



# **The Functioning of Tomato Leaf Stomata and Water Uptake in a Hybrid-lit Greenhouse**

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Tämän opinnäytetyön tavoitteena oli tutkia ilmarakojen toimintaa, haihduntaa ja kalsiumin kulkeutumista tomaatinviljelyssä hybridivalaistuksessa, keskittyen erityisesti kalsiumin puutteen oireisiin, kuten lehtien kalsiumin puutosoireisiin ja latvamätään (blossom-end rot, BER). Työn toimeksiantajana toimi Signify, ja se toteutettiin yhteistyössä Hämeen ammattikorkeakoulun (HAMK) kanssa Lepaan kampuksen kasvihuoneessa.

Tutkimuksen taustalla on haihdunnan keskeinen merkitys ravinteiden kuljetuksessa, sillä kalsium on liikkumaton ravinne, jonka otto riippuu nestevirtauksesta. Tutkimuksessa kerättiin tietoa höyrynpaine-erosta (vapour-pressure deficit, VPD), nestevirtauksesta, ilmaraoista, vedenotosta ja kalsiumpitoisuudesta Aranetin antureilla, porometrillä ja lehtikuvien analyysillä.

Tulokset osoittivat, että kalsiumin puute ei johtunut vähentyneestä vedenotosta, vaan epätasaisesta nestevirtauksesta kasvissa. Lämmitysputket nostivat höyrynpaine-eroa alemmassa kasvustossa, mikä ylläpiti haihduntaa siellä ja näytti rajoittavan kalsiumin kulkeutumista ylempiin lehtiin. Hybridivalaistus vaikutti haihduntaan suurpainenatriumlamppujen lämpösäteilyn kautta. Kellastumisoireet olivat yleisiä, kun taas latvamätää esiintyi harvoin, ja kokonaissadon laatu säilyi hyvänä.

Johtopäätöksenä voidaan todeta, että kalsiumin puutetta tomaatilla luultavasti aiheuttaa ensisijaisesti epätasainen haihdunnan jakautuminen, ei kokonaisvedenoton määrä. VPD:n ja nestevirtauksen seuranta voi auttaa viljelijöitä ennakoimaan ongelmia, ja ilmastosäätelyn keinot, kuten kosteuden hallinta, voivat vähentää kalsiumiin liittyviä kasvuhäiriöitä kaupallisessa viljelyssä.

Avainsanat Tomaatti, haihdunta, kalsium

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Abstract

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The aim of this thesis was to examine stomatal function, transpiration, and calcium transport in tomato cultivation under hybrid lighting, with a focus on calcium deficiency symptoms such as tip-burn and blossom-end rot (BER). The work was commissioned by Signify and carried out in collaboration with Häme University of Applied Sciences (HAMK) at the Lepaa campus greenhouse.

The study was motivated by the role of transpiration in nutrient transport, as calcium is an immobile element whose uptake depends on sap flow. Data on vapour-pressure deficit (VPD), sap flow, stomatal conductance, water uptake, and calcium concentration were collected using Aranet sensors, a porometer, and leaf image analysis.

The results showed that calcium deficiency was not caused by reduced water uptake but by uneven sap flow within the plant. Heating pipes increased VPD in the lower canopy, maintaining transpiration there while limiting calcium flow to the upper canopy. Hybrid lighting also affected transpiration through the heat radiation of HPS lamps. Tip-burn was common, whereas BER was rare, and overall yield quality remained good.

The study concludes that imbalanced transpiration distribution, rather than total water absorption, probably drives calcium deficiency in tomato. Monitoring VPD and sap flow can help growers anticipate problems, while climate control strategies such as humidity management or dehumidification can reduce calcium-related disorders in commercial cultivation.

Keywords: Tomato, transpiration, calcium

Pages 27 pages

# Table of Contents

1	Introduction .....	1
2	Theoretical Background .....	3
2.1	Tomato Growing Conditions .....	4
2.2	Transpiration and Transport of Nutrients in Tomato Plants.....	5
2.3	Calcium Deficiency, Tip-burn, and Blossom-End Rot .....	5
2.4	Stomata in Tomato.....	6
3	Materials and Methods.....	7
3.1	Research Design and Location .....	8
3.2	Measurement Methods .....	9
3.2.1	Water Uptake & Sap Flow.....	9
3.2.2	Stomatal Activity .....	10
3.2.3	Leaf Pictures and Data .....	11
3.2.4	Temperature and Humidity .....	11
3.3	Data Collection and Analysis.....	12
4	Results.....	13
4.1	Total Leaf Area and the Extent of Yellowing.....	13
4.2	Stomatal Activity and Sap Flow.....	15
4.3	Transpiration and Calcium Concentration in the Leaves .....	16
4.4	Lighting .....	19
4.5	Yield Quantity and Quality.....	20
5	Discussion and Conclusions .....	21
5.1	Transpiration.....	21
5.2	Practical Application of Data in Cultivation .....	22
5.3	Hybrid Lighting in Cultivation.....	23
5.4	Limitations of Study and Suggestions for Future .....	23
6	Summary .....	24
	Sources .....	25

## **Kuvat, taulukot ja kaavat**

Figure 1. Sap Flow Sensor Provided by Aranet (Esa Holopainen, 2025).....	10
Figure 2. Total Leaf Area vs. Tip-burn Area 4.9.2024–11.1.2025.....	13
Figure 3. Leaf Sample from 2.10.2024 (Esa Holopainen, 2024a).....	14
Figure 4. Leaf Sample With Tip-burn from 11.12.2024 (Esa Holopainen, 2024b).....	15
Figure 5. VPD and Sap Flow During a 24h Period Showing Close Correlation Between VPD and Sap Flow.....	16
Figure 6. Water Uptake Per Day Per Plant.....	17
Figure 7. VPD in the Lower and Top Canopy During the Experiment.....	18
Figure 8. Average Stomatal Conductance between September and November in Different Canopy Levels.....	18
Figure 9. Calcium Concentrations in Leaf Analyses During the Experiment.....	19
Figure 10. Weekly Tomato Yield from September to April.....	20

## **Vocabulary**

Blossom-end rot (BER) – Nutritional disorder of Solanaceae fruits, caused by calcium deficiency.

Gas exchange – The process where plants take in CO<sub>2</sub> for photosynthesis and release oxygen and water vapour through stomata.

