OPTIMIZING GREENHOUSE TOMATO PRODUCTION: LIGHT AND THE PHYSIOLOGICAL DISORDER EDEMA

A Thesis

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ABSTRACT

Greenhouse production of tomatoes through the use of sophisticated environmental controls and precision hydroponic growing techniques allows for significantly higher yields within a smaller footprint when compared to traditional field production. One of the challenges faced by year-round greenhouse tomato operators in the Northeast U.S. is the low availability of solar radiation during the winter months, which results is a heavy reliance on supplemental lighting to maintain the photosynthetic processes required for suitable yields. During preliminary experiments evaluating multiple daily light integral (DLI) and CO_2 combinations with juvenile tomato plants grown in acrylic miniature growth chambers under cool white fluorescent lights, we began to notice the development of the physiological disorder edema on the lower, oldest leaves. Multiple studies have evaluated the effect of light quality on the development of edema in tomato, with many finding a correlation between increasing rates of edema in UV-deficient environments. Given the UV-filtering characteristics of acrylic and a lack of literature evaluating the interaction of multiple cultivars to edema, the objective of our study was to evaluate the development of edema in one rootstock cultivar, 'Maxifort', and four hybrid scion cultivars: 'Sweetelle,' 'Trust,' 'Merlice,' and 'Torero.'

We began our experiment with 4-week-old tomato plants, with two of each cultivar being placed into four identical acrylic miniature chambers and a remaining eight of each being grown in a control walk-in chamber with no acrylic. Each experimental replication lasted ten days, with plants being assessed for their edema index rating along with affected leaf count of the three oldest compound leaves every two days. At the conclusion of the experiment, plants were evaluated for fresh and dry weight, stem diameter, overall height and total leaf area. We found a significant variation in the edema index between cultivars, with 'Maxifort' and 'Sweetelle'

expressing the most and least symptoms over the 10-day cycle, respectively. All three compound leaves evaluated had a higher edema index when exposed to the acrylic chamber treatment, with severity increasing with leaf age. All cultivars exposed to the treatment, to a different degree, experienced a reduction in fresh weight, dry weight, plant height, and total leaf area. The results of this experiment could have benefits in for selecting existing cultivars or new cultivars from plant breeding efforts with lower susceptibility to edema for greenhouse growers producing in climates that may be conducive to the disorder.

In a separate study conducted to quantity the benefits of an increasing daily light integral (DLI) on commercial-style, high wire hydroponic tomato production, four greenhouses were established with four different lighting treatments (15, 20, 25 and 30 $mol \cdot m^{-2} \cdot d^{-1}$) and controlled using the Light and Shade System Implementation (LASSI) algorithm. Plants were exposed to the treatments for three months, with photosynthetic parameters (net photosynthesis, transpiration, stomatal conductance, and water use efficiency (WUE)) being evaluated three times during the course of the experiment. In addition, each plant was analyzed for number of clusters, number of fruit, total peduncle and fruit weight, first fruit fresh weight, first fruit Brix, first fruit dry weight, and the first fruit FW:DW ratio, with harvests being conducted as needed. From this study, we found no significant difference between treatments in the four photosynthetic parameters, although we did see a significant decrease in net photosynthesis over the course of the experiment. Likewise, there was a significant decrease in the number of harvested clusters, total cluster weight, fresh weight , dry weight, and the FW:DW ratio across the three months of harvest, with plants exposed to 25 $mol \cdot m^{-2} \cdot d^{-1}$ performed significantly worse that the 20 and 30 $mol \cdot m^{-2} \cdot d^{-1}$ treatments. This trend was inverted for Brix content, with the 25 and 15 $mol \cdot m^{-2} \cdot d^{-1}$ treatments having an overall higher average sucrose content than the others.

Due to the interaction of increased plant age at start of the experiment, pressure from the root disease, *Pythium*, and increased environmental stress from high irradiance and heat in the summer, we believe that the experiment should be replicated with younger plants under winter conditions to ensure the best results are achieved. Identifying optimal DLI targets for tomato production can be beneficial for growers looking to determine the optimal light level to target without wasting additional energy on excess light that does not further contribute to yield.

BIOGRAPHICAL SKETCH

Dylan C. Kovach was born in Boynton Beach, Florida, and spent most of his childhood in the city of Ocala, Florida. He grew up enjoying the outdoors, with a large backyard for various projects, which included the garden he cultivated with the loving help of his parents, Christine Kovach (mother) and Glenn Kovach (father). This hobby grew with time, with increased interest in agricultural systems and alternative growing methods, and eventually came to fruition with him attending the University of Florida starting in 2013.

His future in horticulture was shaped by a series of key events that occurred during his undergraduate degree program, with the first being his first horticulture class with Dr. Bala Rathinasabapathi. Not only was this course the catalyst for his switch into Horticultural Sciences, but also laid the foundation for two years of enriching undergraduate research working with greenhouse pepper grafting and cultivation. After the second year of his program, he had the amazing opportunity to intern in horticulture at the Walt Disney World resort, where he found his love for Disney and his passion for working in the field of horticulture. The following Spring, he returned to Disney to work as an agricultural science intern at the Living with the Land greenhouses, which proved to be the defining moment for his destiny in horticulture with greenhouse hydroponic production.

During the final year of his undergraduate program, his interest in a graduate degree that focused on hydroponics and controlled environment agriculture led him to Dr. Neil Mattson, who ultimately accepted him into his master's degree program in the field of horticulture at Cornell University. Since then, he has continued to channel his passion for horticulture through advanced greenhouse vegetable production and looks to continue his work through professional opportunities within the field.

I would like to dedicate this to my parents, Glenn and Christine Kovach, and grandparents, Charles and Catherine Luthin. Your love and guidance have been the cornerstone of my success and have empowered me to overcome the challenges I have faced throughout life. You are my inspiration for what is to come and always bring me joy in your presence. Thank you for all that you have done for me and I love you very much.

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I would like to thank my fellow labmates, Jonathan Allred and Masaki Kurosaki, for all of your help over these past three years in supporting me and my research. You have been there with me through it all and I appreciate all of the time you dedicated not only to my success in graduate school, but for being the wonderful friends that I will cherish for life.

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Finally, I would like to thank all of those unnamed that have touched my life during these past three years, whether it be a simple interaction or being an integral part of my time here at Cornell. Without you, none of this would have been possible.

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CHAPTER 1

Light Quality and the Incidence of Edema in Tomato

Abstract

Light quality plays a key role in the regulation of plant metabolic and physiological processes, with one of these effects being linked to preventing the formation of the disorder edema, which can harm crop performance. Although multiple studies have cited the introduction, or removal, of UV and other short wavelength photosynthetically active radiation (PAR) in the development of the disorder, there is little literature related to the screening of multiple cultivars. Therefore, the objective of this study is to quantify the development of edema in five tomato cultivars: 'Maxifort' (rootstock) and the hybrid scions 'Sweetelle', 'Merlice', 'Trust', and 'Torero'. Two, 4-week-old tomato plants were placed into four identical acrylic miniature chambers and a remaining eight of each being grown in a control walk-in chamber with no acrylic lid. Each treatment received an identical daily light integral (DLI) provided by T5 cool white fluorescent lights. The experimental replication lasted ten days, with plants being assessed for their index rating along with affected leaf count of the three oldest compound leaves every two days. At the conclusion of the experiment, plants were evaluated for fresh and dry weight, stem diameter, overall height and total leaf area. We found a significant variation in the edema index between cultivars, with 'Maxifort' and 'Sweetelle' expressing the most and least symptoms over the 10-day cycle, respectively. All three compound leaves evaluated had a higher edema index when exposed to the acrylic chamber treatment, with severity increasing with leaf age. All cultivars exposed to the treatment, to a different degree, experienced a reduction in fresh weight, dry weight, plant height, and total leaf area. To our knowledge, this study reflects the most comprehensive analysis of screening tomato cultivars for edema in literature.

Introduction

Greenhouse tomato production provides year-round harvests, with an annual U.S. wholesale value of over $418 million dollars annually (2017 Census of Agriculture, 2019). Through the precise control of environmental parameters and growing techniques that promote high density production, commercial greenhouses in the United States and Canada produce in the range of 500 metric tons per hectare per season compared to 34-36 metric tons in field systems (Cook & Calvin, 2005). Due to competition from Canada and Mexico, domestic tomato production has declined by over 30% while importation has increased by approximately 55% since the turn of the century (Guan et al., 2017). Although not traditionally significant field tomato producers, Minnesota and New York contain a high concentration of greenhouse operations with access to off-season, northern markets at a higher premium (Baskins, Bond & Minor, 2019). One of the challenges that greenhouse tomato growers face in higher latitudes is the energy requirement for production. In a study conducted in upstate New York that analyzed energy use of growing environments, greenhouse production required 95% and 87% more energy compared to high tunnels and traditional field production, respectively (de Villiers et al., 2011).

In addition to environmental heating of northern greenhouse operations, lighting is a significant contributor to the energy requirements for tomato production. In a study examining irradiance in the Northeast, the daily integrated light availability of solar radiation can vary greatly throughout the year (Both, 2014). During the months of November through January, which traditionally provide the lowest light levels of the year, Faust and Logan (2018) found that the average daily light integral (DLI) of the Northeast ranges between 5-10 $mol \cdot m^{-2} \cdot d^{-1}$, or approximately 50% of the total light accumulated in Southern growing regions. This reduction is

compounded by the greenhouse cladding used, with a 10-25% reduction in transmittance determined by the glazing material (Both, 2002). With fluctuating and seasonal lighting requirements, supplemental lighting is utilized to provide the necessary daily light integral (DLI) for year-round tomato production.

A physiological disorder that was found under preliminary experiments and reported by producers on several tomato cultivars was edema. Often described as intumescence or enations, edema is an induced, nonpathogenic complication that develops at different levels of intensity depending on the cultivar and, in some cases, between individual plants. Edema is not limited to tomato (*Solanum lycopersicum*), as other plant species such as Ivy Geranium (*Pelargonium peltatum*) (Rangarajan & Tibbitts, 1994) and ornamental sweet potato (*Ipomoea batatas*) (Craver, Miller, Williams & Bello, 2014) have varying levels of sensitivity to this disorder. In most cases, edema is found on plants grown solely under protected agriculture, which includes growth chambers and greenhouses (Lang & Tibbitts, 1983). Edema is often described as a blister or callus-like formation that forms predominately on the bottom veins of leaves (Wollaeger & Runkle, 2014). This swelling is the result of the epidermal layer on the tomato leaf expanding due to cellular elongation, which eventually burst as it reaches its limitation. The cause of tumor proliferation in these plants can be traced to the inheritance of a dominant genetic gene, which when only partially expressed leads to a high predisposition to this complication (Bayer, 1982). Abiotic environmental and physiological conditions have been shown to exacerbate the development of these sores and can have a compounding effect when introduced simultaneously. For example, the use of emulsified oils in spray applications has been shown to exacerbate edema symptoms by reducing stomatal function, therefore impeding plant transpiration and leading to excess water accumulation in the leaves (Sagi & Rylski, 1978). Through the

mechanism of reduced stomatal activity, high relative humidity has long been cited as a major influence in intumescence production (Morrow & Tibbitts, 1988). This finding was contradicted in a previous study as humidity was related to the size and presence of the intumescence rather than its development (Lang & Tibbitts, 1983). Additional causes linked to edema-like symptoms on *S. lycopersicum* include excessive substrate moisture retention, leading to reduced root functionality and transpiration, along with high temperatures in the growing environment (Sagi & Rylski, 1978). Physiological complications related to edema are noted in the form of photosynthetic activity reduction, with Lang et al. (1983) finding tomato hypertrophied palisade and chlorenchyma cells containing little to no chloroplasts.

In a number of studies conducted on the prevalence of edema in tomato, irradiance and light quality was found to play a significant role in preventing the formation of edema on the leaves. In a 2017 study evaluating the market share of supplemental lighting in greenhouse operations, metal halide (MH) and high pressure sodium (HPS) accounted for 98% of installed fixtures within the United States ("Energy Savings Potential", 2017). The industry standard for greenhouse supplemental lighting in tomatoes is high pressure sodium (HPS), which produce significant amounts of light in the yellow/red spectrum (550 – 650 nm) while lacking in short wavelength energy (>500 nm). Greenhouse structures most commonly employ glazing consisting of polyethylene film, acrylic, single or twin-wall polycarbonate, and glass panels, which each have varying levels of light and spectral transmittance. One of the shared characteristics of these materials is their ability to filter UV light (100-400 nm), with acrylic and polycarbonate providing the lowest transmittance at 44 and 18%, respectively (Both, 2002). The availability and dispersion of UV light varies greatly between lighting options, with Bugbee and Nelson (2012) finding nearly identical radiation distribution of UV-B in T12 fluorescent fixtures and

ambient sunlight. Contrarily, metal halide and T5 fluorescent fixtures are shown to provide 74 and 76% less energy in the 287-320 nm range when compared to their total light spectrum, respectively.

It has been shown that the presence of UV light has a high correlation to the development of intumescence in the growing environment, with Lang and Tibbits (1983) finding that plants grown under cool white T12 fluorescent fixtures received sufficient UV-B to prevent the formation of edema. However, it was also uncovered that the introduction of an acrylic barrier increased the occurrence of the disorder, which may lay in the UV filtering nature of the acrylic cover material. Kubota, Eguchi & Kroggel (2017) achieved a 30% reduction of intumescence formation within rootstock cultivar 'Beaufort' by supplementing 6.7 mmol m^{-2} d^{-1} UV-B while Rud (2009) saw a significant reduction in leaf area affected by intumescence with the cultivar 'Maxifort'.

The introduction of far red (710–850 nm) and blue (400-490 nm) light can also have a beneficial effect on the reduction of edema. In a study conducted using supplemental sources of both spectra, end of day far red light (EOD-FR) and blue light used synergistically could significantly reduce the prevalence of edema while unaltering plant growth (Eguchi et al., 2016). In another study conducted using varying ratios of red, blue, and green light on 'Beaufort' tomato seedlings, utilizing a spectrum of higher blue photon flux (PF) reduced intumescence at the expense of plant height (Hernández et al., 2016). In a similar experiment utilizing the F1 hybrid tomato 'Early Girl', Wollaeger & Runkle (2014) found that increasing ratios of blue light or the use of fluorescent lighting led to a reduction in intumescence-affected leaves.

While most literature examines the implications of various treatments on specific susceptible cultivars to edema, relatively little exists regarding commercial scion stock and their

sensitivity to non-pathogenic intumescence. As a result, the objective of this experiment is to document the prevalence of edema in five cultivars of various growing characteristics under UV-deficient conditions.

Materials and Methods

An experiment was conducted to determine the susceptibility of tomato plants to symptoms of edema under low UV conditions. Five cultivars were selected based on their prevalence in commercial greenhouse operations and physiological differences in fruit type and growth structure.

Sweetelle: Indeterminate, baby plum tomato with fruit size ranging from 10-12 grams. Seed from Syngenta International AG (Basel, Switzerland).

Merlice: Indeterminate, round tomato on vine (TOV) with average fruit size of 150-165 grams. Seed from De Ruiter seed company (St. Louis, Missouri).

Trust: Indeterminate, ribbed beefsteak tomato with fruit size of 200-210 grams. Seed from Paramount Seeds (Stuart, Florida).

Rebelski: Indeterminate, flat and ribbed beefsteak tomato with fruit size of 230-260 grams. Seed from De Ruiter.

Torero: Indeterminate, round beefsteak tomato with average fruit size of 250 grams. Seed from De Ruiter.

Prior to the experiment, seedlings of each cultivar were sown into 72-cell plug trays (3.88 cm x 3.88 cm x 5.72 cm; TO Plastics) using a germination mix containing sphagnum peat moss along with finely crushed perlite and vermiculite (LM-1; Lambert Peat Moss, Rivière-Ouelle, Canada). Planting depth was approximately 6 mm with a top dressing of LM-1. Flats were then irrigated with tap water until each cell was fully saturated. For the first 21 days after sowing,

plants remained in plug trays within a walk-in growth chamber (M1 Walk-in; Environmental Growth Chambers, Chagrin Falls OH USA), with environmental conditions of 23ºC day/night temperature controlled using an Argus control interface. Plants were hand watered daily (or as needed) using a liquid fertilizer (15 N -2.19 P - 12.45K Jack's All-Purpose Liquid Feed, J. R. Peter's Inc., Allentown, PA) at a rate of 100 mg $N \cdot L^{-1}$. Lighting was provided by 96 T5 High Output (HO) fluorescent bulbs (Phillips Lighting Company, Amsterdam, Netherlands) in an overhead luminaire covered by panes of flexible acrylic sheathing. Light provided an average photosynthetic photon flux density (PPFD) of 231.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 18 hours daily, resulting in a daily light integral (DLI) of 15 $mol \cdot m^{-2} \cdot d^{-1}$. After 21 days of establishment, the tomato plants were transferred to standard pots (10.2 cm top diameter x 7.3 cm depth x 420 mL maximum dry volume; Dillen – ITML, The HC Companies) and grown with a commercial peat-lite mix (LM-111; Lambert Peat Moss, Rivière-Ouelle, Canada). At transplant, plants were randomly divided into 16 blocks, where each group contained 5 plants (one of each cultivar). Each block was placed back into the growth chamber and allowed to establish for an additional seven days. These plants remained in the growth chamber under the same conditions as previously mentioned. Treatments were applied within two walk-in chambers, each containing two miniature chambers constructed of a plywood base topped with an acrylic box (100 cm x 68 cm x 46 cm) and rigid acrylic lid. For the experiment, mini chamber environmental parameters were set at 23ºC day/night temperature, 70-75% relative humidity, 400 $mg \cdot L^{-1}$ CO_2 using food-grade, compressed gas cylinders (Airgas; Radnor, PA, USA), and an average photosynthetic photon flux density (PPFD) between each of the two main chambers of 157/272 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 1 and 2 active light banks, provided for 18 hours daily and resulting in a daily light integral (DLI) of 15 $mol \cdot m^{-2} \cdot d^{-1}$. Control for temperature, humidity, and CO_2 were achieved using a custom chamber

monitor program (LabVIEW; National Instruments, Houston, TX USA). Instantaneous PPFD and DLI were measured in each main chamber by one quantum sensor located within the most forward mini chamber to the door (LI-190R; LI-COR Inc., Lincoln, NE, USA) and wired to an environmental control system (Argus Control Systems Ltd.; Surrey, British Columbia, Canada).

