WA), which were buried at 30 cm depth in each cultivar × irrigation treatments in blocks 1 and 3.

Pathogen treatments. For this study, tomato seedlings were dip inoculated into a *F. falciforme* spore slurry ($1\times10^6$ spores $mL^{-1}$ 0.1% water agar) for 1 min before transplanting to the field on the following day. Each liter of spore slurry was created by scraping mycelium of *F. falciforme* isolate (CS109) from the surface of seven-day old potato dextrose agar plates that were flooded with 0.5% KCl. The resulting suspension was filtered through two layers of sterile cheesecloth. Spore concentrations in the filtrates were quantified and mixed with enough 0.1% water agar to obtain the desired concentration.

Experimental design. This study took place at the UC Davis Plant Pathology Research Field in Davis, CA. The site is characterized by hot dry summers and cool wet winters (USDA Hardiness Zone 9b) and the soil is a Yolo silty clay loam. The field comprised 14 rows (1.5 m wide and 70 m long), 12 of which were part of the experiment and the remaining two served as borders on either side. The 12 experimental rows were divided into three blocks with four rows in each block so that each irrigation treatment was applied to a single row across all blocks. Each row was planted to four 14 m plots with 3 m borders between them. Two cultivars were used in the study based on field performance

in previous studies; HM3887 was considered a poor performer with low *F. falciforme* tolerance and yields and HM58841 was considered a good performer with greater *F. falciforme* tolerance and yields. Seedlings were single-planted to 30 cm spacing. Each cultivar was planted to two of the plots within each irrigation treatment per block for a total of six replicates across the field for each cultivar × irrigation treatment and a total of 48 plots.

Disease sampling. Symptom incidence was recorded at 0, 2, 6, and 9 weeks after deficit treatment onset (11 weeks after planting). Subplots for canopy symptom monitoring, each consisting of 15 plants, were established within each of the 48 field plots. Canopy decline symptoms were recorded for each plant within these subplots at each time point. Canopy decline symptoms were delineated into categories based on the number of asymptomatic branches (healthy: all branches asymptomatic, early decline:≥1 symptomatic branch, and advanced decline: all branches symptomatic). Vine decline incidence was calculated from the proportion of plants with any decline symptoms to healthy plants. Lower symptoms (foot, crown, and stem rot) were recorded in three randomly selected plants within each of the 48 plots but outside of the monitoring subplots for a total of 144 plants at each time point.

Stem water potential. To establish that plants in the deficit treatments were under water stress, midday stem water potential was measured weekly for three weeks starting at the onset of deficit irrigation treatments for a total of four measurements using a pressure bomb (Model 615, PMS Instrument Co., Albany, OR) (Fig. 2). Measurements were taken in blocks 1 and 3 at weeks 0 and 2, and then in block 2 at weeks 1 and 3. A fully developed leaflet from a young branch was covered with a foil-laminate bag (Stem

Water Potential Bag, PMS Instrument Co.) for 15 min before excision and measurement. One leaflet was selected from each of three randomly selected plants in a “monitoring” subplot in each block per irrigation treatment. Plants were marked so that measurements could be taken from the same plant each time.

Yield and fruit quality. Fruit from all 48 subplots were harvested and separated into three categories: Red marketable (red/pink fruit), green marketable (all green), and rotten (red/pink fruit with any rot including blossom end rot and sunburn). Fruit was then weighed, and a subset of red marketable fruit was collected in 2 ga Ziploc bags for quality analyses (soluble solids (°Brix), hue, and pH) (Processing Tomato Advisory Board, Davis, CA).