High-pressure sodium (HPS) lamp – A traditional greenhouse lighting system that emits broad-spectrum light and produces heat.

Hybrid lighting – Combined use of LED and HPS lighting.

Microclimate – A localized atmospheric environment that differs from the surrounding conditions, sometimes only slightly but in some cases quite substantially.

PAR – Photosynthetically active radiation. Wavelengths between 400–700 nanometres, which plants can utilise in photosynthesis.

Radiation intensity – The strength of light energy from artificial or natural sources that influences plant growth.

Sap flow – The flow of water and nutrients within the stems, branches and roots.

Stomata (sing. stoma) – Microscopic pores on leaves that are responsible for gas exchange.

Tip-burn – A disorder that causes yellowing of the leaves; a symptom of calcium deficiency.

VPD – Vapour-pressure deficit. The difference between the air's saturation point (the maximum water vapour it can hold) and its actual water vapour content, expressed in kilopascals (kPa).

# 1 Introduction

In Finland, tomato (*Solanum lycopersicum* L.) is the most important greenhouse crop, with a national yield of 41 million kilograms in 2024 (Luke, 2025, p. 1). Due to the northern latitude and long winters, Finnish tomato cultivation relies heavily on greenhouse technology to enable production during winter months. Artificial lighting, heating, and carbon dioxide supplementation are applied to maintain yield and fruit quality. Light-emitting diode (LED) technology has transformed greenhouse horticulture, replacing or supplementing traditional high-pressure sodium (HPS) lamps. Greenhouses in Finland are generally moving towards LED lighting systems, replacing older, less efficient HPS lights. This can lead to greenhouses with a hybrid lighting system, as the HPS lights are gradually replaced with LED lighting. These changes in greenhouse technology not only influence energy efficiency but also directly affect plant physiology. Light quality and intensity shape fundamental processes such as photosynthesis, transpiration, and nutrient transport. Stomatal function is highly responsive to environmental conditions within the greenhouse. Consequently, disruptions in stomatal function or transpiration can impair calcium transport, which is strongly associated with disorders like blossom-end rot (BER) in tomatoes (White, 2003, pp. 487–488). This disorder is a persistent concern in Finnish greenhouse production, where calcium deficiency in rapidly growing tissues is suspected to be a major cause.

This thesis investigates the effects of greenhouse environmental conditions on stomatal function and transpiration, as well as the occurrence of blossom-end rot in a hybrid-lit greenhouse during the lighting season. The study examines the climate conditions, plant's water uptake, stomatal function, and their combined impact on blossom-end rot occurrence, total yield, and crop quality. Additionally, the goal is to provide growers with examples of how they can use sensor-generated data in their operations.

This study seeks to answer the following research questions: (1) to determine whether or not there is a connection between the occurrence of blossom-end rot in tomatoes and insufficient calcium transport to the plant's crown, (2) to identify the most significant environmental factors affecting stomatal opening and closing in a hybrid-lit greenhouse during the growing season, and (3) to

observe how fluid (sap) flow differs between the lower and upper parts of the tomato plant in such an environment, revealing insights into plant transpiration.

The study was conducted in collaboration with Häme University of Applied Sciences (HAMK), where the experiment took place in the Lepaa campus greenhouse, Aranet, which provided the necessary sensors, and Signify, the commissioning company of this project. Aranet is a technology company that specializes in wireless monitoring. Aranet designs, develops, and manufactures its own products, such as sensors, base stations, and software platforms. Signify (formerly Philips Lighting) is a Dutch-based corporation and an industry leader in lighting technologies. Signify offers products and IoT services to consumers and professionals.

## 2 Theoretical Background

Tomato (*Solanum lycopersicum* L.) is one of the most familiar and commonly cultivated vegetables in greenhouses in the world. In 2023, global production reached nearly 190 million tonnes, making the tomato one of the leading vegetable crops worldwide (FAOSTAT, 2023, p. 1). Tomatoes are grown across diverse climates and production systems, ranging from open-field cultivation to high-tech greenhouses. Tomatoes contain essential vitamins (A, C, and K), minerals, and bioactive compounds, namely lycopene, an antioxidant. (Salehi et al., 2019, p. 202)

This literature review provides an overview of physiological and environmental factors affecting tomato cultivation, and it examines key aspects of greenhouse tomato growing, transpiration, nutrient transport, calcium deficiency, tip-burn, and blossom-end rot. This chapter also discusses VPD as a driving force behind stomatal activity and VPD's relation with the aforementioned factors. Emphasis is placed on how temperature, humidity, and light shape the canopy microclimate and affect stomatal activity and calcium transport through transpiration. These factors determine the rate of water loss from the leaves, which in turn influences the water flow and nutrient transport through the xylem.

Previous studies have shown that calcium deficiency and related disorders (tip-burn, BER) are primarily linked to environmental factors that influence stomatal behaviour and transpiration, including temperature, humidity, radiation intensity, and vapour-pressure deficit (VPD). Together, these factors govern water flow in the plant and thus determine calcium distribution across the canopy. Given that microclimatic variation may disrupt sap flow between canopy layers and cause uneven calcium allocation, this study focuses on examining the environmental and physiological parameters most strongly associated with calcium transport and related disorders, including VPD, sap flow, and stomatal activity.

The theoretical background in this thesis consists mainly of peer-reviewed studies published within the past decade, with a focus on the latest studies, supported by technical reports concerning commercial tomato production. While most recent sources provide credible and up-to-date findings, some earlier publications (e.g. White, 2003; Saure, 1998) were included to provide foundational understanding regarding calcium transport and other relevant

topics. Sources were critically evaluated, with emphasis placed on peer-reviewed and academically credible publications.