At experiment initiation (Day 0), two groups (10 plants) were randomly selected for placement within each miniature chamber. An additional four groups remained in the seedling chamber as the control treatment and the final two groups were destructively harvested. Plants that were selected for destructive harvest were analyzed for edema index, number of leaflets, number of affected leaflets, stem diameter using a digital caliper (Mitutoyo; Kanagawa, Japan); overall plant height from the soil line to the apical meristem, internodal distance between the cotyledons and first branch, leaf area of the first four branches (Li-3100C Area Meter; LI-COR Inc., Lincoln, NE USA), fresh weight, and dry weight.

Data was collected throughout the 10-day experiment cycle, with the edema index, total leaflet number, and number of affected leaflets of the three bottommost compound leaves being measured every two days (six data points) from Day 0 to Day 10. The edema index was measured on a scale from 1-6, with an increasing value signifying advancing symptoms and a greater amount of affected tissue (Figure 1.2). All leaflets that measured at least 10 mm in length were included in the count and leaflets that contained any amount of edema were labeled as affected. At the conclusion of the final lighting cycle on Day 10, plants were photographed individually and in groups to provide visual analysis of each cultivar between treatments and replications. Plants were then evaluated for the same growth and biomass parameters as analyzed in the initial destructive harvest on Day 0.

Between April and June 2019, a total of four experimental cycles were conducted. Two mixed models were developed with fixed and random effects to quantify the development of edema over time and percent affected leaflets (Table 1.1.A.) and to evaluate the effect of the disorder across cultivars in the form of biomass parameters, which include stem diameter, overall height, total leaf area, fresh weight, and dry weight (Table 1.1.B.). Nonsignificant terms were removed using backwards stepwise method to obtain the final models. Post hoc multiple comparisons with a Bonferroni correction at $P \leq 0.05$ were used to further identify significant differences between the treatments. Both statistical analyses were processed using JMP statistical software (JMP Pro 11; SAS Institute, Cary, NC).

Table 1.1. The mixed model fixed and random effects used to analyze the physiological development of edema and the destructive harvest biomass parameters

A. Physiological Development of Edema	
Fixed Effects	Random Effects
Run	Mini Chamber (Nested) [Run Number, Macro Chamber]
Macro Chamber	Plant ID (Nested) [Micro Chamber, Macro Chamber, Run Number]
Cultivar	
Macro Chamber*Cultivar	
Day	
Macro Chamber *Day	
Cultivar*Day	
Macro Chamber*Cultivar*Day	
B. Final Destructive Biomass Parameters	
Fixed Effects	Random Effects
Macro Chamber	Run Number
Cultivar	Mini Chamber (Nested) [Macro Chamber]
Macro Chamber*Cultivar	

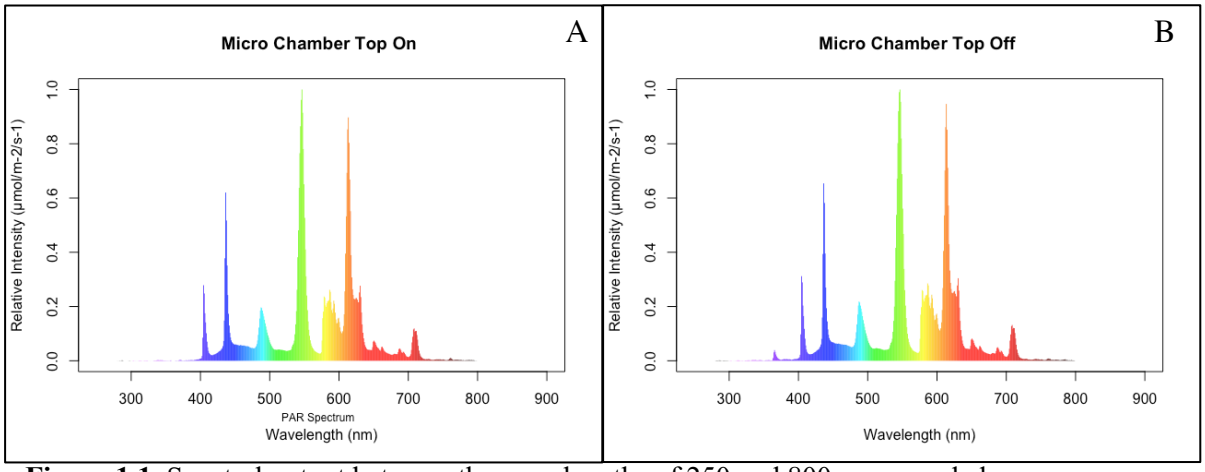


Figure 1.1. Spectral output between the wavelengths of 250 and 800 nm recorded as a measurement of relative intensity (µmol·m^{-2}·s^{-1}). Data was collected from Mini Chamber 18, which resides in Macro Chamber 17, and was taken from within the acrylic box with (A) and without (B) the acrylic lid. Measurements were taken using a spectroradiometer (PS-300; Apogee Instruments, North Logan, UT, USA)

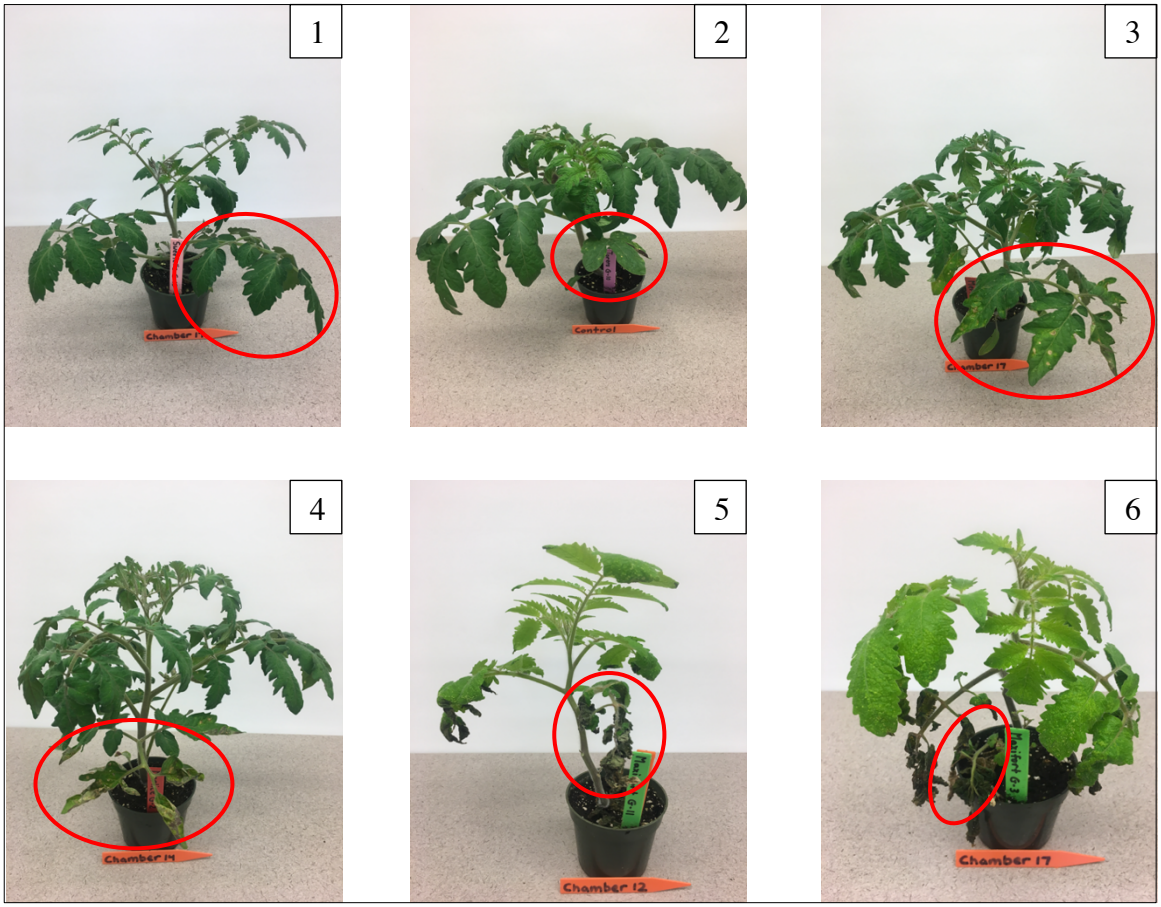


Figure 1.2. Edema index values from 1-6 noted in top right corner. The index value refers to the bottom compound leaf of each plant as denoted by the red outline, with the exception of index #6 with the abscised leaf.

Table 1.2. Edema index description for each value from 1-6.

Edema Index Value	Description
1	No edema present
2	1-10% of the compound leaf area affected, minimal isolated intumescence on terminal leaves
3	11-50% of the compound leaf area affected, dense intumescence on terminal leaflet with pronounced topical necrotic spotting
4	51-75% of the compound leaf area affected, pronounced upward leaf curling, prolific top leaf surface necrosis
5	76-100% of the compound leaf area affected, full senescence of leaflets
6	Complete abscission of compound leaf

Results

Edema Index

During the 10-day evaluation period, edema index was recorded every two days to determine its development over time in the control and acrylic treatment chamber conditions. There was a significant effect of cultivar, day, and their interaction observed in each of the three leaves (Table 2.1). With some exceptions, the trend of cultivar susceptibility at each day could be ranked, from most affected to least, as 'Maxifort', 'Merlice', 'Torero', 'Trust', and 'Sweetelle' (Figure 2.1). The rootstock cultivar 'Maxifort' expressed significant edema symptoms prior to the onset of the experiment and continued to exhibit the most severe symptoms compared to other cultivars, with a 66-75% increase in edema over the next most affected cultivar, 'Merlice', on Day 0 (Figure 2.1). Consequently, Maxifort experienced only a further 11% increase in leaf #1 mean edema index while compared to a 45-65% increase in symptoms for the other cultivars between Day 0 and Day 10. When comparing compound leaves #1 (oldest) and #3 (youngest most recently mature leaf) to the development of edema over the 10-day experiment cycle, the older leaf #1 showed more severe symptoms, but exhibited similar advancement as the younger leaf #3. Leaf #1 showed an increase in edema index of 11 and 23% in 'Trust' and 'Sweetelle',

respectively, while a similar increase in the progression of edema of 12 and 22% was seen with ‘Merlice’ and ‘Maxifort’ in leaf #3. Between days 6 and 10, there was no significant difference between the mean edema index within each of the cultivars ‘Merlice’ and ‘Torero’ across all three leaves. For ‘Sweetelle’, little advancement in symptoms was noted between days 6 and 10, however ‘Trust’ developed more advanced symptoms during this time frame.

The significant effect of the macro chamber (control chamber vs. chambers with acrylic mini chambers) on mean edema index over time was also noted. As there was no significant difference observed in the mean edema index of all cultivars between the two treatment macro chambers (which each contained two acrylic mini chambers), the data from these two macro chambers, 15 and 17, were combined for statistical analysis and denoted as the model parameter “Treatment Chamber” (Table 2.1./2.2.). There was a significant difference in mean edema index between the treatment and control macro chambers, with the treatment chamber showing a higher mean edema index when compared to the control at days 4 (leaf #2), 6 (leaf #1), and 8 (leaf #3) until the conclusion of the experiment run (Day 10) (Figure 2.2). Between the beginning (day 0) and end (day 10) of the experiment, there was less than a 1% difference in the development of edema in leaf #2 and 3 in their respective treatments. The average edema index of leaf #1 within the treatment mini chambers during increased by 44.5% over the course of the experiment, or 7.6% less than the development of edema in leaves #2 and 3. Likewise, leaf #1 grown within the control increased by 33%, or 12% lower than the average of the other two leaves. There was a positive correlation between leaf age and the development of symptoms in both treatments, with the increasing age of the leaf leading to a higher edema index. When comparing between leaf #1 (oldest) and leaf #3 (youngest) of plants within the control treatment, leaf #1 had a 23 and 17% higher edema index on day 0 and day 10, respectively. Plants exposed

to the acrylic mini chamber treatment showed greater variation between the oldest and youngest leaves on days 0 (26%) and 10 (20%) while the separation between both days remained nearly identical across both treatment (±.1%).

The interaction between the treatment and control chambers and cultivars was significant for leaf #1 and 2, although not for leaf #3. There was a significant difference between the treatment and control in the cultivar 'Merlice' in both leaves while 'Sweetelle' and 'Torero' were only significant in leaf #2, again with treatment chamber showing greater edema than control.

Percentage of Affected Leaflets

The mixed model representing the percent affected leaflets per compound leaf was significant as a three-way interaction between the treatment chamber, cultivar, and time for both leaves #1 and #2 (Table 2.1.). In both leaves, the cultivars 'Maxifort' and 'Torero' were not significantly different between the control and treatment (Figures 2.4 and 2.5). 'Torero' did exhibit a significant increase in leaflets affected over time. The cultivar 'Merlice' saw a similar developmental pattern in percentage of leaflets affected between treatment and control at Day 2, although this trend was non-significant for the remainder of the 10-day treatment period. The cultivars 'Trust' and 'Sweetelle' saw no significant differences in leaflets affected between the treatment and control for the first four days of the experimental cycle, with significance occurring on day 8 for leaf #1 and day 6 for leaf #2.

The pattern of leaflets affected follows a grouped trend, with the cultivars 'Sweetelle' and 'Trust' experiencing delayed manifestation of symptoms and a significantly smaller percentage of leaflets affected when compared to the other cultivars. 'Torero' and 'Merlice' form the next group, with the percentage of leaflets affected under the treatment greatly increasing until day 6,

where it begins to plateau near 100% affected leaves. Plants of both cultivars grown under the control follow a similar trend, although with reduced severity, across both leaves. 'Maxifort' forms the final group and the outlier, with nearly 100% affected leaflets across both leaves at Day 0, which reflects the previously stated predisposition to edema prior to the start of the experiment.

Fresh/Dry Weight

The effects of cultivar and treatment chamber were recognized as significant elements as a result of the mixed model (Table 2.2.) There was a significant difference between the treatment and control chambers for all cultivars, with an average 28% greater fresh weight in the control chamber when compared to the treatment chambers (Figure 2.6.A). 'Maxifort' exhibited the greatest impact on fresh weight due to the chamber treatments, with the average mean fresh weight being 42% smaller when compared to the control, and it was more severely affected than the next most sensitive cultivar to fresh weight, 'Sweetelle'. For 'Maxifort' dry weight was affected by chamber, with a 36% decrease in the treatment vs. the control chamber. Likewise, the fresh to dry weight ratio between the treatment and control chambers of 'Sweetelle', 'Merlice', 'Trust', and 'Torero' were similar (±2%) while Maxifort had a decrease of 6%.

Stem Diameter/Overall Height/Total Leaf Area

There was no significant interaction of stem diameter between each cultivar and the chambers (Figure 2.6.C) There were two significant interactions of cultivar and treatment chamber in regard to plant height, with the mean overall height of 'Maxifort' and 'Sweetelle' being 18 and 20% higher in the control, respectively. Although not significant, it can be noted

there was a pattern whereby height of plants averaged 12% greater within the control chamber for all cultivars when compared to the mean plant height of the treatment chambers. All cultivars grown under the control had a significantly higher leaf area, with an average 35% higher surface area across all cultivars and a 51% increase in 'Maxifort' over the treatment.

Table 2.1. Mixed model analysis for the effects of experiment replication and full factorial interaction of cultivar, day, and treatment chambers on edema index and percent of affected leaves over a 10-day period. Random effects included mini chambers nested within the treatment/control chambers, experimental replication and plant ID nested within mini chamber, treatment/control chambers, and experimental replication.