Statistical analyses. Analyses were conducted in RStudio 2021.09.0. Incidence of early and advanced decline and plant mortality were observed over time and, due to symptom progression over the season (i.e., early decline incidence decreasing as plants succumbed to the pathogen and advanced decline and mortality increasing), the time point of 8 weeks post DI onset was found to best highlight differences in disease incidence among treatments. Therefore, disease incidence (lower: foot, crown, and stem rot; canopy: early and advanced decline, mortality) was analyzed based on percentage data derived from each block, treating block as replicate, for data collected at 8- weeks post DI treatment onset. Prior to statistical analysis, percentage data were transformed using an arcsine square root transformation. Yields (red marketable, green, and rotten fruit) and fruit quality (Brix, hue, and pH) were analyzed based on data derived from each block, treating block as replicate. Data comparisons across irrigation level and irrigation method (ET vs. VWC) were conducted within each cultivar using ANOVA (lme4

package; two-way ANOVA). Irrigation method and irrigation level were treated as fixed effects, whereas block was treated as a random effect.

**Results and discussion**

Deficit irrigation (DI) did not influence early or advanced decline or mortality incidence in either cultivar (Table 1). We did not observe a significant effect of DI on foot, crown, or stem rot in HM58841; this was also true for HM3887 except for increased foot rot under DI in the VWC irrigation method ($P$ = 0.011) (Table 2). While this was the only observed significant effect of DI on disease incidence, higher on average disease incidence was observed in both cultivars. For example, higher decline and mortality incidence were observed under DI in both cultivars in the VWC irrigation method (Table 1). Similarly, under the ET irrigation method we observed more foot and crown rot in HM3887 and more crown and stem rot in HM58841 under DI (Table 2). Within the VWC irrigation method, in addition to the significantly increased foot rot under DI, we also observed more crown and stem rot under DI. There were also instances where disease incidence was lower under DI. For example, early decline incidence was lower under DI within the ET irrigation method for both cultivars compared to other treatments. Our results support the supposition that reduced irrigation influences disease outcomes in various ways, ranging from disease enhancement to no effects to disease suppression (Swett, 2020).

Most tomato studies quantify reduced irrigation effects on yield, rather than on specific disease symptoms. Of these studies, many demonstrate reduced tomato yields under reduced irrigation (Cantore et al., 2016; Giuliani et al., 2016; Obreza et al., 1996). However, in our study, DI treatments did not influence yield (red, green, rotten) in either

cultivar (Table 3). We observed significantly higher Brix under DI in HM58841 ($P$ = 0.018) and significantly lower hue (redder fruit) under DI in HM3887 ($P$ = 0.038) for both irrigation methods (Table 4). These findings are in line with other studies that found increased Brix under reduced irrigation (Cantore et al., 2016; Ripoll et al., 2016; Veit-Kohler et al., 1999). All disease symptoms (early and advanced decline; mortality; foot, crown, and stem rot incidence) were similar under the two irrigation methods in both cultivars and irrigation levels (OPT vs. DI). We observed similar yields (red, green, rotten) in the two irrigation methods across cultivars and irrigation level. The two irrigation methods also resulted in similar fruit quality (°Brix, hue, pH) in both cultivars and irrigation levels. While there have been studies comparing irrigation based on ET and VWC in turf and soybean (McCready and Dukes, 2011; Sui and Vories, 2020), our study is the first, to the authors' knowledge, to examine the effect of irrigation method on plant disease development.

**Conclusion**

This study shows that deficit irrigation (DI) can pose a potential risk for *F. falciforme* vine decline in processing tomatoes depending on cultivar. Implementing DI based on evapotranspiration or soil volumetric water content resulted in similar disease incidence, yield, and fruit quality. In other words, both irrigation scheduling methods are feasible for predicting disease risk in a field setting. Deciding which method to use will likely depend on such factors as crop type, soil texture homogeneity, and acreage.

**Acknowledgments**

Funding for this research was provided by the USDA Western Sustainable Agriculture Research Education Graduate Student grant (GW19-191).

**Literature cited**

Bureau of Reclamation. (2020). Summary of Water Supply Allocations. https://www.usbr.gov/mp/cvp-water/ allocations.html.