## 2.1 Tomato Growing Conditions

The tomato (*Solanum lycopersicum* L.) is an herbaceous plant that belongs to the Solanaceae family. It has a chromosome number of  $2n = 24$  (Wu & Tanksley, 2010, p. 1). Other members of the nightshade family include, for example, pepper, eggplant, and potato. The ideal daytime temperature range in tomato cultivation is between 21 and 27°C and the optimal nighttime temperature is 17 to 18°C (Bayer, 2019, p. 1). Tomato responds to temperature changes and elevated temperatures are known to have a negative effect on tomato yield. Fruit set in tomatoes decreases at temperatures above 35°C (Ro et al., 2021, p. 2). Studies have shown that peak net photosynthesis rate for tomato was achieved in light conditions of 300–450  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , with 300  $\mu\text{mol m}^{-2} \text{s}^{-1}$  being most energy efficient (Fan et al., 2013, p. 54). Tomato benefits from CO<sub>2</sub> enrichment up to a saturation point of 1000–1300 ppm, seedlings needing slightly lower levels of 800–1000 ppm (Ministry of Agriculture, Food and Agribusiness, 2022, p. 1). Tomato needs a balanced supply of macro- and micronutrients for optimum growth and yield. Nitrogen, phosphorus, and potassium are the most important, phosphorus for root development, and a high potassium supply to support fruit quality. Calcium and magnesium are also essential to prevent disorders such as blossom-end rot, while micronutrients like boron, iron, and zinc should be added only if deficiencies occur (Sainju et al., 2003, p. 1–4). Nitrogen over-fertilization in tomato causes excessive leaf growth that competes with fruits for calcium (Joy & Hudelson, 2024, p. 1).

Far-red light (700–800 nm) increased tomato yield, while not affecting fruit quality (Vincenzi et al., 2024, p. 11). The study found that yield increased with the far-red light illumination and that far-red light increased yield as effectively as PAR light. However, Ji et al. (2019) observed that far-red treatment caused more severe leaf damage, which may reduce the tomato plant's resistance to powdery mildew. VPD for tomato was found to be the most sensitive indicator of stem sap flow in the fall–winter period, while light was the primary indicator in the spring–summer period (Mao et al., 2017, p. 412). VPD is the main factor in

regulating stomatal behaviour and can, in theory, be used to predict plants' irrigation needs (He et al., 2024, p. 614–618).

## 2.2 Transpiration and Transport of Nutrients in Tomato Plants

In transpiration, water is transported in the plant, from the roots to leaves to the atmosphere through stomatal pores. This water movement is caused by root pressure, along with the water potential difference between leaves and external air. As water evaporates, it leaves behind tension which pulls water upward through the xylem. Transpiration plays a role in many plant activities, including cooling down the plant, and driving nutrients from the roots through xylem to leaves and flowers (Sharma, 2024, p. 1). External factors such as VPD, temperature and light intensity affect transpiration. A high VPD raises the water content difference between the air and the leaf, driving water loss and thus calcium movement in the plant (Yu et al., 2022, p. 1).

Tomato crops develop dense canopies that create distinct microclimates within the growing space. Temperature, humidity, light intensity, and air circulation differ between canopy levels and position in the greenhouse. Šalagovič et al. (2024, p. 1) showed that sensors installed in the canopy uncovered microclimatic gradients, with temperature differences up to 3°C and vapour-pressure deficit differences up to 0.6kPa in a commercial greenhouse. Jerszurki et al. (2021, pp. 1, 8) state that the microclimate heterogeneity inside a greenhouse is largely unknown, yet it can influence yield and plant production. It was further found that while air temperature exhibited considerable vertical variation, leaf temperature gradients were much smaller, reflecting the plant's capacity to regulate its own temperature.

## 2.3 Calcium Deficiency, Tip-burn, and Blossom-End Rot

Calcium is important in maintaining cell walls, particularly in shoot tips, young leaves and developing fruits (White, 2003, pp. 487–489). In tomato fruits, calcium is needed in sufficient concentrations during cell expansion stages to stabilize pectins to prevent cell wall collapse. Because calcium is an immobile nutrient in the phloem, it cannot be redistributed by the plant. Calcium is transported in water within the plant, so the amount of calcium transported is

directly related to the amount of sap flow in the plant. Insufficient calcium in tomato causes blossom-end rot (BER) in fruits and in leaves it manifests as yellowing (tip-burn) (Saure, 1998, pp. 131–132; Joy & Hudelson, 2024, p. 1). (Hocking et al., 2016, pp. 6, 12)

Fruits affected by BER are characterised by lesions at the bottom of the fruit that later darken. This disorder appears during the cell expansion stage when calcium needs peak. BER often starts to manifest when fruits are very small, under a few millimetres in diameter. Young fruits are very susceptible to BER since they grow at a fast rate. Since transpiration is stronger in leaves than in fruits, calcium uptake is prioritised toward foliage, causing the blossom end of fruits to be deficient in calcium. (Shrefler, n.d., p. 1)

## 2.4 Stomata in Tomato

Stomata are miniscule pores on the plant leaves through which the plant absorbs carbon dioxide and releases moisture in the form of water vapour. The state of the stomata depends on several factors, such as air and leaf temperature, humidity in the growing environment, radiation intensity, and the physiological needs of the plant. In tomato cultivation, high radiation intensity can trigger stomatal closure (O’Carrigan et al., 2014, p. 68). When stomata are open, evaporation from the leaf builds negative pressure which then draws water from the roots through capillary action, simultaneously transporting dissolved nutrients. Among these, as an immobile nutrient calcium is particularly dependent on the transpiration stream for distribution within the plant.

Stomata control almost all gas exchange in plants. They regulate the plant's CO<sub>2</sub> uptake for photosynthesis, and by opening and closing, they decrease or increase the plant's transpiration. By regulating gas exchange, the plant aims to balance photosynthetic activity and water loss (Harrison et al., 2019, p. 769). Environmental factors like humidity, light intensity, temperature and CO<sub>2</sub> concentration affect the functioning and development of tomato stomata (Driesen et al., 2020, p. 14).

Driesen et al. (2020, p. 22) uncovered that light intensity correlates with the quantity of stomata. In the study, it was observed that increasing light intensity

leads to a higher number of stomata in tomato plants;  $50 \mu\text{mol m}^{-2} \text{s}^{-1}$  of PAR light resulted in 1,109 stomata/ $\text{mm}^2$ , whereas an intensity of  $550 \mu\text{mol m}^{-2} \text{s}^{-1}$  produced 1,604 stomata/ $\text{mm}^2$ . O’Carrigan et al. (2014, pp. 68–69) found that high light intensity reduces stomatal aperture width. High air humidity was found to increase both stomatal density and length (Driesen et al., 2020, p. 18).