Leaf Number	Main Effects & Interactions	Edema Index	Percentage Affected Leaflets
1	Experiment Replication	***	**
	Cultivar	***	***
	Day	***	***
	Cultivar•Day	***	***
	Treatment/Control Chambers	**	**
	Treatment/Control Chambers•Cultivar	*	**
	Treatment/Control Chambers•Day	***	***
	Treatment/Control Chambers•Cultivar•Day	NS	***
2	Experiment Replication	***	**
	Cultivar	***	***
	Day	***	***
	Cultivar•Day	***	***
	Treatment/Control Chambers	***	***
	Treatment/Control Chambers•Cultivar	*	**
	Treatment/Control Chambers•Day	***	***
	Treatment/Control Chambers•Cultivar•Day	NS	***
3	Experiment Replication	*	NS
	Cultivar	***	***
	Day	***	***
	Cultivar•Day	***	***
	Treatment/Control Chambers	*	NS
	Treatment/Control Chambers•Cultivar	NS	**
	Treatment/Control Chambers•Day	***	***
	Treatment/Control Chambers•Cultivar•Day	NS	*

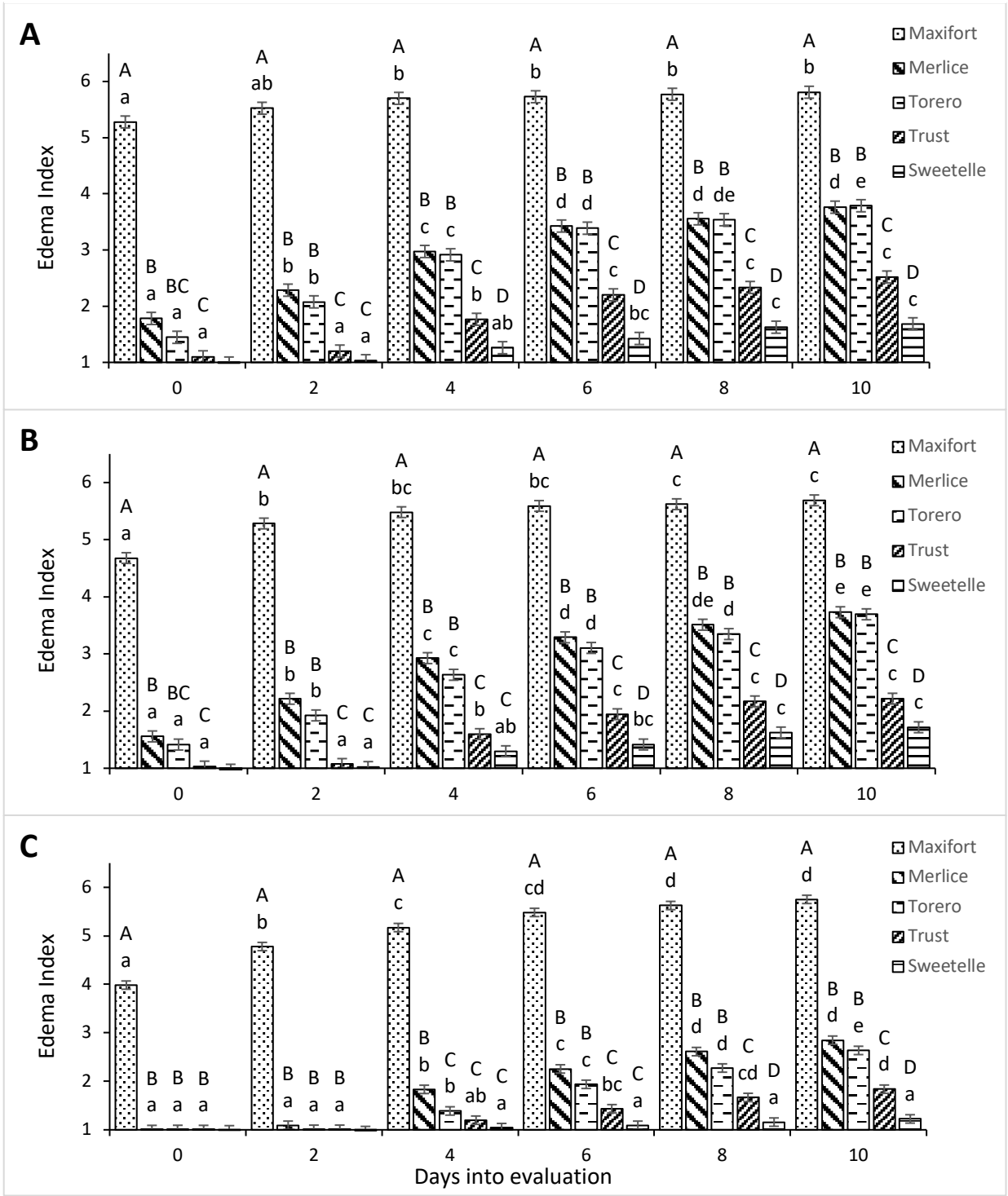
NS, *, **, * Nonsignificant or significant at P ≤ 0.05, 0.01, or 0.001 respectively**

Table 2.2. Mixed model analysis for the effects of cultivar, treatment chambers, and their interaction on morphological parameters measured at harvest. The random effect included the mini chamber nested within the experiment replication and treatment/control chambers.

Main Effects & Interactions	Stem Diameter	Overall Height	Total Leaf Area	Fresh Weight	Dry Weight
Cultivar	***	***	***	***	***
Treatment/Control Chambers	NS	**	***	***	***
Treatment/Control Chambers•Cultivar	*	***	***	*	**

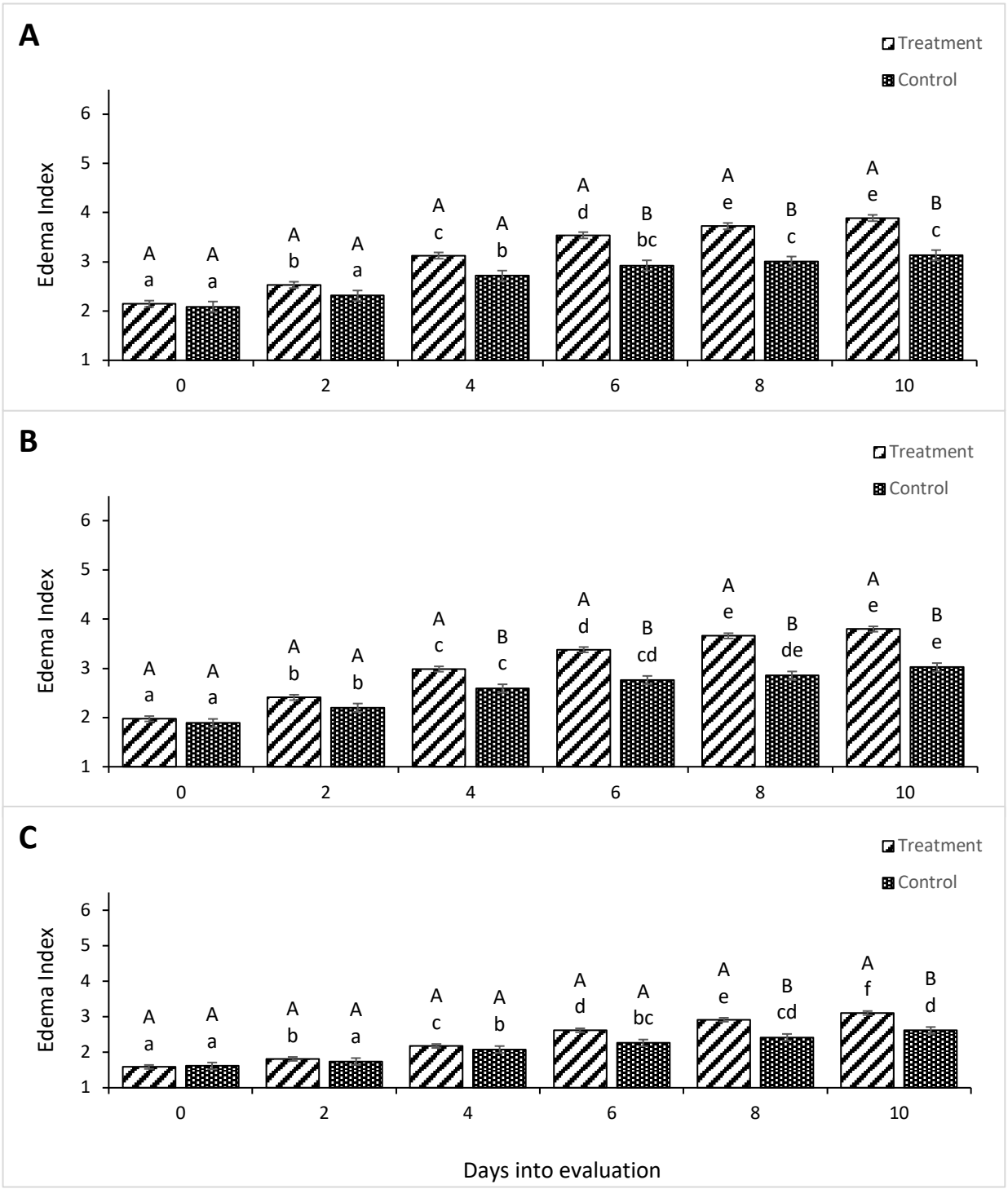
NS, *, **, * Nonsignificant or significant at P ≤ 0.05, 0.01, or 0.001 respectively**

Figure 2.1. Edema index as a function of the least square mean for leaf #1 (oldest expanded leaf, A), leaf #2 (B), and leaf #3 (most recently expanded leaf, C) of the cultivars 'Maxifort', 'Merlice', 'Torero', 'Trust', and 'Sweetelle' over 10 days.



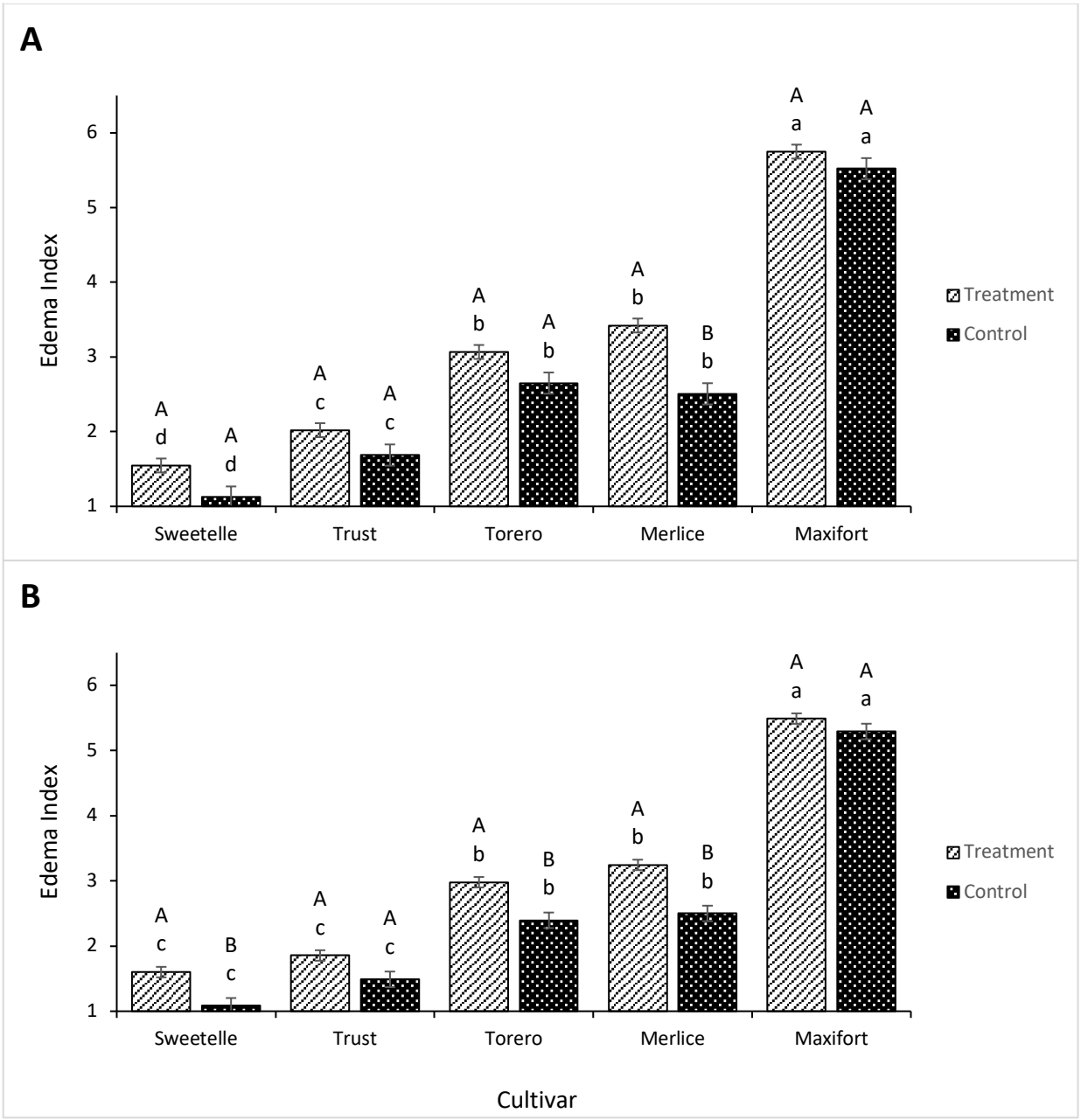
Uppercase letters indicate significance between cultivars on the same day while lowercase the same cultivar across the days of measurement using a Bonferroni multiple comparisons correction (alpha=0.05). Error bars signify ± standard error (SE).

Figure 2.2. Edema index as a function of the least square mean for leaf #1 (oldest expanded leaf, A), leaf #2 (B), and leaf #3 (most recently expanded leaf, C) of the treatment and control macro chambers over 10 days.



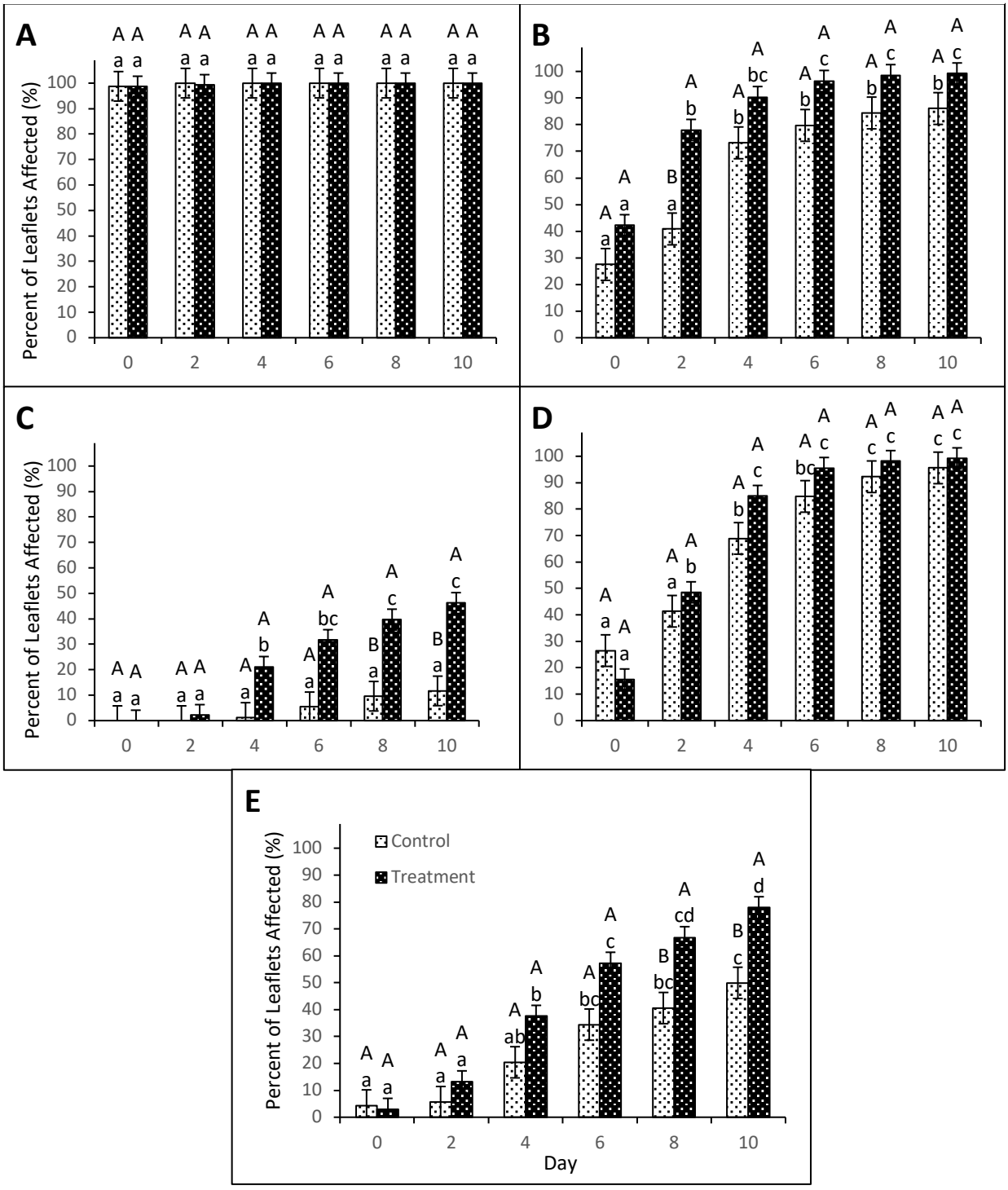
Uppercase letters indicate significance between treatments on the same day while lowercase the same treatment across the days of measurement using a Bonferroni multiple comparisons correction (alpha=0.05). Error bars signify ± standard error (SE).

Figure 2.3. Edema index as a function of the least square mean for leaf #1 (oldest expanded leaf, A) and leaf #2 (B) of the five cultivars within the treatment and control macro chambers. Leaf #3, the youngest most recently expanded leaf, was not significant.