CA Dept of Food and Agriculture. (2020). California's Top 10 Agricultural Commodities. https://www.cdfa.ca.gov/statistics/

Cantore, V., Lechkar, O., Karabulut, E., Sellami, M.H., Albrizio, R., Boari, F., Stellacci, A.M., and Todorovic, M. (2016). Combined effect of deficit irrigation and strobilurin application on yield, fruit quality and water use efficiency of "cherry" tomato (*Solanum lycopersicum* L.). Agric. Water Manage. *167*, 53–61 https://doi.org/10.1016/j.agwat. 2015.12.024.

Del Castillo Mu nera, J., Belayneh, B., Ritsvey, A., Koivunen, E.E., Lea-Cox, J., and Swett, C.L. (2019). Enabling adaptation to water scarcity: identifying and managing root disease risks associated with reducing irrigation inputs in greenhouse crop production – a case study in poinsettia. Agric. Water Manage. *226*, 105737 https://doi.org/10.1016/j.agwat.2019.105737.

Giuliani, M.M., Gatta, G., Nardella, E., and Tarantino, E. (2016). Water saving strategies assessment on processing tomato cultivated in Mediterranean region. Ital. J. Agron. *11* (*1*), 69–76 https://doi.org/10.4081/ija.2016.738.

McCready, M.S., and Dukes, M.D. (2011). Landscape irrigation scheduling efficiency and adequacy by various control technologies. Agric. Water Manage. *98* (*4*), 697–704 https://doi.org/10.1016/j.agwat.2010.11.007.

Obreza, T.A., Pitts, D.J., McGovern, R.J., and Spreen, T.H. (1996). Deficit irrigation of micro-irrigated tomato affects yield, fruit quality, and disease severity. J. Prod. Agric. *9* (*2*), 270–275 https://doi.org/10.2134/jpa1996.0270.

Ripoll, J., Urban, L., Brunel, B., and Bertin, N. (2016). Water deficit effects on tomato quality depend on fruit developmental stage and genotype. J Plant Physiol *190*, 26–35 https://doi.org/10.1016/j.jplph.2015.10.006.

Sui, R., and Vories, E. (2020). Comparison of sensor-based and weather-based irrigation scheduling. Appl. Eng. Agric. *36*, 375–386 https://doi.org/10.13031/aea.13678.

Swett, C.L. (2020). Managing crop diseases under water scarcity. Annu Rev Phytopathol *58* (*1*), 387–406 https://doi.org/10.1146/annurev-phyto-030320-041421. PubMed

UC IPM. (2021). Irrigation of Processing Tomatoes. https://www2.ipm.ucanr.edu/agriculture/tomato/irrigation- of-processing-tomatoes/.

USDA Economic Research Service. (2019). Potatoes and tomatoes are the most commonly consumed vegetables. https://www.ers.usda.gov/data-products/chart-gallery/gallery/chart-detail/?chartId=58340.

USDA NASS. (2021). 2021 California Processing Tomato Report. 1–2. https://www.nass.usda.gov/ Statistics_by_State/California/Publications/Specialty_and_Other_Releases/Tomatoes/2021/202105ptom.pdf.

Veit-Kohler, U., Krumbein, A., and Kosegarten, H. (1999). Effect of different water supply on plant growth and fruit quality of *Lycopersicon esculentum*. J. Plant Nutr. Soil Sci. *162* (*6*), 583–588 https://doi.org/10.1002/(SICI)1522-2624(199912)162:6<583:AID-JPLN583>3.0.CO;2-P.