Since calcium is transported with water in plants, low transpiration due to high relative humidity can cause calcium deficiency, which causes blossom-end rot. Blossom-end rot is commonly found in humid conditions, since high relative humidity causes stomatal closure and malfunctioning (Carvalho et al., 2015, p. 1). Relative humidity directly affects VPD. VPD provides a more accurate measure of evaporative demand of the plant, since VPD regulates stomatal opening (Merilo, 2018, p. 857). Light intensity influences both stomatal development and aperture width, high irradiation causing stomatal closure (O’Carrigan et al., 2014, pp. 68–69). Stomatal closure in reaction to high irradiation can be thought of as a water saving response in which the plant is trying to conserve water on hot days.

### **3 Materials and Methods**

This chapter provides information about materials and methods, such as research design and location, various measurement methods, data collection, and sensors used in the experiment. The aim was to connect environmental conditions in a greenhouse to transpiration, stomatal behaviour, and calcium transport. The section focuses on how the experiment was conducted at a commercial-style greenhouse, discussing monitoring of environmental factors including temperature, relative humidity, VPD, and light intensity.

Parameters such as sap flow, stomatal conductance, and leaf calcium concentration were studied. Automatic sensor data and manual measurements were used to assess the microclimatic variations in different canopy levels. This chapter also discusses sensors and instruments used in the experiment as well as the schedule and frequency of measurements.

### 3.1 Research Design and Location

This study was conducted as an exploratory observational experiment in a commercial-style greenhouse at Häme University of Applied Sciences (HAMK), Lepaa campus between November 2024 and February 2025. No control group was used in this study due to cost constraints; instead, data were interpreted relative to environmental changes and physiological responses within the monitored plant. Because the sensors were prohibitively expensive, only one set was used.

Key physiological and environmental factors were continuously monitored using Aranet sensors. Data collected included: irrigation input, amount of drain water, temperature, relative humidity (RH), leaf surface area, temperature, and sap flow, stomatal conductance, measured in both the upper and lower canopy. A time series dataset was created from the data produced by sensors and the porometer, which was then compared to the surrounding environmental conditions. Data collected from the greenhouse environment by the Priva system was used in conjunction with data gathered by Aranet sensors. The greenhouse used hybrid lighting:  $280 \mu\text{mol m}^{-2} \text{s}^{-1}$  from top LED lighting and  $90 \mu\text{mol m}^{-2} \text{s}^{-1}$  from LED interlighting. The intensity of the HPS (high-pressure sodium) lighting was  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Total light intensity was  $470 \mu\text{mol m}^{-2} \text{s}^{-1}$ , not including natural light, amount which was negligible during the experiment. Photoperiod was set to 16/8. DLI (daily light integral) not including natural light was  $27 \text{ mol m}^{-2} \text{ day}^{-1}$ . Temperature levels were set at  $23\text{--}24^\circ\text{C}$  during the day and at  $18^\circ\text{C}$  at night. The greenhouse is equipped with heating pipes, which had notable effects on canopy temperature and humidity levels. The greenhouse has a  $\text{CO}_2$  enrichment system that was set on 1,000 ppm during daytime hours.

The observed plant was changed twice a month as plants did not stay fixed in the same spot. Plants were lowered and repositioned every other week as part of routine greenhouse operations. The individual stems and leaves varied over time, affecting test results and introducing variability. To minimise this, measurement methods were standardised to ensure comparability between observations. The studied variety was 'Encore' and the planting density used was  $2.5 \text{ plants/m}^2$ .

## 3.2 Measurement Methods

This chapter examines the range of methods employed in this experiment. Data collection on environmental conditions, water uptake, stomatal activity, leaf size, yellowing and sap flow is discussed. These methods provided a comprehensive picture of how greenhouse climate interacts with tomato physiology, enabling continuous monitoring and detailed analysis of the data gathered. This chapter also discusses the sensors and instruments used in the experiment.

In this experiment, infrared, temperature/humidity, and sap flow sensors, along with a porometer, were used for data collection. The process relied on both automated sensor readings and manual measurements to ensure accurate interpretation. Infrared sensors, temperature/relative humidity sensors, sap flow sensors, and a porometer formed the core of the measurement system. These devices enabled the monitoring of the microclimate at different canopy levels. Data from the Aranet sensors and the greenhouse's Priva system complemented each other and were cross-checked for accuracy.

### 3.2.1 Water Uptake & Sap Flow

Water uptake was determined by calculating the difference between the amount of water given to the plants and the amount of drainage water. Water uptake was recorded by the Priva greenhouse control system, while drainage was collected and measured by the greenhouse staff. Continuous tracking of water uptake helped to determine whether calcium deficiency symptoms could be linked to insufficient water absorption.

Sap flow was measured using two sap flow sensors supplied by Aranet, one in the top canopy and other in the lower canopy. Sap flow sensors operate using the thermal dissipation method, in which the sensor is equipped with a heater and thermistors. Heater and thermistors are housed in a collapsible, heat-insulating cylinder (Figure 1). Upper and lower thermistors detect the temperature difference caused by the flow of sap and it is then interpreted in the system to estimate the rate of sap flow.

Figure 1. Sap Flow Sensor Provided by Aranet (Esa Holopainen, 2025).



The placement of sap flow sensors was determined by the number of fully developed leaves from the top and bottom of the plant. The fifth leaf from the top and the fifth leaf from the bottom were selected to represent the upper and lower canopy, respectively. The sap flow sensors recorded measurements at one-minute intervals.

### 3.2.2 Stomatal Activity

Stomatal conductance measurements were recorded with a hand-held SC-1 porometer (Decagon Devices, USA), which was used weekly between 8 and 9 a.m. In addition, the leaf porometer was also used to measure stomatal activity for two hours before and after the lights were switched on and off. The device measures stomatal conductance, which describes the rate that water vapour exits through the stomata, expressed in  $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ . These readings

provide a clear and direct indication of the plant's gas exchange under varying environmental conditions.

To measure variation in stomatal conductance between plant canopy levels, leaves were selected from the upper, middle, and lower canopy levels. At each measurement time, a leaf from a different canopy level was selected, to provide readings from all canopy levels at approximately the same time. This procedure was repeated over a two-hour period, timed to coincide with the switching on and off the lights. Another more often used measurement approach was to measure stomatal conductance from only the lower and upper canopy of the plant. The fifth fully developed leaf from the top represented the upper canopy, and the fifth leaf from the bottom represented the lower canopy.