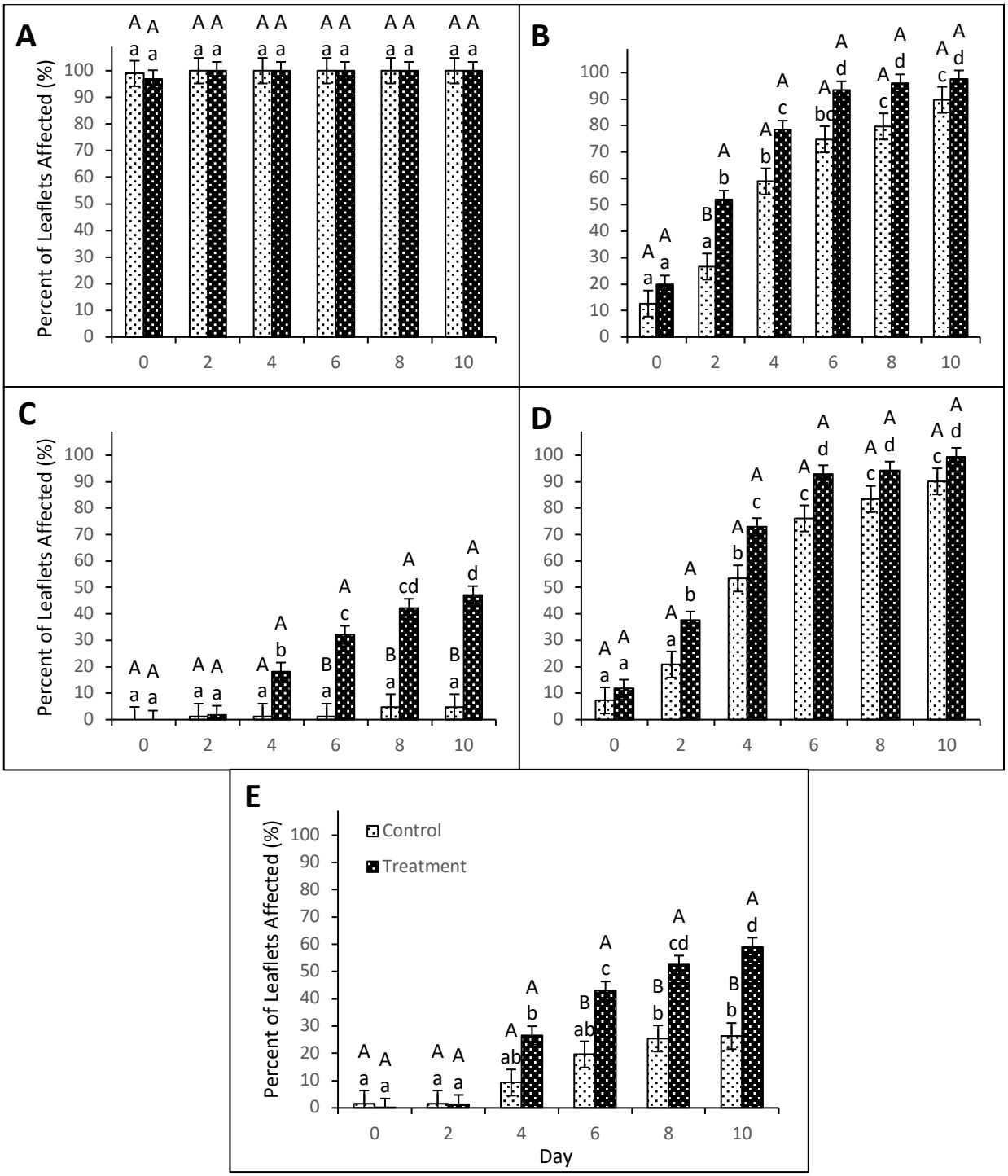
Uppercase letters indicate significance between treatments with the same cultivar while lowercase the same treatment across each cultivar using a Bonferroni multiple comparisons correction (alpha=0.05). Error bars signify ± standard error (SE).

Figure 2.4. Percent of leaflets affected on Leaf #1 as a function of the least square mean for the cultivars 'Maxifort' (A), 'Merlice' (B), 'Sweetelle' (C), 'Torero' (D), and 'Trust' (E) over the 10 day evaluation period.



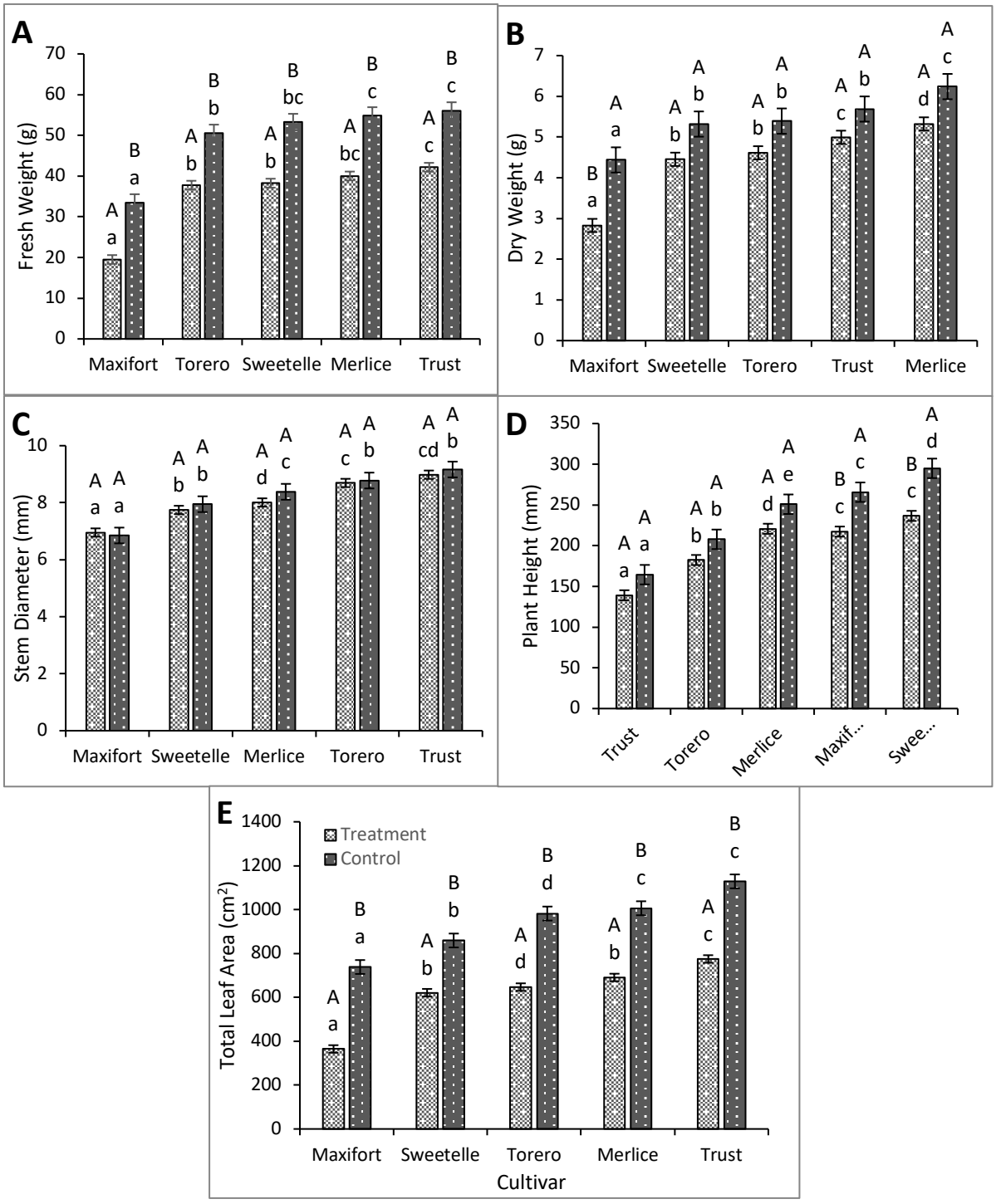
Uppercase letters indicate significance between treatments on the same day of measurement while lowercase the same treatment across each day of measurement using a Bonferroni multiple comparisons correction (alpha=0.05). Error bars signify ± standard error (SE).

Figure 2.5. Percent of leaflets affected on Leaf #2 as a function of the least square mean for the cultivars 'Maxifort' (A), 'Merlice' (B), 'Sweetelle' (C), 'Torero' (D), and 'Trust' (E) over the 10-day evaluation period



Uppercase letters indicate significance between treatments on the same day of measurement while lowercase the same treatment across each day of measurement using a Bonferroni multiple comparisons correction (alpha=0.05). Error bars signify ± standard error (SE).

Figure 2.6. Least square mean fresh weight (A), dry weight (B), stem diameter (C), overall height (D), and total leaf area (E) of the cultivars 'Maxifort', 'Merlice', 'Torero', 'Trust', and 'Sweetelle' after 10 days under the control and treatment macro chambers.



Uppercase letters indicate significance between treatments with the same cultivar while lowercase the same treatment across each cultivar using a Bonferroni multiple comparisons correction (alpha=0.05). Error bars signify ± standard error (SE).

Discussion

Edema Index Characterization

The traits used to measure edema in tomato have not been previously standardized and take into account qualitative and quantitative properties across the plant. In previous studies assessing the development of abiotic intumescence, researchers have developed index scales that involved visual assessments of callus development, leaf abscission, wilting (Lang and Tibbits, 1983), and percentage of leaf surface tissue affected (Eguchi et al., 2016). Other analyses focused more on the individual leaflets on a compound leaf, quantifying the number of healthy and affected leaflets along with the percentage leaf area affected (Rud, 2009), and general observation of intumescence on a plant level (Zhao, 2008). For this experiment, we found a combination of these techniques, the qualitative edema index as well as the quantitative percentage of leaflets affected, was sufficient for providing an assessment of edema sensitivity based on time, cultivar, and treatment chamber. Beyond cultivar specific responses, the experiment set out to determine if acrylic treatment chambers exacerbated symptoms.

Cultivar selection had a profound effect on the outcome of the experiment, with a significant difference noted between the rootstock and hybrid cultivars. Across multiple studies, the effects of environmental parameters have previously been studied for one (Lang and Tibbits, 1983; Kubota et al., 2017) or two (Rud, 2009; Zhao et. al.,2008) cultivars. As in our experiment, the premature onset of edema symptoms in the rootstock cultivar ‘Maxifort’ has been noted by Zhao (2008), who found intumescence injury occurring at the development of 7-9 compound leaves. This finding is also concluded in work performed by Rud (2009), who found

intumescence development on compound leaf 7 after 12 and 14 days, respectively. This result coincides with the developmental age of 'Maxifort' in this experiment, which began to show symptoms during the propagation phase prior to the start of the experiment, with an average edema index of 4.6/5 measured across the three oldest compound leaves measured across all replicates at the beginning of the experiment on day 28. As a result of increased early onset of edema, this limited the overall increase in the edema index in 'Maxifort' over the 10-day experimental cycle, with this effect being most notable in the older leaf tissue. The advancement of symptoms over time in the form of the mean edema index was cultivar, chamber, and leaf specific, with 'Maxifort' being the most and 'Sweetelle' the least affected. Likewise, the acrylic chamber treatments enhanced the effect of edema, with leaf #3 (youngest) being less affected that leaf #1 (Figure 2.1.) The delayed and reduced incidence of edema in younger leaves is illustrated in work performed by Kubota et al. (2017), who found significantly higher levels of edema in the older compound leaf #1, which correlates with the results of higher levels of edema being found in the two older leaves in our study.

Influence of UV Light on Edema

Although we understand, to some degree, the development of intumescence as a physiological disorder, it is still unknown exactly how environmental parameters directly affect the formation of intumescence. The presence of UV light is a well-documented factor that can reduce the incidence and severity of edema in tomatoes, with Kubota et al. (2017) and Rud (2009) finding that the rootstock cultivars 'Beaufort' and 'Maxifort' both reacted favorably to the availability of UV-B light, with a significant reduction in the percent affected leaves, respectively. Although our study did not specifically treat with UV light, it is suspected that the

extreme sensitivity of the rootstock cultivar ‘Maxifort’ to low UV conditions resulted in its disposition to edema prior to the start of the experiment and, inadvertently, led to no observed trend in percent leaves affected as a result of the experiment. This level of sensitivity was not witnessed in the four hybrid cultivars, thought we did observe an increase in the incidence of edema when exposed to the UV filtering acrylic chambers. When evaluating the severity of edema within the compound leaves, Kubota et al. (2017) found a decrease in the incidence and severity of edema within younger leaves, which reflects the findings in our study as the cultivar ‘Merlice’ along with ‘Sweetelle’, and ‘Torero’ saw a decrease incidence in younger leaves as compared to the oldest leaf. In further support of the role of UV light, Lang and Tibbits (1983), also saw a significant reduction in the edema index using UV-transmitting acrylic with the cultivar ‘Oxheart’. Contrarily, Rud (2009) and Zhao et. Al. (2008) did not find any development of edema in the hybrid cultivars ‘Trust’ and ‘Florida-47’, respectively. This contradiction may be attributed to the propagation environment, in which both experiments cultured plants in greenhouse conditions and, subsequently, may have led to some sunlight UV exposure when compared to a growth chamber. Other possible explanations may be linked to environmental temperature control, with a temperature setpoint of 23 °C day/night in this experiment when compared to similar night and significantly warmer (average 31 °C) daytime temperatures in their reports.

Across all cultivars, Rud (2009) and Kubota et al. (2017) reported a significant reduction in fresh weight associated with the UV-limited growing environment, with ‘Maxifort’ and ‘Beaufort’ exhibiting a 42% and 50% reduction in shoot fresh weight, respectively, as compared with controls under cool white fluorescent lights in controlled environment chambers. Alternatively, with plants grown under glass greenhouse conditions, Rud (2009) found no

significant difference between the control and treatment with ‘Maxifort’ while ‘Trust’ exhibited a decrease in fresh weight. Kubota et. al. (2017) saw a reduction in dry weight in plants exposed to UV, while Rud (2009) saw a significant difference only in the cultivar ‘Trust’. In our study, the disproportionate decrease in dry weight compared to fresh weight can be partially explained by the necrotic lesions and other abnormalities that led to the partial/full desiccation of leaves. As a result, the plants lacked a significant amount of leaf area with live tissue, leading to a greater discrepancy in fresh weight. In our study, the difference of overall height was significant in ‘Maxifort’ and ‘Sweetelle’, with an 18% decrease in the height of ‘Maxifort’ compared to 6% in the study conducted by Rud (2009). The effect of edema on leaf area was also highly significant in all cultivars during this experiment and is supported by the findings of Kubota et.al. (2017), with ‘Maxifort’ and ‘Beaufort’ experiencing a 51 and 60% decrease in leaf area as a result of low-UV conditions, which compares to an average 51% decrease in the leaf area of ‘Maxifort’ in our study. As noted by Lang et. al. (1983), there is an inherent lack of chloroplasts in the voided areas affected by edema, which in turn negatively affects the photosynthetic capabilities of the plant and reduces the available energy required for proper growth. Therefore, it is possible that edema has an indirect role in reducing the overall height and leaf area of a plant through these symptoms. In addition, leaf area was greatly affected by the partial/complete desiccation of the lower leaves within the treatment chambers, leading to stunted and deformed leaflets with a lower surface area.

There appears to be no clear consensus in literature about the optimum dosage of UV light, although Kubota et. Al (2017) suggests within the range of 12.3 and 14 mmol m^{-2} d^{-1} UV-B to prevent the formation of edema in tomato seedlings. In our study, we were able to achieve 8.42 mmol m^{-2} d^{-1} accumulated UV-B with the mini chamber acrylic top off (Table 3.3.). While

this was a 78% increase over the treatment with the top on, our experiment did not achieve the recommended rate and resulted in the development of edema in our control treatment.

Alternative Contributing Factors to Edema

Intumescence in tomato and other crops is also thought to be a result of other factors beyond lack of UV-light, which includes overall light quality, air quality, humidity, temperature, and soil/substrate moisture (Pinkard, 2006). In our experiment, the acrylic mini chambers we used for treatments utilized a heat exchange unit with chilled water to provide dehumidification and, to some extent, cooling. The chambers were designed for use in smaller crops such as baby leaf greens, and for our tomatoes, over time it became apparent that the chambers were extended past their capacity to control relative humidity to be < 70%. Limitations in control of humidity and correspondingly high rootzone moisture during the course of the experiment may have contributed to the development of edema. In a study evaluating the effect of humidity, soil substrate moisture, and light levels on tomato intumescence, Sagi and Rylski (1978) found that a high relative humidity of 80% exacerbated the formation of edema symptoms in tomato. This work is supported by the findings of Lang and Tibbits (1983), who reported that relative humidity level of 92% (as compared to 30% in control) led to higher instances of intumescence. Air quality may contribute to edema, for example Lang and Tibbits (1983) reported higher levels of edema when exposed to contaminants found in pressurized laboratory air over longer periods. As a result of higher humidity levels in our acrylic mini chambers, soil substrate moisture was retained longer and required less frequent watering. In a study examining the effect of rootzone moisture on rootstock cultivar ‘Maxifort’ and ‘Florida-47’, Rud (2009) found that ‘Maxifort’ was significantly affected by rootzone moisture while the hybrid ‘Florida-47’ was unaffected.