**Figures**

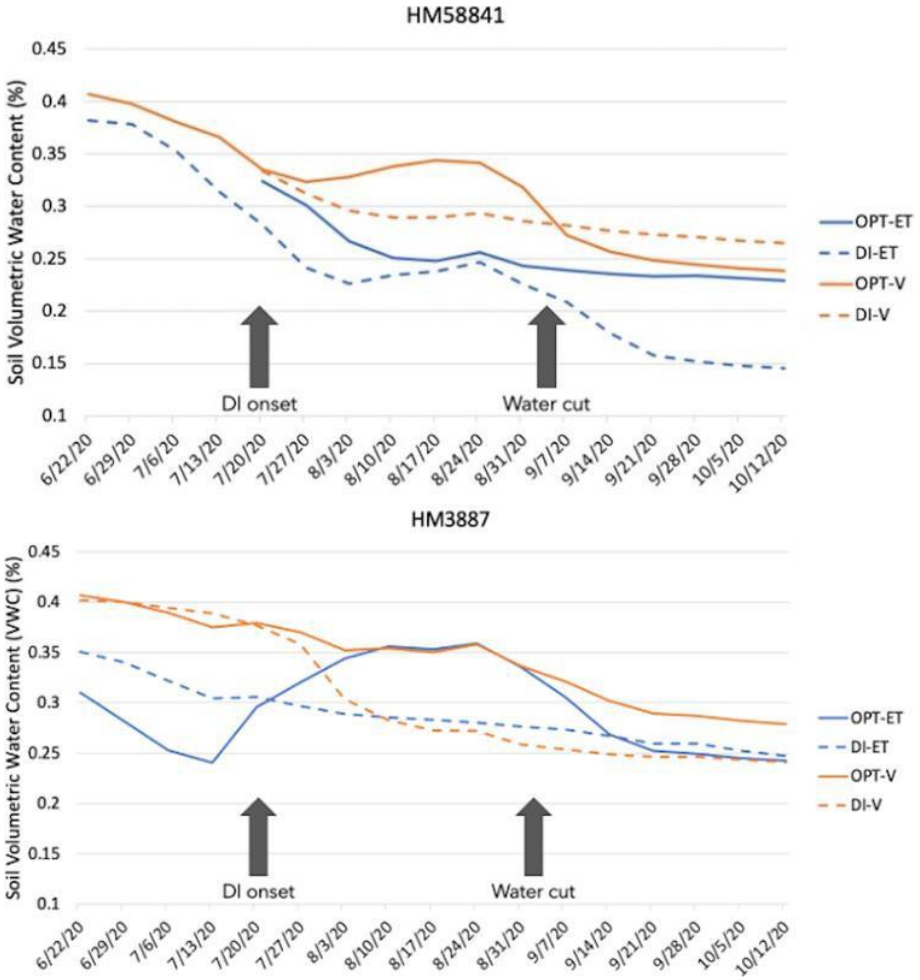



**Figure 1.** Soil volumetric water content in the HM58841 and HM3887 cultivars in the four irrigation treatments.

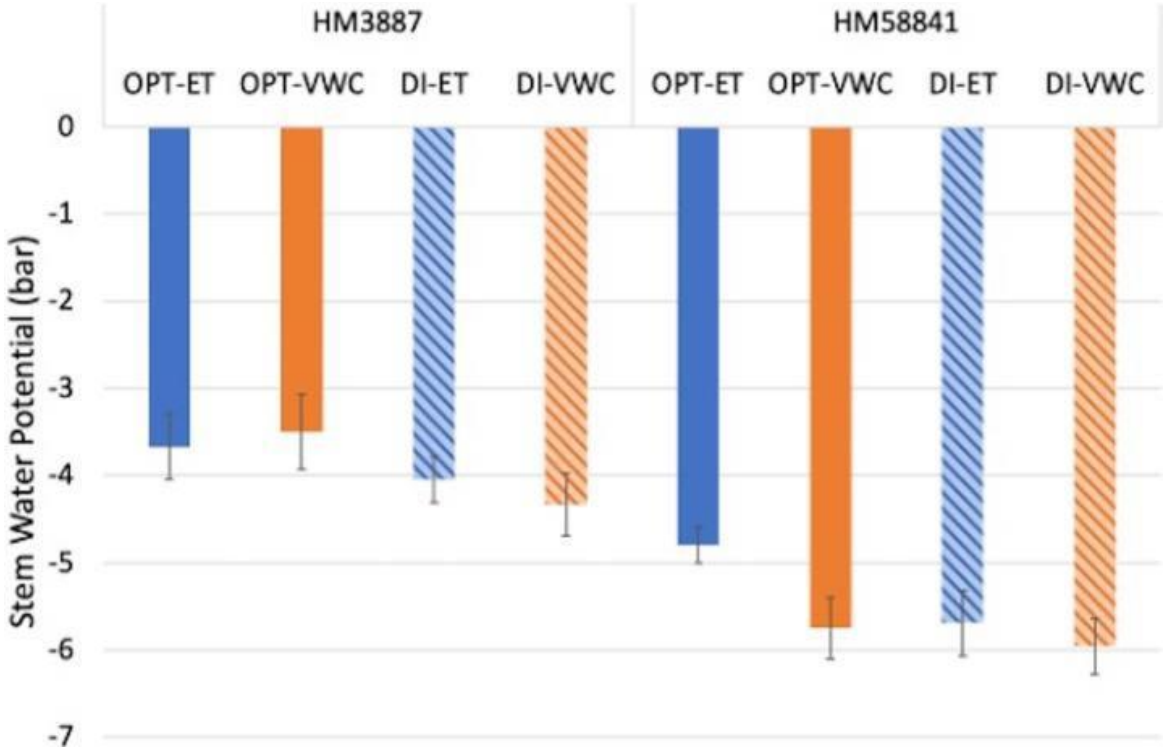



**Figure 2.** Stem water potential at 2 weeks post DI onset in the HM3887 and HM58841 cultivars.

**Tables**

**Table 1.** Aboveground disease incidence in both cultivars in the four irrigation treatments 8 weeks post DI onset.

| Irrigation level | Irrigation method | HM58841 | | | HM3887 | | |
|---|---|---|---|---|---|---|---|
| | | Early decline | Advanced decline | Plant mortality | Early decline | Advanced decline | Plant mortality |
| OPT | ET | 0.2 ± 0.1 a | 0.1 ± 0.1 a | 0.0 ± 0.0 a | 0.3 ± 0.1 a | 0.0 ± 0.0 a | 0.0 ± 0.0 a |
| | VWC | 0.1 ± 0.0 a | 0.0 ± 0.0 a | 0.0 ± 0.0 a | 0.1 ± 0.1 a | 0.0 ± 0.0 a | 0.0 ± 0.0 a |
| DI | ET | 0.1 ± 0.0 a | 0.0 ± 0.0 a | 0.0 ± 0.0 a | 0.1 ± 0.1 a | 0.1 ± 0.0 a | 0.1 ± 0.1 a |
| | VWC | 0.1 ± 0.0 a | 0.0 ± 0.0 a | 0.1 ± 0.1 a | 0.1 ± 0.2 a | 0.0 ± 0.0 a | 0.1 ± 0.1 a |
| *P* value irrig. level | | 0.763 | 0.827 | 0.339 | 0.588 | 0.218 | 0.169 |
| *P* value irrig. method | | 0.763 | 0.366 | 0.330 | 0.451 | 0.891 | 0.877 |