### **3.2.3 Leaf Pictures and Data**

Leaf condition was documented on a weekly basis by photographing selected leaves and analysing the images digitally. Purpose of this method was to provide a way to monitor the calcium deficiency symptoms, particularly tip-burn and other yellowing and browning of the leaves. The data was then compared with environmental measurements (VPD, temperature, humidity) and physiological variables (sap flow, stomatal conductance, leaf calcium content).

Five plants were chosen randomly in the greenhouse for leaf pictures. All leaf photographs were taken from the upper canopy, specifically from the fifth fully expanded leaf below the plant top. This leaf position was chosen because calcium deficiency symptoms typically appear first in young leaves, where the demand for calcium is high. Focusing on a single leaf position across the measurement period allowed comparing data between weeks to reveal trends in the development of calcium deficiency symptoms.

### **3.2.4 Temperature and Humidity**

Temperature and humidity were continuously monitored to assess the microclimate conditions within the canopy levels and to calculate VPD, which is a key factor in stomatal activity and transpiration. Data were then analysed and compared with physiological observations and measurements, such as sap flow and stomatal conductance.

An Aranet infrared sensor was utilised to measure leaf temperature in upper and lower canopy. IR-sensors were set so that they were pointing at the leaves. Aranet T/RH (temperature/relative humidity) IP67 sensor was used to measure temperature and humidity in upper and lower canopy. T/RH sensors were placed on the same level with sap flow and IR sensors. Canopy levels were determined based on leaf count, and the instrument sets were placed on the level of the fifth leaf from the top and on the fifth leaf from the bottom. The sensors provided reading at one-minute intervals, which were transmitted to the Aranet Cloud platform. The collected data were cross-checked with values from greenhouse's Priva climate system to ensure consistency and reliability.

### **3.3 Data Collection and Analysis**

All sensor data (temperature, relative humidity, sap flow, and leaf temperature) were collected in 1-minute intervals and then timestamped and logged into Aranet Cloud. Before analysing, raw data were checked for anomalies, such as missing values, sensor dropouts, errors, and outliers like sap flow spikes. Unreliable data were identified through inspection and removed. Data from Aranet Cloud and Priva were synchronized, and a cross-analysis on sensor and porometer data was performed.

To assess variability between plant canopy levels (upper and lower), data were organized accordingly. Differences in sap flow, temperature, relative humidity, and VPD were analysed between these canopy levels to test the hypothesis of insufficient calcium transport to the upper canopy. Porometer measurements were timed so that stomatal activity was measured for 4 hours when the lights were turned on and off, taking measurements alternating between top and bottom canopy. Porometer measurements in the day were taken from up to down, with every leaf measured. Porometer measurements were then categorized as upper, middle, or lower leaf readings to analyse stomatal activity in different plant parts. Leaf images were compiled and then processed using ImageJ software for measurement of leaf area and tip-burn affected area. Visual symptoms like tip-burn and yellowing were compared with sensor data and leaf analysis data to determine causality.

## 4 Results

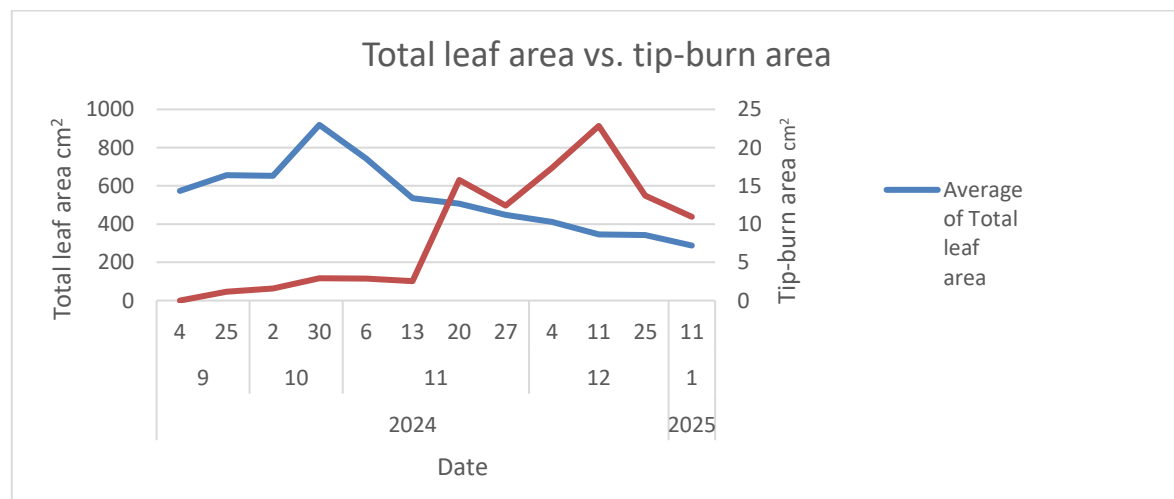
The following chapter summarizes the study's primary findings, based on the research questions and measurement objectives. The results cover changes in leaf area and yellowing, stomatal activity and sap flow patterns, transpiration and calcium concentration, lighting effects, and yield quantity and quality. Data are shown in figures and tables, with focus on differences between canopy levels and trends observed during the experiment.

The results are presented according to major physiological and environmental parameters to illustrate how the plants responded to changes in microclimatic conditions. Trends in environmental parameters and plant physiological responses were observed during the measurement period, which allows for comparison across different stages and canopy levels.

### 4.1 Total Leaf Area and the Extent of Yellowing

Yellowing of the leaves was observed from September to the end of the measurement period at the end of January. The data collected show that total leaf area had a descending trend throughout the experiment, conversely leaf area affected by tip-burn increased during the experiment (Figures 2–4).

Figure 2. Total Leaf Area vs. Tip-burn Area 4.9.2024–11.1.2025.



Leaf imaging revealed clear changes in both total leaf area and the proportion of yellowed or tip-burned tissue over the course of the experiment. At the

beginning of the experiment in September, the leaves appeared mostly healthy, and the affected area was minimal. As the measurement period progressed, the proportion of damaged tissue increased steadily while the overall leaf area began to decline.

Figure 3. Leaf Sample from 2.10.2024 (Esa Holopainen, 2024a).