Table 2.3. Total accumulated photon flux density (PFD) for UV-A and UV-B with the mini chamber top on and off. Values were calculated using data collected from the spectral output shown in Figure 1.1.

	Wavelength (nm)	Micro Chamber Top On ($mmol \cdot m^{-2} \cdot d^{-1}$)	Micro Chamber Top On ($mmol \cdot m^{-2} \cdot d^{-1}$)	Percent Increase (%)
UV-B	(280-320)	4.73	8.42	78%
UV-A	(320-400)	41.5	135	225%

Conclusion

In summary, in our experiment, sensitivity to edema was well characterized between cultivars, with significant differences being documented between the rootstock 'Maxifort' (most affected) and 'Sweetelle' (least affected). Symptoms of edema progressed over the 10-day observation period, with developmental rates being cultivar-specific. The positioning of the compound leaf on the plant played a significant role in the onset and severity of edema, with older leaves experiencing symptoms of edema earlier and with greater severity. The acrylic mini chamber treatment, with higher relative humidity, lower availability of UV light, and a significant decrease in air exchange rates, had, to a varying degree, promoted development of edema, with each cultivar expressing more symptoms of the disorder when compared to the control. Consequently, this increased incidence of edema was negatively correlated to the measured biomass parameters, with significantly lower fresh and dry weight, plant height, and leaf area being recognized in the plants grown in the acrylic mini chambers.

To our knowledge, this paper reports the most comprehensive information, to date, on the sensitivity of multiple tomato cultivars to edema. The acrylic mini chambers and the methodology presented here could be useful for additional cultivar screenings for edema, which may be beneficial for selection and breeding of cultivars for tolerance of edema in conducive environments. Likewise, this methodology can also provide the framework for future

experiments that evaluate specific environmental parameters and the physiological origins of edema.

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CHAPTER 2

Effect of Light on Yield, Quality, and Photosynthetic Parameters in Greenhouse Tomato Cultivar 'Merlice'

Abstract

Supplemental lighting in greenhouse applications has been shown to offer significant benefits in increasing yields and extended harvest for growers producing in climates with insufficient solar radiation during the winter months. While previous studies have evaluated the difference in tomato crops grown under ambient and supplemental lighting along with the targeting of a specific daily light integral (DLI) with various supplemental lighting sources, there is little literature evaluating multiple DLI targets to optimize greenhouse tomato production. Our study utilized four glass greenhouse sections with high wire hydroponic tomato production using the tomato on vine scion 'Merlice' grafted to the rootstock 'Maxifort'. Each greenhouse was established with a different lighting treatment (15, 20, 25 and 30 $mol \cdot m^{-2} \cdot d^{-1}$) and controlled using Light and Shade System Implementation (LASSI) to achieve our daily target. Plants were exposed to the treatments for three months, with photosynthetic parameters (net photosynthesis, transpiration, stomatal conductance, and water use efficiency [WUE]) being evaluated three times during the course of the experiment. In addition, plants were harvested during a three-month period to collect data on the number of fruit clusters, number of fruit per cluster, total peduncle and fruit weight, first fruit fresh weight, first fruit Brix, first fruit dry weight, and the first fruit fresh to dry weight (FW:DW) ratio. From this study, we found no significant difference between treatments in the four photosynthetic parameters, although we did see a significant decrease in net photosynthesis over the course of the experiment. Likewise, there was a

significant decrease in the number of harvested clusters, total cluster weight, fresh weight, dry weight, and the FW:DW ratio as the plants aged. As well, the plants exposed to 25 $mol \cdot m^{-2} \cdot d^{-1}$ performed significantly worse that the 20 and 30 $mol \cdot m^{-2} \cdot d^{-1}$ treatments, which may have been due to a higher incidence of the root disease *Pythium*. This trend was inverted for Brix content, with the 25 and 15 $mol \cdot m^{-2} \cdot d^{-1}$ treatments having an overall higher average sucrose content than the others.

Introduction

Greenhouse tomato production provides year-round harvests while maintaining economic significance, with over $418 million wholesale value annually in the United States (*2017 Census of Agriculture*, 2019). As a result of production techniques that favor high density cropping systems and environmental control networks, commercial greenhouses in the United States and Canada produce approximately 500 metric tons per hectare per season compared to 34-36 in field systems (Cook & Calvin, 2005). Due to increased market proliferation and production costs in Canada and Mexico, domestic tomato production has declined by over 30% while importation has increased by approximately 55% since the turn of the century (Guan et al., 2017). Although not traditionally significant tomato producers, Minnesota and New York contain a high concentration of greenhouse operations with access to off-season, northern markets at a higher premium (Baskins et al., 2019). One of the challenges that greenhouse tomato growers face in higher latitudes is the energy requirement for production. In a study conducted in upstate New York that analyzed energy use of growing environments, greenhouse production required 95% and 87% more energy compared to high tunnels and traditional field production (de Villiers et al., 2011).

In northern greenhouse operations, lighting is a significant contributor to the energy requirements for tomato production. In a study examining irradiance in the Northeast, the daily integrated light availability of solar radiation can vary greatly throughout the year (Both, 2014). Greenhouse glazing material also plays a significant role in transmittance of photosynthetically active radiation (PAR), with a 10 and 25% reduction in available light energy provided using glass and polycarbonate, respectively. Compounded with light diffused through overhead infrastructure, greenhouse structures can reduce the light absorbed at the plant canopy by up to 50% (Both, 2002).

As the industry standard for greenhouse supplemental lighting, high pressure sodium (HPS) fixtures utilizes a magnetic or digital ballast to provide energy to a sodium core to produce significant amounts of light in the yellow/red spectrum (550–650 nm). These fixtures are noted for their relatively low cost, high output, and small footprint when compared to other lighting technologies. With significant improvements in wall-plug efficacy and decreasing capital costs over previous years, light emitting diode (LED) fixtures are slated to capture $3.6 billion dollars in capital by the turn of the decade (Runkle et al., 2014). As with both of these technologies, there are deviations in cost and efficiency in various fixtures that can significantly alter expenditures associated with implementing these systems. Furthermore, both lighting options produce varying levels of heat, with HPS bulbs generally producing more thermal and radiant heat when compared to diodes. In a study comparing hybrid lighting strategies using LED and HPS fixtures, it was found that greenhouses operating with a higher ratio of HPS fixtures required less heating during morning and winter operations while hampering greenhouse cooling capabilities in warmer conditions (Dueck et al., 2012).

Both forms of supplemental lighting provide a variety of benefits to the grower, with the ability to control photoperiod and provide the necessary daily light integral (DLI) for the crop being critical for maintaining consistent yields and quality throughout the year. Supplemental lighting provided beyond the ambient photoperiod has been shown to increase tomato growth and subsequent fruit yield, with Demers et al. (1998) finding that an optimal photoperiod of 14 hours at a photosynthetic photon flux density (PPFD) of 110 $\mu mol \cdot m^{-2} \cdot day^{-1}$ increases yields and growth by up to 57% when compared to the ambient treatment. During Demers et al. (1998) experiment, young tomato plants exposed to continuous lighting did see a significant benefit in growth and yield, although mature plants provided diminishing returns and suffered chlorotic symptoms with excessive exposure. In two experimental cycles, with one conducted each in the Spring and Fall, evaluating the effect of beginning and end of day (EOD) greenhouse HPS supplemental lighting to ambient lighting conditions, Blom and Ingratta (1984) found that extending the photoperiod of the tomato plants to 18 hours (11 hours of ambient conditions with seven hours of supplemental lighting) provided a 25% to 28% increase in total yield and harvested fruit during the first month of spring and a 23 to 25% increase the following fall, respectively. A similar study evaluating the response of pepper to various photoperiods was conducted, with improved yields observed at up to 20 hours of light per day while utilizing overhead HPS supplemental lighting at a PPFD of 110 $\mu mol \cdot m^{-2} \cdot day^{-1}$ (Demers et al., 1998).

Additional canopy lighting has been shown to increase photosynthetic activity in tomato, with Dorais et. al (2002) finding a 67% increase in net photosynthesis of the fifth leaf with an additional 50 $\mu mol \cdot m^{-2} \cdot day^{-1}$ of supplemental HPS lighting. This finding reflects work performed by McAvoy and Janes (1989), who found the highest net photosynthetic response in young leaf tissue undergoing initial fruit set and a subsequent decreasing rate with leaf maturity.

Another experiment exposed plants to 12 hours of supplemental, intracanopy LED lighting during the day or night in summer or winter at an average PPFD of 165 $\mu mol \cdot m^{-2} \cdot day^{-1}$. From this research, it was established that net photosynthesis measured in the winter and summer showed a significant increase and subsequent decrease over the control in the mid and lower canopy, respectively. These results have been confirmed in other crops, as greenhouse cucumber production under supplemental lighting saw a significant increase in net photosynthesis under overcast conditions, with leaf weight, chlorophyll, and dry matter content increasing considerably when compared to the ambient light crop (Hao & Papadopoulos, 1999).

As an outcome of increased leaf photosynthetic rates, it is well documented that supplemental lighting leads to an increase in overall yield in tomato crops. In a study comparing the yield of year-round greenhouse tomatoes grown under ambient and ambient plus 6.5 $moles \cdot m^{-2} \cdot day^{-1}$ of HPS supplemental lighting, fresh fruit yields of one crop and two crop cycles per year increased by 75 and 66%, respectively (McAvoy and Janes, 1988). In another study examining the effect of two planting densities and photosynthesis photon flux densities (PPFD) on commercial-style greenhouse tomatoes, Dorais et. al (1991) found that by increasing the available PPFD from 100 to 150 $\mu mol \cdot m^{-2} \cdot day^{-1}$ over a 16-hour photoperiod during months of September through May led to a 10% and 14% increase in total yield when grown at 2.3 and 3.5 $plants \cdot m^{-2}$, respectively. When comparing the effect of overhead lighting using HPS fixtures to intracanopy lighting using LED arrays, with both providing an average daily light integral (DLI) of 9 $mol \cdot m^{-2} \cdot d^{-1}$, there was no statistical difference between treatments while both achieved a 65% and 70% average increase in total harvested fruit weight and harvest fruit as compared to ambient light control, respectively (Gómez et al., 2013). In another study utilizing intracanopy lighting in tomatoes, supplemental fluorescent lighting provided for 16 hours at 40 to 140

$\mu mol \cdot m^{-2} \cdot day^{-1}$ lead to a significant increase in yield from fruit set to green fruit maturation (Tewolde et al., 2016). In research comparing lettuce growth under five treatments with 1000 $\mu l \cdot L^{-1}$ CO_2 and varying daily integrated light levels between 8 and 22 $mol \cdot m^{-2} \cdot d^{-1}$, it was concluded that increasing DLI levels lead to continuously higher shoot dry weight, with 17 $mol \cdot m^{-2} \cdot d^{-1}$ being ideal for head lettuce production (Both et al., 1997); greater DLIs increased plant biomass but also led to high incidence of the physiological disorder, tip burn.

While supplemental lighting has been well reported for yields and photosynthetic activity in tomato, to our knowledge, there is no published data that analyzes the outcome of multiple DLI treatments on commercial-style greenhouse tomato production in the Northeast. This study could benefit growers looking to optimize their lighting regimes for a balance between yields and costs associated with supplemental lighting. As a result, the focus of this study is to analyze four DLI treatments on greenhouse tomato (*Solanum lycopersicum* 'Merlice') for fruit yield, size, Brix, and photosynthetic parameter.

Methods and Materials

An experiment was conducted to evaluate the effect of supplemental lighting on yield and quality of grafted tomato plants. Two cultivars were selected based on their known compatibility and prevalence in commercial greenhouse operations in the Northeast. 'Merlice', an indeterminate, round tomato on vine (TOV) (De Ruiter Seed Company, St. Louis, Missouri) and 'Maxifort', a vigorous, vegetative cultivar (Johnny's Selected Seeds; Fairfield, Maine) were chosen as the scion and rootstock, respectively. Six sheets, each consisting of 96 cells (3.6 cm length x 3.6 cm width x 4.0 cm height; Grodan; Roermond, NL) were soaked in tap water for 10 minutes to condition the material. 294 seeds of each cultivar were sown into three rockwool

sheets, with each placed within a standard 1020 flat (54.5 cm x 27.8 cm x 6.2 cm; TO Plastics, Clearwater, MN). Plants were grown in a glass greenhouse at 23ºC/18ºC temperature day/night and were provided supplemental lighting for 6 hours/day at an average PPFD of 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Each flat was irrigated with fertilizer water (15 N -2.19 P - 12.45K; Jack's All-Purpose Liquid Feed, J. R. Peter's Inc., Allentown, PA) at a rate of 150 mg $N \cdot L^{-1}$ as needed.

Five days after sowing, it was observed that both cultivars were experiencing slow and delayed germination. To correct this issue, plants were moved to a growth chamber (M1 Walk-in; Environmental Growth Chambers, Chagrin Falls, OH), with environmental conditions of 23ºC/20ºC day/night temperature controlled using an Argus Controls interface (Argus Titan Controller; Argus Control Systems Ltd., Surrey, BC). Plants were hand watered daily (or as needed) using a liquid fertilizer (15 N -2.19 P - 12.45K; Jack's All-Purpose Liquid Feed, J. R. Peter's Inc., Allentown, PA) at a rate of 100 mg $N \cdot L^{-1}$. Lighting was provided by 96 T5 High Output (HO) fluorescent bulbs (Technical Consumer Products, Aurora, Ohio) in an overhead luminaire covered by panes of flexible acrylic sheathing with an average photosynthetic photon flux density (PPFD) of 260.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ provided for 16 hours daily resulting in a daily light integral (DLI) of 15 $mol \cdot m^{-2} \cdot d^{-1}$. After six additional days, the three trays containing 'Maxifort' were placed underneath a slotted chamber bench to reduce light and, consequently, induce plant elongation while slowing growth.

After 17 days from sowing, the stem diameter compatibility of 'Merlice' and 'Maxifort' was adequate for grafting. Each plant was cut at approximately a 45º angle below the cotyledons using a single edge razor blade (Red Devil, Pryor, Ohio) and paired using a 1.5 mm silicone grafting clip (Johnny's Selected Seeds; Fairfield, ME). Each of the three nursery flats containing the grafted tomato plants was placed in a white, non-porous flat (TO Plastics), topped using a

humidity dome (Curtis Wagner Plastics Corp.; Houston, TX), and sealed using plastic wrap. Plants were slowly acclimated to the conditions of the main chamber, with the cling wrap and humidity dome being removed 4 and 7 days after grafting. On day 8 after grafting, the plants were returned to the chamber benchtop level to grow under previous conditions.

Three weeks after grafting, 196 grafted 'Merlice'/'Maxifort' tomato plants were transplanted into conditioned rockwool blocks (10.2 cm length x 10.2 cm wide x 6.4 cm height; Grodan) and placed on benchtop level. The greenhouse was maintained at a day/night temperature of 23ºC/17 ºC and provided with supplemental lighting at an average of 167 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for a supplemental daily light integral (DLI) of 9.6 $mol \cdot m^{-2} \cdot d^{-1}$ over a 16 photoperiod. Irrigation was provided using a liquid fertilizer (15 N -2.19 P - 12.45K) at 150 mg $N \cdot L^{-1}$.

Three days prior to final transplanting, preparations were made to the growing system in four greenhouses (10.7 m length x 2.9 m width x 4.3m high growing space). Each greenhouse was constructed with three rows facing East-West, with the middle row being 3.2 m on center and the two outside rows being 1.1 m from the wall/boundary. Each row was constructed using 6 cinder blocks (19.4 cm length x 19.4 cm width x 40.6 cm height; Home Depot, Atlanta, GA) equally spaced along 3.7 m of dimensional lumber (3.8 cm length x 18.4 cm width; Home Depot). Each row then received three rockwool slabs (15.2 cm width x 7.6 cm height x 91.4 cm length; Grodan) conditioned with tap water for 10 minutes, in which a square slit (10.2 cm length x 10.2 cm wide) was made every 30.5 cm on center to allow for 10 rockwool blocks. Irrigation tubing (2.1 cm inner diameter; Dripworks, Willits, CA) was attached along the side of the lumber on each row using cable staples (1.4 cm; Home Depot), with pressure compensated emitters (1.9 L/hour; Netafim; Tel Aviv, Israel), micro irrigation tubing (3.2 mm inner diameter x 45.7 cm

length; Dripworks), and arrow stakes providing consistent irrigation to the rockwool blocks. Fertigation was achieved using a 1:100 custom, two stock hydroponic solution (Table 3.1.) diluted into a 200 L drum at 2.4 ± 0.1 dS/m and a pH of 6.5 ± 0.2. The final solution was then distributed using a gravity-fed, 1/10 horsepower centrifugal pump (TE-4-MD-HC; Little Giant, Fort Wayne, IN) and provided to the plants at an equal rate. Supplemental lighting was supplied by twelve 600W high pressure sodium fixtures (P.L. Light Systems Inc, Beamsville, ON) providing an average photosynthetic photon flux density (PPFD) of 398.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ as needed to reach the specified daily light integral (DLI) target for each treatment. One day following the final transplant, each plant had its apical meristem removed to promote lateral bud initiation. Each plant was attached to a wire spanning the length of the greenhouse offset 0.46 m from the center of each row using a tomato trellising spool and trellis clips (Johnny's Selected Seed). Each plant was then selected for two dominant lateral branches after four weeks of growth, which were then attached using the same method. Daily (or as needed) plant management tasks included lowering of tomato plants, attachment of tomato clips as needed, and removal of lower leaves up to the lowest truss for increased airflow under the leaf canopy.