**Table 2.** Belowground disease incidence in both cultivars in the four irrigation treatments 8 weeks post DI onset.

| Irrigation level | Irrigation method | HM58841 | | | HM3887 | | |
|---|---|---|---|---|---|---|---|
| | | Foot rot | Crown rot | Stem rot | Foot rot | Crown rot | Stem rot |
| OPT | ET | 0.8 ± 0.2 a | 0.8 ± 0.2 a | 0.8 ± 0.2 a | 0.6 ± 0.2 a | 0.5 ± 0.2 a | 0.5 ± 0.2 a |
| | VWC | 0.8 ± 0.1 a | 0.8 ± 0.1 a | 0.8 ± 0.1 a | 0.5 ± 0.2 a | 0.4 ± 0.2 a | 0.4 ± 0.2 a |
| DI | ET | 0.8 ± 0.2 a | 0.8 ± 0.2 a | 0.8 ± 0.2 a | 0.8 ± 0.2 b | 0.8 ± 0.3 a | 0.8 ± 0.3 a |
| | VWC | 0.8 ± 0.2 a | 0.7 ± 0.1 a | 0.7 ± 0.1 a | 1.0 ± 0.0 b | 0.8 ± 0.1 a | 0.8 ± 0.1 a |
| *P* value irrig. level | | 0.854 | 0.847 | 0.847 | 0.011 | 0.106 | 0.106 |
| *P* value irrig. method | | 0.630 | 0.614 | 0.614 | 0.969 | 0.804 | 0.804 |

**Table 3**. Yields in both cultivars in the four irrigation treatments at harvest (10 weeks post DI onset).

| Irrigation level | Irrigation method | HM58841 | | | HM3887 | | |
|---|---|---|---|---|---|---|---|
| | | Red marketable | Green marketable | Damaged | Red marketable | Green marketable | Damaged |
| OPT | ET | 34.8 ± 9.4 a | 15.2 ± 7.8 a | 2.6 ± 0.9 a | 32.7 ± 4.3 a | 12.0 ± 4.7 a | 6.9 ± 0.2 a |
| | VWC | 33.7 ± 11.3 a | 11.5 ± 3.9 a | 2.9 ± 0.7 a | 34.9 ± 10.0 a | 7.3 ± 0.8 a | 5.4 ± 1.1 a |
| DI | ET | 40.0 ± 6.1 a | 18.2 ± 7.9 a | 3.4 ± 0.7 a | 40.1 ± 4.2 a | 18.5 ± 6.3 a | 7.1 ± 2.8 a |
| | VWC | 47.3 ± 4.5 a | 20.7 ± 5.7 a | 3.9 ± 0.4 a | 38.6 ± 3.8 a | 15.7 ± 2.9 a | 6.1 ± 2.1 a |
| *P* value irrig. level | | 0.270 | 0.272 | 0.062 | 0.948 | 0.965 | 0.799 |
| *P* value irrig. method | | 0.700 | 0.337 | 0.319 | 0.395 | 0.538 | 0.510 |

**Table 4.** Fruit quality in both cultivars in the four irrigation treatments at harvest (10 weeks post DI onset).

| Irrigation level | Irrigation method | HM58841 | | | HM3887 | | |
|---|---|---|---|---|---|---|---|
| | | °Brix | Hue | pH | °Brix | Hue | pH |
| OPT | ET | 5.0 ± 0.1 a | 20.0 ± 0.1 a | 4.4 ± 0.0 a | 4.8 ± 0.2 a | 20.1 ± 0.3 b | 4.4 ± 0.1 a |
| | VWC | 4.9 ± 0.1 a | 20.8 ± 0.3 a | 4.3 ± 0.0 a | 4.5 ± 0.1 a | 19.8 ± 0.1 b | 4.4 ± 0.0 a |
| DI | ET | 5.2 ± 0.1 b | 19.9 ± 0.3 a | 4.4 ± 0.0 a | 4.9 ± 0.1 a | 19.4 ± 0.2 a | 4.4 ± 0.1 a |
| | VWC | 5.2 ± 0.1 b | 20.8 ± 0.5 a | 4.4 ± 0.0 a | 5.0 ± 0.3 a | 19.3 ± 0.3 a | 4.4 ± 0.0 a |
| *P* value irrig. level | | 0.018 | 0.345 | 0.927 | 0.120 | 0.038 | 0.841 |
| *P* value irrig. method | | 1.000 | 0.104 | 0.186 | 0.618 | 0.366 | 0.841 |