The photographs show that symptoms gradually worsened over time. The most severe development of tip-burn symptoms occurred in November–December, when the extent of yellowing increased by more than nine-fold compared to September–October. These observations are consistent with earlier findings in the literature, which describe calcium immobility as a key factor leading to deficiency symptoms first appearing in young leaves.

Figure 4. Leaf Sample With Tip-burn from 11.12.2024 (Esa Holopainen, 2024b).



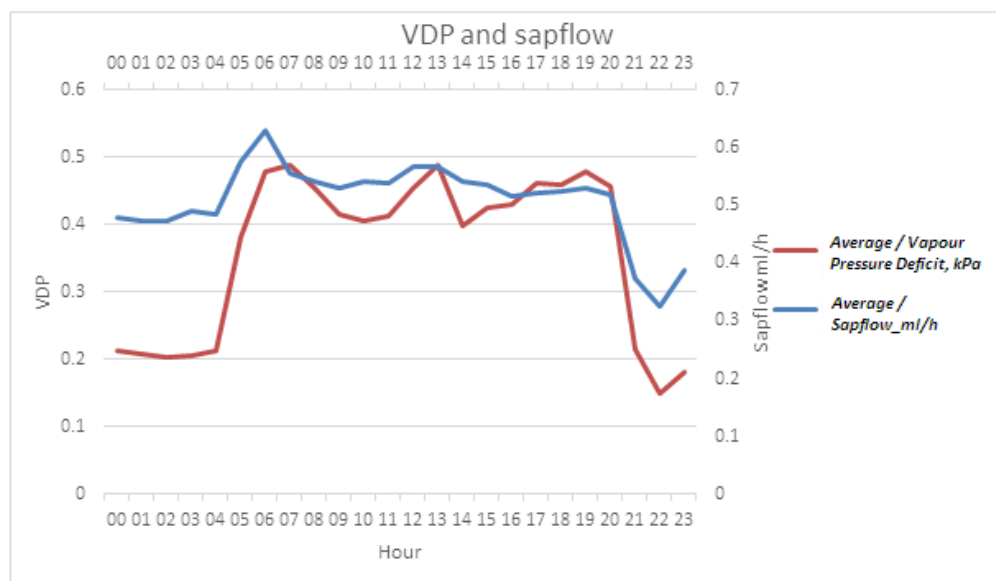
This sharp rise coincided with the period when vapour-pressure deficit (VPD) was higher in the lower canopy than in the upper canopy (Figure 7). In December and early January, the relative severity of tip-burn symptoms decreased by nearly half, despite a continuing decline in total leaf area.

## 4.2 Stomatal Activity and Sap Flow

Stomatal activity and sap flow data showed a strong connection to VPD, confirming its central role in regulation gas exchange and transpiration. Both porometer measurements and sap flow data indicated that increase in VPD led to proportional increase in transpiration (Figure 5). The lower canopy exhibited consistently higher stomatal conductance and sap flow compared to the upper canopy. Porometer data provided direct evidence of stomatal activity at the leaf

level. Measurements carried out during stable morning conditions showed that stomatal conductance in the lower canopy was on average 20–30% higher than in the upper canopy. This suggests that microclimatic conditions near the heating pipes promoted greater water loss in the lower canopy. Porometer measurement sessions around lighting transitions revealed clear changes: when HPS lights were turned on, stomatal conductance rose rapidly in the upper canopy, while turning them off led to an immediate decline in conductance and sap flow.

Figure 5. VPD and Sap Flow During a 24h Period Showing Close Correlation Between VPD and Sap Flow.



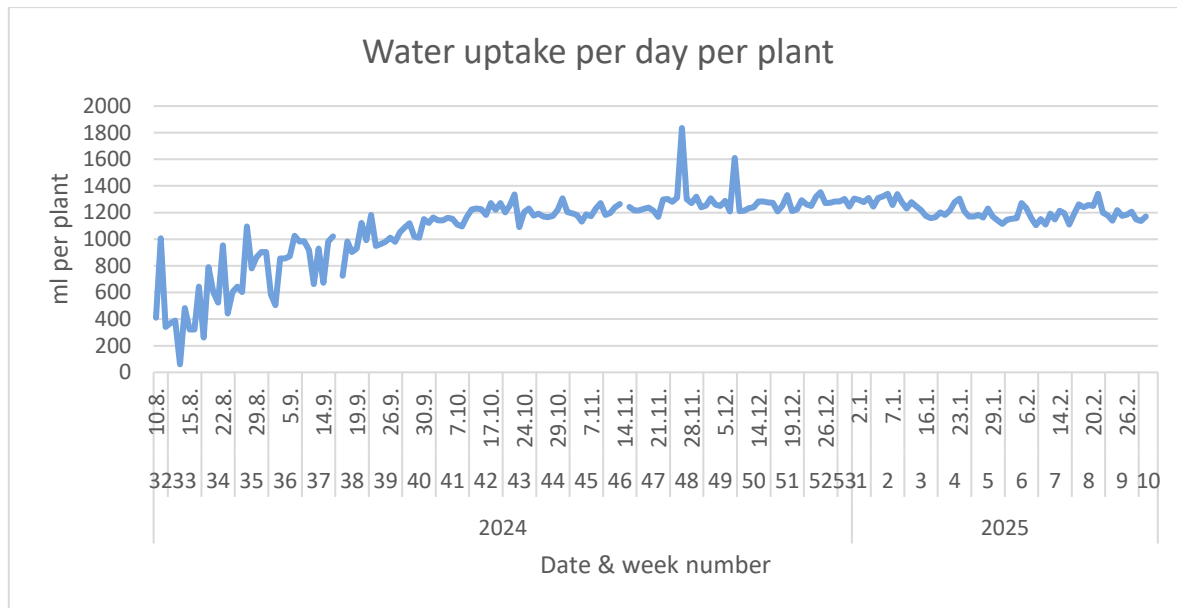
Sap flow sensors confirmed these patterns. Throughout the experiment, sap flow in the lower canopy remained stronger, even at night. This is most evident in November and December, when the heating pipes were on, increasing lower canopy temperatures and thus the local VPD. As a result, transpiration continued overnight in the lower canopy, while the upper canopy experienced restricted sap flow.