At experiment initiation, tomato plants in each greenhouse section were exposed to one of four different daily light integral (DLI) treatments, with each greenhouse receiving a target of 15, 20, 25, or 30 $mol \cdot m^{-2} \cdot d^{-1}$. Lighting targets were controlled using the Light and Shade System Implementation (LASSI) control system (Albright et. al., 2000) integrated with a LI-190R quantum sensor (LI-COR Inc., Lincoln, NE USA) to utilize the deployable shade cloth system (Svensson; Kinna, SE) and supplemental lighting to achieve daily lighting requirements. Each integral was recorded daily starting on June 18th, 2019 and until the conclusion of the experiment on September 6th, 2019.

Data collection began approximately seven months post-sowing, with each of the three months of harvesting representing a time segment for data analysis. Each greenhouse was harvested on a per-need basis (harvests occurred 2 to 3 times weekly), with the number of fully mature fruit clusters, total fruit per cluster, and fresh weight yield per cluster documented in-house. In each mature cluster, the tomato fruit closest to the stem abscission point was analyzed for fresh weight and Brix (HI96801 Refractometer; Hanna Instruments, Woonsocket, RI). After two days of drying at 80 C in a mechanical convection oven (Model 645; Thermo Scientific, Waltham, MA), each fruit was then analyzed for dry weight using a digital scale (PL6001E; Mettler Toledo, Columbus, OH). Data was collected from all plants with fully developed lateral branches, which if not developed, were excluded from the collection process. If the apical meristem was lost during the experiment, that branch continued to be harvested but was not included in the final analysis. These measures were taken to reduce incomplete/incorrect data that did not represent unaffected plants within the treatment and, with a high number of replicates (Table 3.2) within each treatment, should not have adversely affected the outcome of the experiment. Each parameter was analyzed using a mixed model, with a post-hoc comparison and Bonferroni correction at $P \leq 0.05$ being used to further identify significant differences based on lighting treatment.

Three replications of gas exchange measurements were conducted using an infrared gas analyzer (IRGA) (LI-6400; LI-COR Inc., Lincoln, NE) in three-week intervals leading up to the conclusion of the experiment. Three plants per treatment were chosen at random to be analyzed using the terminal leaflet on the fifth compound leaf below the apical meristem, where they were exposed to ten instantaneous light levels in succession: 0, 15, 30, 60, 120, 250, 500, 1000, 1500, and 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at an ambient CO_2 and relative humidity of 400 µl/L and 70 ± 10%,

respectively. The photosynthetic parameters, including net photosynthesis, stomatal conductance, transpiration, and water use efficiency (WUE), were analyzed on an individual basis using a mixed model, with nonsignificant terms being removed using the backwards stepwise method to obtain the final model. Post hoc multiple comparisons with a Bonferroni correction at $P \leq 0.05$ were used to further identify significant differences between the parameters (Figure 4.2). Least square means were obtained from the triple interaction of each parameter, with the exception of WUE being insignificant, and were used as data points for developing nonlinear, best-fit curves (Table 4.6.). A mechanistic model was selected to analyze net photosynthesis while transpiration and stomatal conductance were modeled using a biexponential 5P model. Both methods of developing fit curves allowed for net negative values to be graphed while also providing average R-square values of .914, .991, and .967, respectively. Values associated with the fit curve formula for each parameter were tabularized and analyzed using separate mixed models, with nonsignificant terms being removed using backwards stepwise method to obtain the final models. Post hoc multiple comparisons with a Bonferroni correction at $P \leq 0.05$ were used to further identify significant differences between the treatments and letters were used to show significance (Table 4.1). All statistical analyses were processed using JMP statistical software (JMP Pro 11; SAS Institute, Cary, NC).

Figure 3.1. Daily Light Integral (DLI) values recorded in correspondence to their treatment, with 15 mol (A), 20 mol (B), 25 mol (C), and 30 mol/m^{-2}/d^{-1} (D). The average DLI of each treatment was adjusted to remove inconsistencies and errors in the recording of daily values (for example, due to times when there was a lost wireless signal (DLI value of 0 mol·m^{-2}·d^{-1})).

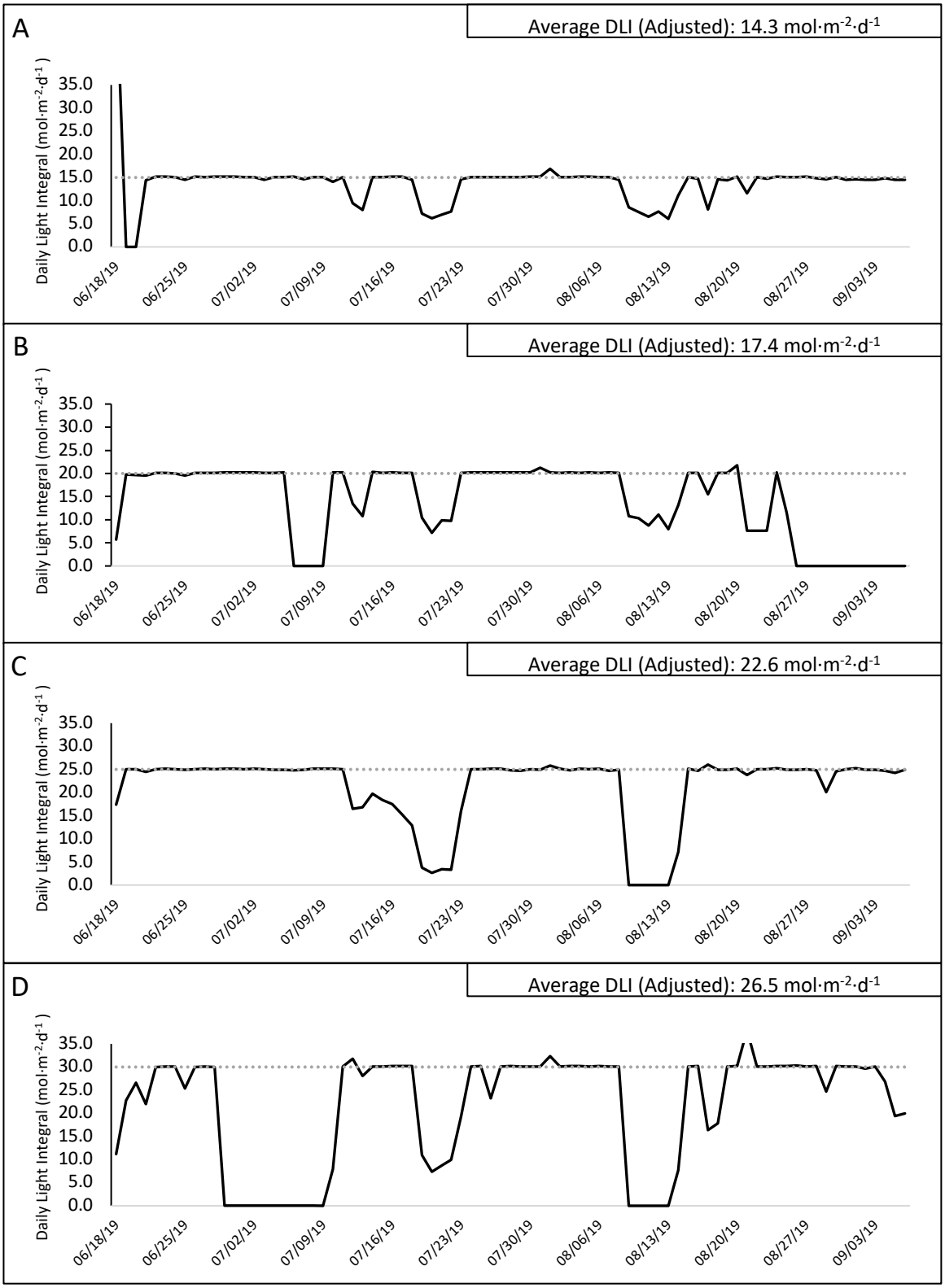


Table 3.1. Nutrient composition of the two-stock hydroponic nutrient solution

Element	Target (mg/L)	Tap Water (mg/L)	Nutrients Added (mg/L)	Final Solution (mg/L)
N	190	0.84	189.2	190
P	47	0.41	46.6	47
K	350	1.57	348.4	350
Ca	200	63.9	136.1	200
Mg	60	14.1	45.9	60
S	116	0	61.5	61.5
Cl	89	0	36.1	36.1
Fe	2	0.04	2	2
Cu	0.05	0.05	0	0.05
Mn	0.55	0.01	0.54	0.55
Zn	0.33	0	0.33	0.33
Bo	0.4	0.02	0.38	0.40
Mb	0.05	0	0.05	0.05

Target value from the 3-stage tomato nutrient solution (Kroggel & Kubota, 2018)

Table 3.2. Number of replicates within each treatment greenhouse

Treatment	Number of replicates
15 $mol \cdot m^{-2} \cdot d^{-1}$	43
20 $mol \cdot m^{-2} \cdot d^{-1}$	46
25 $mol \cdot m^{-2} \cdot d^{-1}$	54
30 $mol \cdot m^{-2} \cdot d^{-1}$	50

Replicates refer to each growing point on the v-cordon of the 30 tomato plants per greenhouse, with a maximum of 60 replicates possible per treatment

Results

Net Photosynthesis

Over the three months of data collection, photosynthetic parameters were measured three times to determine the effect of each treatment over time. From the mixed model results, it was found that there was a significant difference in the triple interaction between measurement replication, instantaneous light intensity, and the DLI treatment within all parameters excluding

water use efficiency (Table 4.1.). Evaluating each of the remaining parameters was further performed using the least square mean values of each interaction with best-fit, non-linear curves, which resulted in three sets of graphs related to each parameter (Figures 4.2-4.4). Net photosynthesis, which was evaluated using a mechanistic growth curve, exhibited no significant difference within the same day of measurement, although there were differences across the three measurements in the same treatment (Figure 4.2). The asymptote of the 15 $mol \cdot m^{-2} \cdot d^{-1}$ treatment significantly decreased across all three runs, with a combined 45% decrease in maximum photosynthetic capability between the first and last measurements. Likewise, the 20 and 30 $mol \cdot m^{-2} \cdot d^{-1}$ treatments saw a 71 and 53% decrease in the asymptote between the first and third measurements, respectively. The scale and growth rate of the photosynthetic curves were also significantly different between the first and last measurements of the 20 and 30 $mol \cdot m^{-2} \cdot d^{-1}$ treatments, with the scale increasing by 23 and 27% and the growth rate by 66 and 51%.

Transpiration/Stomatal Conductance

Transpiration and stomatal conductance curves were achieved by plotting the least square means against a biexponential 5P curve, which accounted for a decrease in overall net transpiration and subsequent exponential increase at low and high light levels, respectively (Figures 4.3, 4.4). There was no significant difference between DLI treatments within each day of measurement for transpiration or stomatal conductance parameters (Tables 4.3, 4.4), although there was an observed decrease across measurement runs. Between the first and last measurement date, there was an average decrease of all treatments of 75 and 77% for stomatal conductance and transpiration, respectively. Of the treatments, the plants exposed to 20 $mol \cdot m^{-}$

$^{2}\cdot d^{-1}$ saw the greatest reduction over time while the 25 $mol\cdot m^{-2}\cdot d^{-1}$ treatment were the least affected in both measurements.

Biomass Data

A mixed model was used to analyze and test the significance of seven biomass parameters, with differences being measured across time (Figure 4.4.) and as an average of the three months of harvest (Figure 4.6.). There was a significant difference in the number of clusters harvested between treatments in only the first month, with the 15 $mol\cdot m^{-2}\cdot d^{-1}$ treatment having a 17% greater output compared to the 30 $mol\cdot m^{-2}\cdot d^{-1}$ treatment (Figure 4.4.). Across all treatments, there was a significant decrease of 26% in the average total number of harvested clusters between the first and subsequent months in all treatments. As an average of the treatments over the three months, there was no significant difference in the number of clusters harvested (Figure 4.5.) between DLI treatments. Likewise, there was no difference in the average number of fruits harvested within both measurements. All treatments saw a decrease in the average total truss and fruit weight harvested over time, with a 47% decrease in the average of all treatments between the first and last month. The 25 $mol\cdot m^{-2}\cdot d^{-1}$ treatment performed significantly worse than all other treatments in the first month, with a 42% smaller yield compared to the average of the other treatments and a continued trend as the lowest producer for the remainder of the experiment (Figure 4.5.) As a result, the cumulative fruit yield over three months was significantly lower in the 25 $mol\cdot m^{-2}\cdot d^{-1}$ treatment than all other treatments (Figure 4.5.)

The trend of decreasing size and yield also reflected in the average first fruit fresh and dry weight, with there being a 37 and 40% decrease between the first and last month's harvests for each parameter, respectively. Between the first and second month, there was a noticeably greater decrease in dry weight vs. fresh weight, with a separation of 22%. When comparing

between treatments, the 25 mol·m^{-2}·d^{-1} treatment had a significantly lower first fruit fresh weight across all months while only being significantly different in the first month for dry weight. There was a significant increase in the fresh weight measurements of both the cluster and individual fruit in the second month between the 15 and 30 mol·m^{-2}·d^{-1} treatment.

As a function of the fresh weight to dry weight ratio, there was no significant interaction between any of the treatments in the same month of harvest. Similarly, there was no significant difference in the same treatment over time, with the exception being the 25 mol·m^{-2}·d^{-1} treatment in the second month of harvest. All previously mentioned parameters followed a trend, with the highest to lowest performances being 30, 20, 15 and 25 mol·m^{-2}·d^{-1} (Figure 4.5).

The measurement of Brix had an inverse trend when compared to the other parameters, with the average fruit from the 25 mol·m^{-2}·d^{-1} treatment having the highest Brix content over all three months. Between the first and second months of harvest, there was a decrease in Brix across all treatments by an average 20%, with the 25 mol·m^{-2}·d^{-1} treatment experiencing the greatest decrease of 36%. Between the second and third months, the Brix values increased by 12%, with the 25 mol·m^{-2}·d^{-1} treatment showing the least variation between all cultivars.

Table 4.1. Mixed model analysis for the full factorial interaction of instantaneous light, measurement replication, and DLI treatments on photosynthetic parameters. Random effects included Plant ID nested within greenhouse and the interaction of the experimental replication and run nested within the greenhouse

Main Effects & Interactions	Net Photosynthesis	Stomatal Conductance	Transpiration	Water Use Efficiency
Instantaneous Light	***	***	***	***
Measurement Month	***	***	***	NS
Instantaneous Light•Measurement Replication	***	***	***	NS
DLI Treatment	*	NS	NS	NS
DLI Treatment•Instantaneous Light	***	NS	NS	NS
DLI Treatment•Measurement Replication	NS	NS	NS	NS
Measurement Replication•DLI Treatment•Instantaneous Light	***	*	***	NS

NS, *, **, * Nonsignificant or significant at P ≤ 0.05, 0.01, or 0.001, respectively.**

Table 4.2. Net photosynthesis parameters reported from the mechanistic growth curve derived from the least square means ± standard error of the mixed model. Numbers to the left of the 'Treatments' within the table signify the month of measurement.

Treatment ($mol \cdot m^{-2} \cdot d^{-1}$)		Asymptote		Scale		Growth Rate	
1	15	21.31 ± 1.06	A	1.08 ± .04	A	.0030 ± .0005	A
	20	18.98 ± .46	A	1.07 ± .02	A	.0031 ± .0003	A
	25	15.63 ± .55	A	1.06 ± .04	A	.0037 ± .0005	A
	30	15.18 ± .50	A	1.15 ± .03	A	.0036 ± .0004	A
2	15	12.83 ± .33	B	1.17 ± .03	A	.0041 ± .0003	A
	20	11.06 ± .72	AB	1.22 ± .08	AB	.0046 ± .0010	A
	25	15.86 ± .37	A	1.20 ± .02	A	.0034 ± .0003	A
	30	12.88 ± .65	AB	1.20 ± .05	AB	.0038 ± .0006	AB
3	15	11.64 ± .50	C	1.17 ± .05	A	.0053 ± .0008	A
	20	5.48 ± .30	B	1.47 ± .09	B	.011 ± .002	B
	25	10.03 ± .69	A	1.21 ± .08	A	.005 ± .001	A
	30	7.16 ± .35	B	1.49 ± .08	B	.0074 ± .001	B

Uppercase letters indicate significance differences between the same DLI treatment across month of measurement (1, 2, or 3) using a Bonferroni multiple comparisons correction (alpha=0.05). Error bars signify ± standard error (SE).

Table 4.3. Transpiration parameters reported from the biexponential 5P curve derived from the least square means ± standard error of the mixed model. Numbers to the left of the 'Treatments' within the table signify the month of measurement.