### 4.3 Transpiration and Calcium Concentration in the Leaves

Total water uptake did not fluctuate significantly during the season (Figure 6), showing that calcium deficiency is not caused by plants absorbing less water and thus less calcium. Instead, this observation supports the hypothesis that

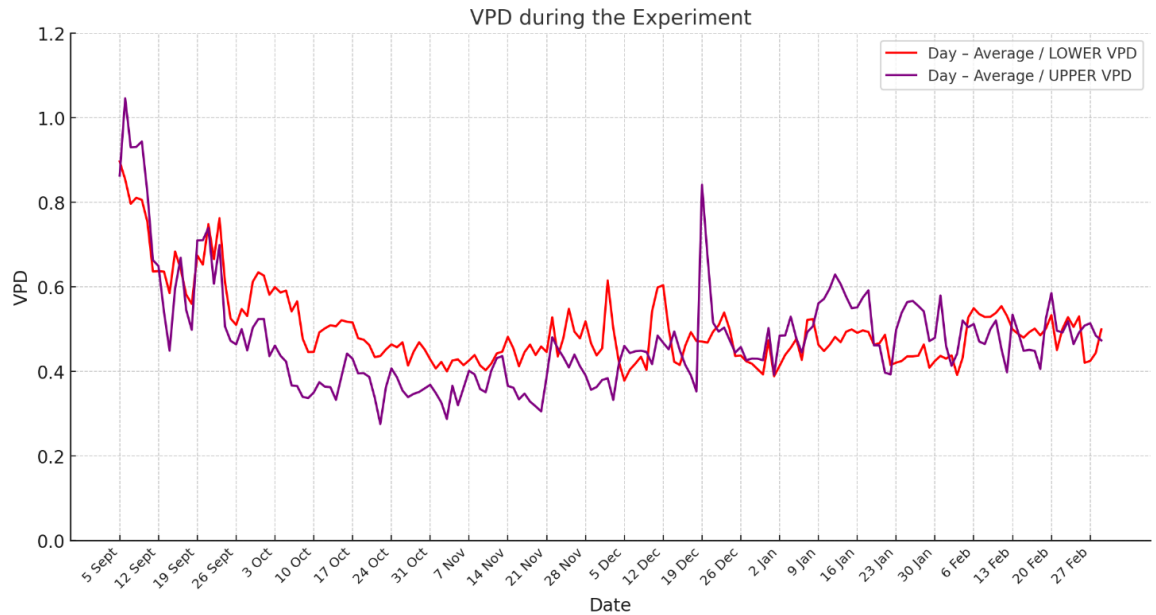
calcium deficiency and tip-burn symptoms are caused by uneven distribution of water and nutrients within the plant.

Figure 6. Water Uptake Per Day Per Plant.



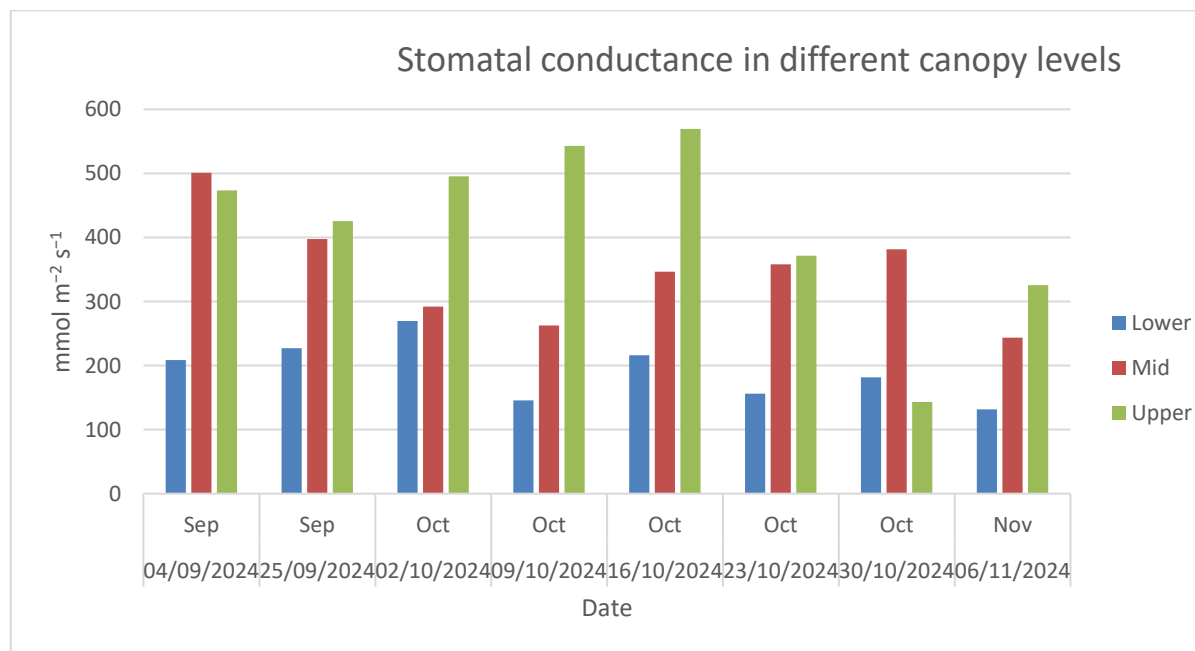
Different canopy levels of the plant varied greatly in stomatal conductance during the experiment, with the upper canopy exhibiting the highest conductance from September through mid-October (Figure 8). After this period, stomatal conductance in the upper canopy declined significantly. Meanwhile, stomatal conductance in the lower canopy remained relatively stable and from November onward exceeded that of the upper canopy.

Figure 7. VPD in the Lower and Top Canopy During the Experiment.