Treatment ($mol \cdot m^{-2} \cdot d^{-1}$)		Asymptote	Scale 1	Decay Rate 1	Scale 2	Decay Rate 2
1	15	0.68 ± 0.84	1.72 ± 0.80	-0.00043 ± 0.00013	2.97 ± 0.08	0.062 ± 0.004
	20	1.49 ± 0.2	0.32 ± 0.17	-0.00084 ± 0.00021	1.49 ± 0.08	0.070 ± 0.009
	25	0.80 ± 0.26	0.71 ± 0.24	-0.00055 ± 0.00011	0.72 ± 0.04	0.040 ± 0.005
	30	-3.50 ± 3.45	0.40 ± 0.04	$2.67e^{04}$ ± 0	5.27 ± 3.44	$-1.40e^{-04}$ ± $8.19e^{-05}$
2	15	0.29 ± 0.29	0.81 ± 0.27	-0.00046 ± $9.95e^{05}$	0.58 ± 0.03	0.039 ± 0.005
	20	0.52 ± 0.19	0.52 ± 0.18	-0.00050 ± 0.00011	0.61 ± 0.03	0.082 ± 0.009
	25	0.54 ± 0.31	1.11 ± 0.30	-0.00041 ± $7.51e^{-05}$	0.69 ± 0.03	0.048± 0.005
	30	0.31 ± 0.20	0.59 ± 0.18	-0.00052 ± 0.0001	0.92 ± 0.03	0.052 ± 0.004
3	15	-7.29 ± 37.61	7.83 ± 37.59	$-5.32e^{-05}$ ± 0.00024	0.77± 0.06	0.053 ± 0.009
	20	4.65 ± 18.57	-4.63 ± 18.57	$4.83e^{-05}$ ± 0.0002	0.23 ± 0.02	0.09 ± 0.03
	25	0.47 ± 0.15	0.15 ± 0.13	-0.00089 ± 0.00037	0.16 ± 0.07	1.77 ± $9.96e^{09}$
	30	0.08± 0.06	0.05 ± 0.04	-0.0012 ± 0.0004	0.50 ± 0.04	0.038 ± 0.007

There were no significant differences in parameters by treatment at each time using Bonferroni multiple comparisons correction (alpha=0.05)

Table 4.4. Stomatal conductance parameters reported from the biexponential 5P curve derived from the least square means of the mixed model. Numbers to the left of the 'Treatments' within the table signify the month of measurement.

	Treatment ($mol \cdot m^{-2} \cdot d^{-1}$)	Asymptote	Scale 1	Decay Rate 1	Scale 2	Decay Rate 2
1	15	0.11 ± 0.05	0.08 ± 0.04	-0.0005 ± 0.0002	0.394 ± 0.008	0.080 ± 0.004
	20	0.18 ± 0.01	0.004 ± 0.006	-0.0015 ± 0.0008	0.45 ± 0.01	0.095 ± 0.007
	25	0.07± 0.03	0.06 ± 0.03	-0.0004 ± 0.00014	0.060 ± 0.003	0.061 ± 0.008
	30	-0.89 ± 4.80	1.02 ± 4.80	$-3.61e^{-05}$ ± 0.00016	0.045 ± 0.004	26.15 ± 0
2	15	0.04± 0.02	0.05 ± 0.01	$-0.00049 \pm 8.47e^{-05}$	0.051 ± 0.002	0.053 ± 0.005
	20	0.06 ± 0.02	0.049± 0.02	-0.0005 ± 0.0001	0.081 ± 0.003	0.10 ± 0.01
	25	0.04 ± 0.03	0.12± 0.03	$-0.00039 \pm 7.22e^{-05}$	0.066 ± 0.003	0.052 ± 0.005
	30	0.04 ± 0.03	0.06 ± 0.03	-0.0004 ± 0.0001	0.082 ± 0.003	0.055 ± 0.004
3	15	0.22 ± 0.29	-0.16 ± 0.28	0.0002 ± 0.0003	0.063 ± 0.004	0.061 ± 0.008
	20	0.029 ± 0.007	0.025 ± 0.003	0.08 ± 0.03	-0.043 ± 0.006	0.0010 ± 0.0004
	25	0.07 ± 0.05	0.003 ± 0.02	-0.001 ± 0.003	-0.002 ± 0.03	0.006 ± 0.192
	30	0.013± 0.009	0.005 ± 0.006	-0.0011 ± 0.0006	0.062 ± 0.005	0.037 ± 0.007

There were no significant differences in parameters by treatment at each time based on a Bonferroni multiple comparisons correction (alpha=0.05)

Table 4.5. R^2 values reported from the best fit curves of net photosynthesis, transpiration, and stomatal conductance as an average of each of the four treatments over three measurement replications

	Treatment ($mol/m^2/d$)	Net Photosynthesis	Transpiration	Stomatal Conductance
1	15	.93	0.997	0.998
	20	.98	0.992	0.998
	25	.95	0.997	0.989
	30	.94	0.998	0.997
2	15	.97	0.997	0.996
	20	.83	0.997	0.98
	25	.98	0.998	0.995
	30	.90	0.998	0.999
3	15	.91	0.987	0.687
	20	.87	0.989	0.992
	25	.80	0.964	0.997
	30	.91	0.979	0.973

Figure 4.1. Net photosynthesis of plants within the four treatment greenhouses during the first (A), second (B) and third (C) data collection cycles. Best fit curves were achieved using a mechanistic growth model, with the asymptote, scale, growth rate, associated standard error, and R^2 values reported from the output (Tables 4.2;4.5)

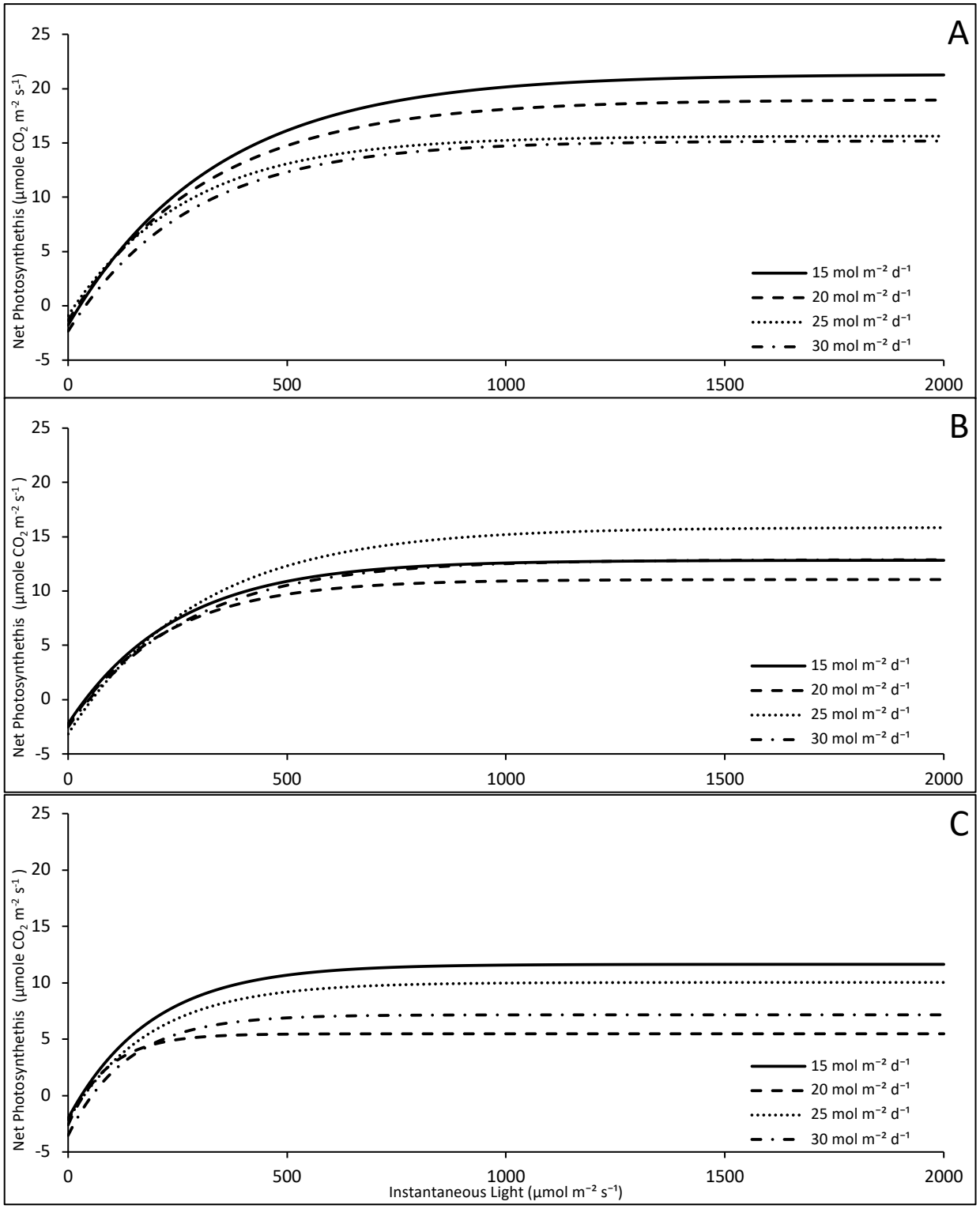


Figure 4.2. Plant transpiration within the four treatment greenhouses during the first (A), second (B), and third (C) data collection cycles. Best fit curves were achieved using a biexponential 5P model, with the asymptote, scales, decay rates, associated standard error, and R^2 values reported from the output (Table 4.3;4.5).

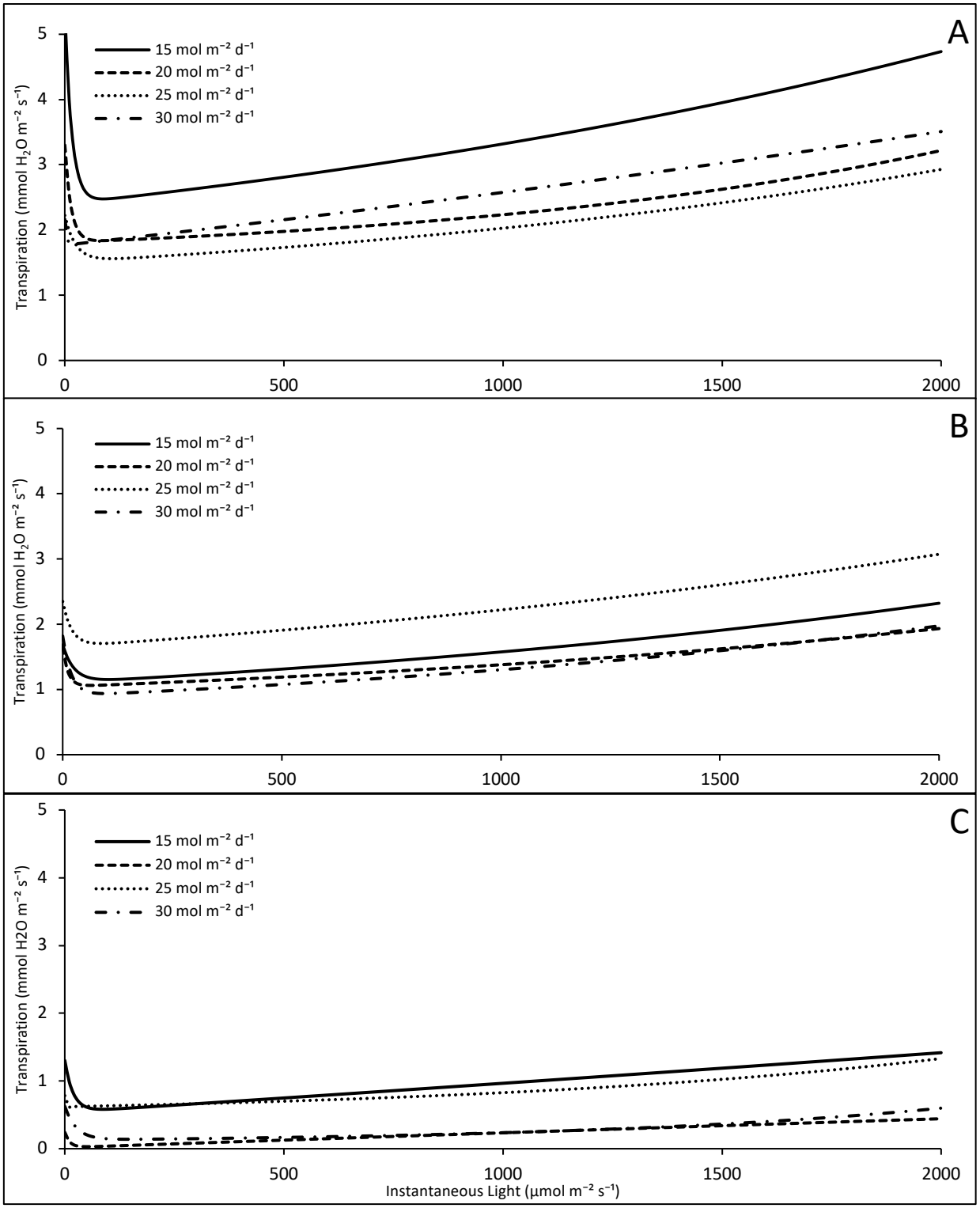


Figure 4.3. Plant stomatal conductance within the four treatment greenhouses during the first (A), second (B), and third (C) data collection cycles. Best fit curves were achieved using a biexponential 5P model, with the asymptote, scales, decay rates, associated standard error, and R^2 values reported from the output (Table 4.4;4.5).

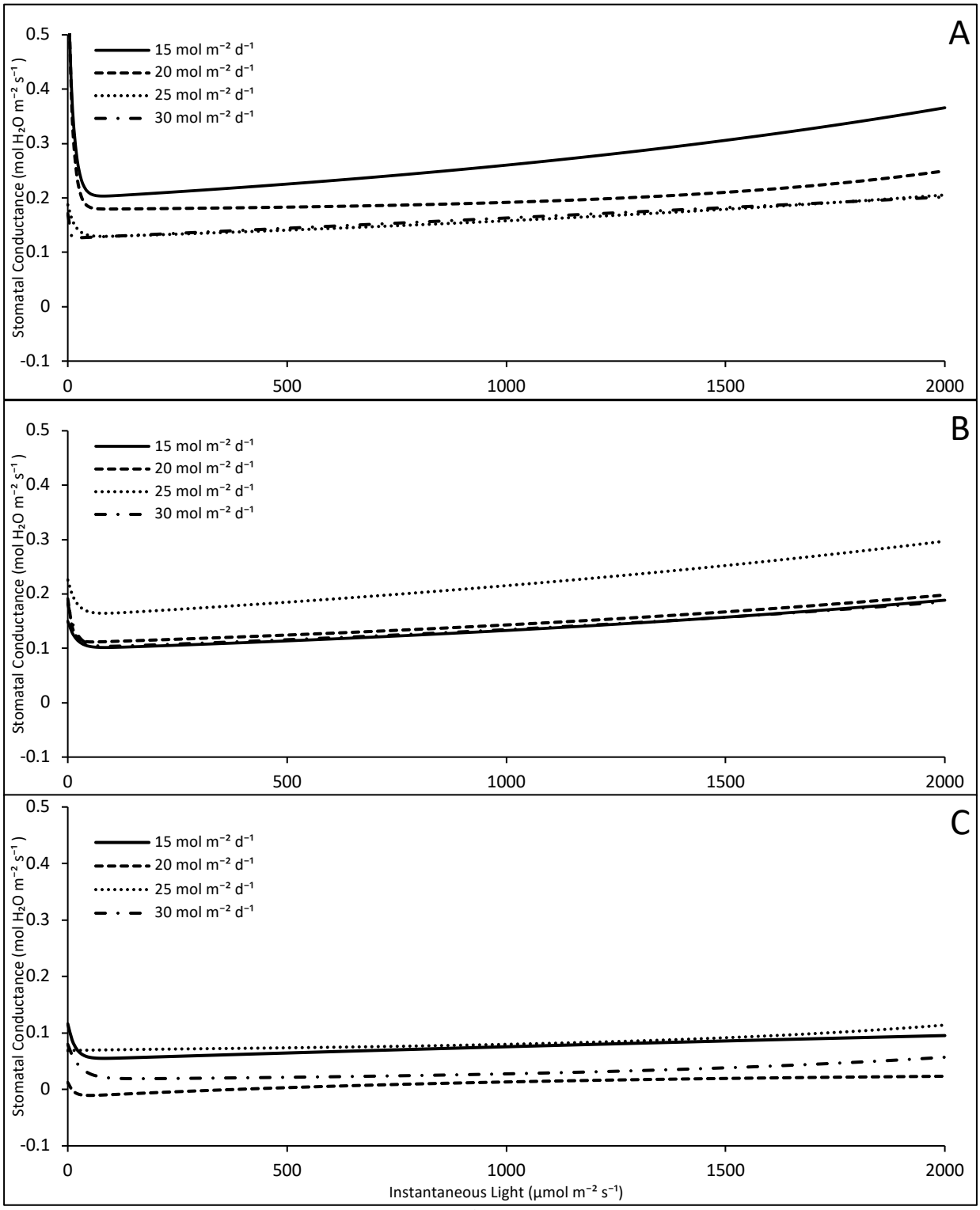
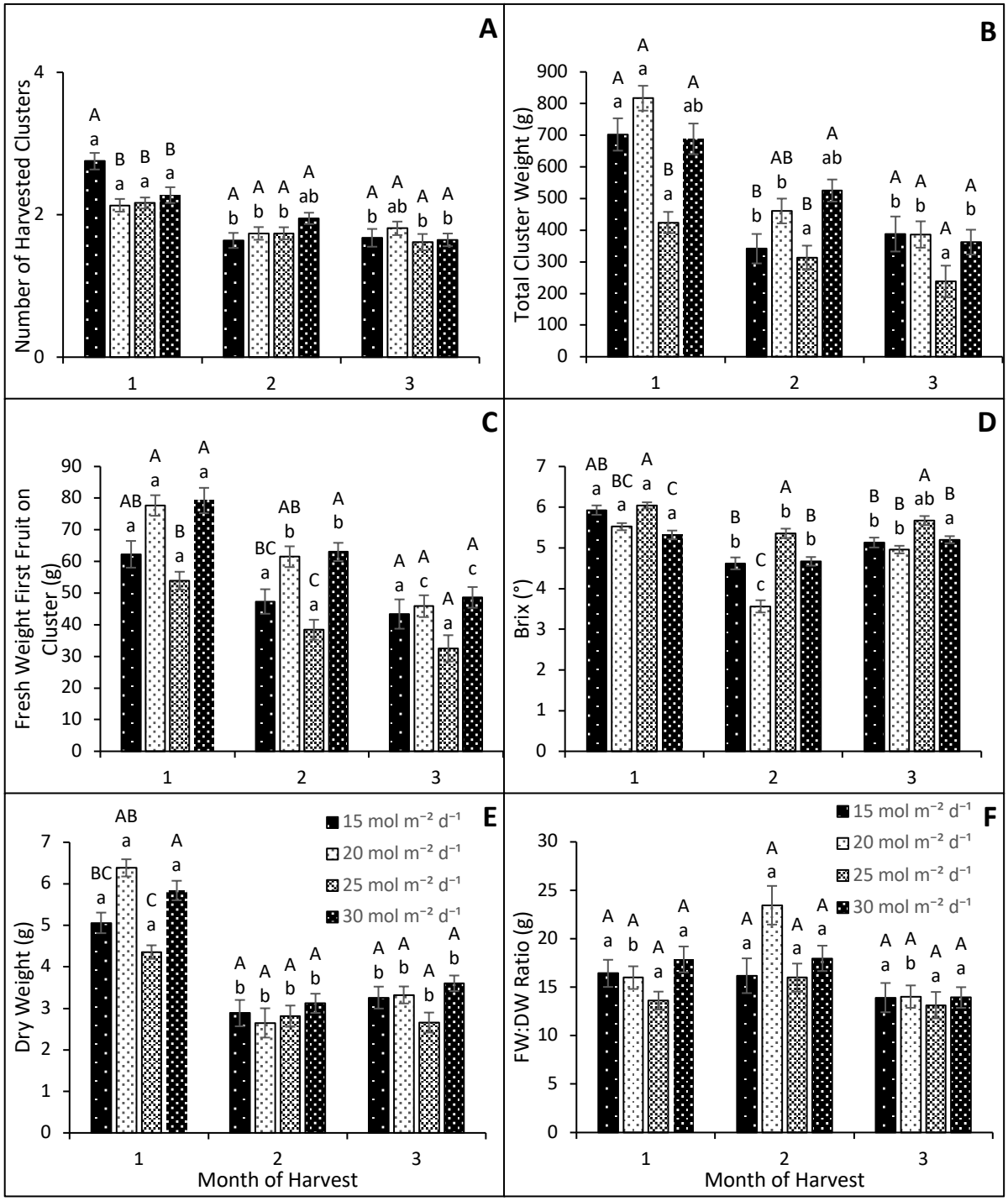
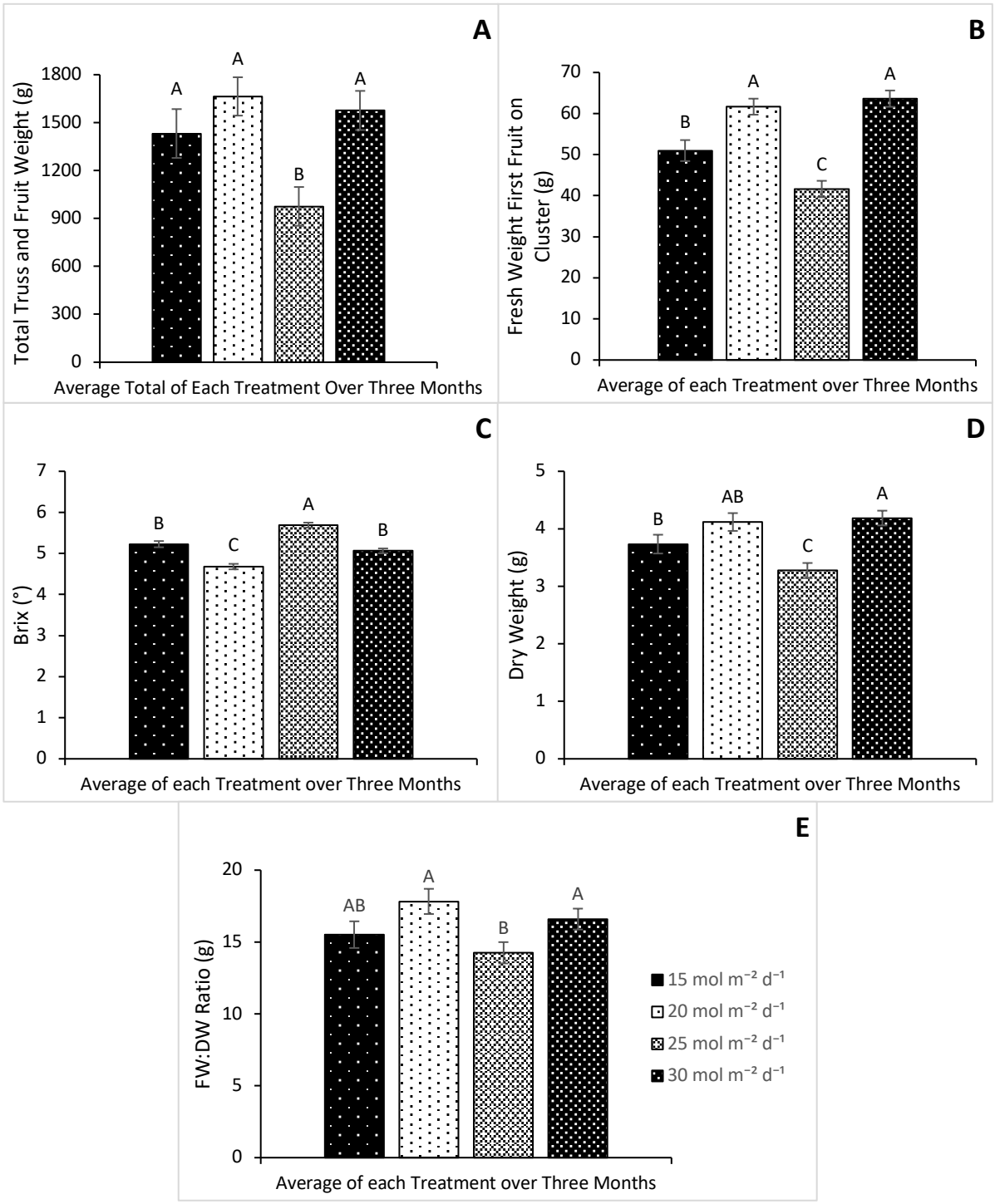


Figure 4.4. Least square mean number of: harvested fruit clusters (A), total cluster fresh weight (including peduncle and fruit) (B), average first fruit fresh weight (C), average first fruit Brix (D), average first fruit dry weight (E), and average first fruit fresh:dry weight ratio (FW:DW Ratio) (F) of the four treatments over three months of harvest.



Uppercase letters indicate significance across treatments during the same month and lowercase the same treatment across the three months of harvest using a Bonferroni multiple comparisons correction (alpha=0.05). Error bars signify ± standard error (SE).

Figure 4.5. Least square mean of total cluster (peduncle and fruit weight) (A), average first fruit fresh weight (B), average first fruit Brix (C), average first fruit dry weight (D), and average first fruit fresh/dry weight (E).



Uppercase letters indicate significance across treatments using a Bonferroni multiple comparisons correction (alpha=0.05). Error bars signify ± standard error (SE).

Table 4.6. Prediction Models for Best Fit Curves

Measured Parameter	Net Photosynthesis	Transpiration/Stomatal Conductance
Best Fit Curve Type	Mechanistic Growth	Biexponential 5P
Formula	$a * (1 - b * exp(-c * i))$	$a + b * \exp(-c * i) + d * \exp(-f * i)$
Formula Parameters	a Asymptote b Scale c Growth Rate i Instantaneous Light	a Asymptote b Scale 1 c Decay Rate 1 d Scale 2 f Decay Rate 2 i Instantaneous Light

Discussion

Photosynthetic Parameters: Plant Age

The decline in maximum net photosynthesis measured across the duration of the experiment, as denoted by the asymptotic value (Table 4.2), may be due to various biotic and abiotic factors. One of the suspected causes of decline in the plant's gas exchange capabilities is related to the age of the plant, with net photosynthesis rates declining with the increasing age of the leaf measured on the same plant on the same day (Xu et. al, 1995, 1997). Alternatively, we found little research related to the relationship between plant age and the photosynthetic capability of morphologically similar leaves measured over time. In a study that evaluates the interaction of plant age to the photosynthetic capability of the uppermost fully expanded leaf in cotton, Peng & Krieg (1991) found that photosynthesis rates decreased between 27 and 38% between days 70 and 115, with peak net photosynthesis occurring halfway through the trial. Although tomato and cotton plants have significant physiological differences, both plants utilize the C3 metabolic pathway for photosynthesis and may be similarly affected by the breakdown in efficiency of these systems, leading to a decrease in net photosynthesis. In another study, Dwyer & Stewart (1986) found a correlation between increasing plant age to decreasing photosynthesis

rates on an average plant level in maize (*Zea Mays* L.). When examining the net photosynthesis of same age foliage in two tree species (Pinus contorta and P. ponderosa), Yoder et. al. (1994) found a decrease of up to 30% in older trees, which was suspected as a result of lower hydraulic conductance in the vascular system. Given the nature of increasing stem length in high wire tomato production over time, it is possible that the interaction of plant size and reduced hydraulic conductivity led to a decrease in the maximum potential net photosynthesis.

Photosynthetic Parameters: *Pythium*

As an alternative outcome of plant age, increased exposure and susceptibility to pathogens may have also adversely affected the net photosynthetic rate of the tomato plants over time. Shortly after introducing the lighting treatments, a varying number of plants in each greenhouse began to show symptoms of water stress, which under closer evaluation was determined that the root systems in the rockwool bags were affected, to varying degrees, by the root pathogen *Pythium*. Beyond a reduction in root mass, pythium has been shown to reduce total leaf area, height, shoot fresh and dry weight, and carbon exchange rates within plants, although not directly affecting net photosynthesis efficiency of hydroponically cultivated pepper (Sutton et al., 2006). In another study examining the effect of pythium in cucumber roots at various inoculum levels, there was a significant reduction in root and leaf dry matter accumulation with higher levels of the pathogen while net photosynthesis was not significantly affected (Panova et. al., 2011). Contrarily, Panova et. al. (2004) found that there was a reduction in net photosynthesis and transpiration with a high concentration of pythium at higher rootzone temperatures in tomato, which correlates with a significant decrease in root and shoot dry weight in this study. Degradation of the root structure due to pythium reduces root functionality and,

subsequently, stomatal conductance as the plant cannot maintain hydraulic conductivity, with Aldahadha et. al. (2012) finding an overall reduction in transpiration of 14% in inoculated wheat. Likewise, a decrease in water availability has been shown to decrease the xylem vessel diameter in grape vines (Vitis vinifera L.), which reduces the maximum potential hydraulic conductivity and subsequently results in a lower level of transpiration and stomatal conductance (Lovisolo & Schubert, 1998).

Photosynthetic Parameters: Environmental Stress

A possible explanation for the decrease in photosynthetic parameters over the course of the experiment may be the interaction of plant age, environmental stress and subsequent worsening of tomato plant health due to pythium. With lighting treatments starting in June and running through the remainder of the summer months, increased irradiance and canopy temperatures from the high-pressure sodium lamps may have placed the tomato plants in increased osmotic stress, therefore lowering their photosynthetic potential. Fluctuations in rootzone temperature also play a significant role in the proliferation of pythium (Sutton et. al., 2006), which may have advanced the spread of the pathogen over time and, consequently, placing more strain on the plants.

Biomass Parameters: Daily Light Integral (DLI)

As stated previously, there was an incremental increase in the total truss and fruit weight, average first fruit fresh weight, dry weight, and fresh weight to dry weight ratio with the increasing daily light integral (DLI), with the exception being the outlier in the 25 $mol \cdot m^{-2} \cdot d^{-1}$ treatment. Increased yield with increasing DLI (up to a point) is consistent with other literature.

Greenhouse tomato production is generally light intensive, with an optimal DLI for production being between 20 and 30 $mol \cdot m^{-2} \cdot d^{-1}$ (Dorais, 2003; Faust, 2001). In our work, an increase in the available light for tomato production from 15 to 20 $mol \cdot m^{-2} \cdot d^{-1}$ led to an increase in the average total fruit and truss fresh weight of approximately 18%. This compares to a study conducted by Dorais et. al (1991), who found an overall increase in yield when increasing the supplemental lighting exposure of a tomato crop from 5.76 to 13.7 $mol \cdot m^{-2} \cdot d^{-1}$. Contrarily, this study also found a 14% increase in the number of fruit while our study found no significant increase across the treatments. This discrepancy may be due to the much lower DLI in Dorais et al. (1991) vs. our experiment. In another study evaluating the effect of intracanopy LED vs. overhead HPS lighting of a tomato crop, Gómez and Mitchell (2014) found that supplementing 9 $mol \cdot m^{-2} \cdot d^{-1}$of either lighting regiment led to an approximately 33% increase in fruit weight ($kg \cdot m^{-2}$) and a similar increase in fruit number.

Pythium and Brix

The average soluble sugars (Brix) per fruit was significantly higher in the 25 $mol \cdot m^{-2} \cdot d^{-1}$ treatment with the trend of decreasing Brix with treatments that had higher yields of fruit fresh/dry weight. One of the possible causes of this trend is osmotic stress induced by the presence of pythium in the rootzone of these plants. The plants in the 25 $mol \cdot m^{-2} \cdot d^{-1}$ treatment were more broadly affected by the symptoms of pythium, which is reflected in the lower yield when compared to the other light treatments. As a result of decreased stomatal conductance and transpiration, less water accumulation occurs within the fruit, leading to a lower FW:DW ratio and, consequently, a fruit with a higher concentration of soluble solids. This hypothesis is supported by a study that evaluates drought stress on sugar accumulation in satsuma mandarin fruit, which concludes that fruit mass and the content of sucrose within the fruit are inversely

related, with plants exposed to increasing levels of drought expressing a reciprocating increase in sugar (Yakushiji et. al., 1998).

Chapter 2 Experiment Evaluation

In this experiment, there were a series of factors that affected the outcome of the experiment. One of the issues discussed previously was the age of the plants, with plants having existed within the same production system for seven months prior to the start of the experiment. As a result of the advanced age prior to the start of the experiment, the plants and growing systems within the greenhouse were exposed to increased irradiance and temperature, increasing the stress on the plants and allowing to the opportunistic pathogen pythium to exploit the rootzone of the tomato plants. Although curative measures were taken to treat the pathogen, the prevalence of decaying roots and increased moisture resulted in the continued reoccurrence of pythium and a decrease in the vigor of the tomato plants. In hindsight, if time would have allowed, I would have repopulated the treatment greenhouses with a new series of tomato plants following appropriate sanitization measures as well as delaying the experiment to begin in the fall and run into the winter months to take advantage of lower irradiance and temperatures.

If disease is encountered in future experiments, I would recommend addressing this as a variable in the statistical model (i.e. develop a quantitative measure for disease severity that could be used to correlate disease to yield).

Conclusion

From the results of our experiment, we did not find any significant differences between the treatments in each of the photosynthetic parameters, although we did see a significant

decrease in the maximum average net photosynthesis between the first and last measurements of all treatments minus the 25 $mol \cdot m^{-2} \cdot d^{-1}$ greenhouse. Although not statistically significant, there was also a pattern whereby the rates of transpiration and stomatal conductance decreased as the length of treatment increased. This relationship of decreasing measurement values over time can be related to a variety of factors that adversely affected the tomato plants, which included the overall plant age, increased exposure to higher irradiance and greenhouse temperatures during the summer months, and the subsequent exposure to the root-borne pathogen *Pythium*.

Biomass parameters also saw a decrease over the duration of the experiment, with a significant decrease in the number of clusters, total average fruit and truss weight, average first fruit fresh weight, and average first fruit dry weight on average across all four treatments. Within these same parameters, plants exposed to 25 $mol \cdot m^{-2} \cdot d^{-1}$ performed significantly worse than the 20 and 30 $mol \cdot m^{-2} \cdot d^{-1}$ treatments, although this trend was reversed when evaluating Brix, which may be attributed to a lower FW:DW ratio and a subsequently higher percentage of soluble solids. There was a positive trend between an increasing DLI and yield parameters, with the 20 and 30 $mol \cdot m^{-2} \cdot d^{-1}$ treatments having a significantly higher total average fruit and truss weight and average first fruit fresh weight than the 15 $mol \cdot m^{-2} \cdot d^{-1}$ treatments. Due to limitations created by the previously stated issues that occurred during this experiment, corrections can be made in future experiments to ensure young, healthy plants are being evaluated. The methodology described in this experiment can be beneficial for future studies evaluating the interaction of DLI.

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