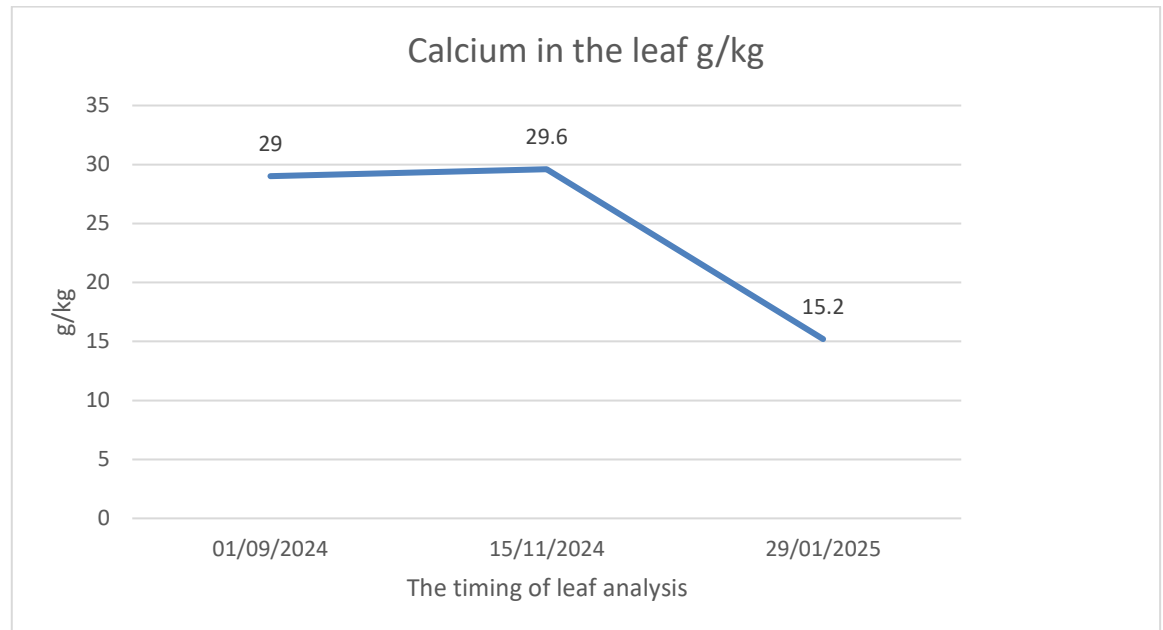
This indicates that transpiration concentrated in the older, lower canopy leaves. The decline in the upper canopy conductance coincided with the period when tip-burn symptoms intensified. Continuous activity of the lower canopy, particularly during night-time due to heating pipes, maintained sap flow towards older tissues, seemingly inhibiting sap flow and thus, calcium to the upper canopy.

Figure 8. Average Stomatal Conductance between September and November in Different Canopy Levels.



Leaf analysis showed that the concentration of calcium in the analysed leaves declined by 51% from November to January during the experiment (Figure 9). This decline occurred despite consistent irrigation, pointing to disruption in calcium transport within the plant. The decline corresponded with sap flow data showing reduced water movement in the upper canopy during late autumn and early winter.

Figure 9. Calcium Concentrations in Leaf Analyses During the Experiment.



The decline in calcium concentration coincided with the period of highest tip-burn incidence. Young expanding leaves at the top of the plant, where calcium demand was greatest, became deprived of calcium, leading to visible deficiency symptoms. Leaf imaging data support these findings.

#### 4.4 Lighting

The amount of PAR-light remained stable during the day throughout the experiment. On a typical day, the PAR-light level did not fluctuate much, averaging about  $450 \mu\text{mol m}^{-2} \text{s}^{-1}$  when all lights were turned on. This steady lighting level composed of top LEDs, interlighting LEDs and HPS lamps. Some minimal fluctuations were experienced due to weather conditions and the use of light-blocking screens. Light intensity did not vary significantly, but due to lighting composition, there were observable physiological effects. HPS lights emit a significant amount of heat radiation, which contributed to higher leaf

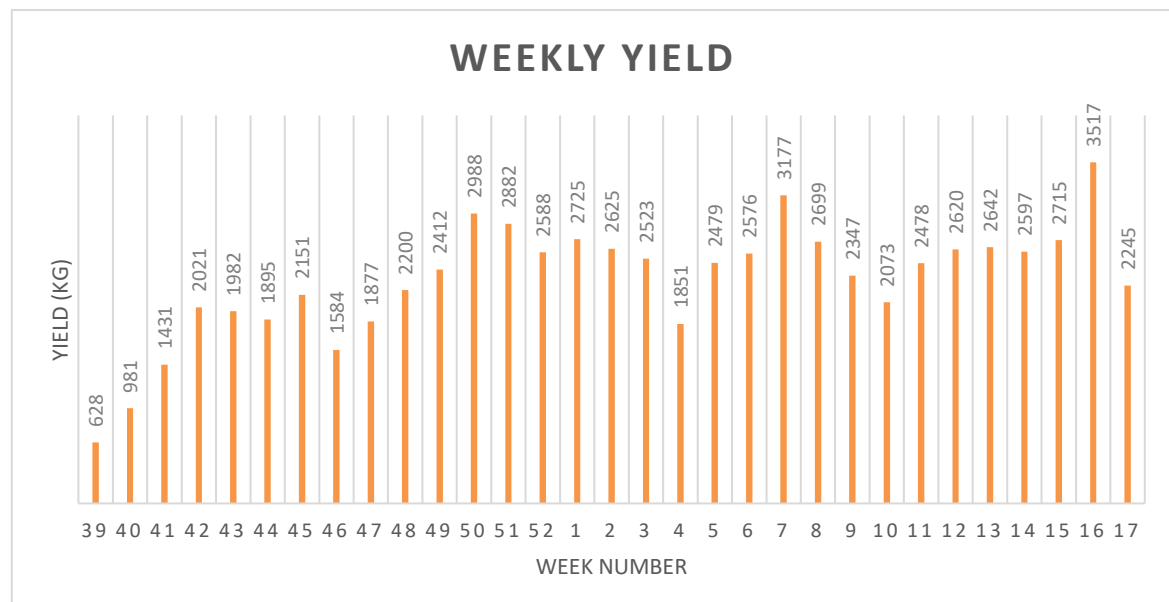
surface temperature in the upper canopy. This radiant heat caused an increase in VPD in the upper canopy.

Additionally, measurements taken after the HPS lights were turned off at 15:00 showed a measurable decline in sap flow in the upper canopy. Within 45 minutes, sap flow declined by approximately 12%, or 0.09 ml/h, showing that changes in radiation also had immediate effects on transpiration. Results confirm that the overall quantity of light remained constant and that minimal fluctuations in light intensity had negligible impact on sap flow, VPD or stomatal functioning in general.

## 4.5 Yield Quantity and Quality

Harvest data show (Figure 10) that fruit production remained largely stable during the experiment, production reaching its highest point in early December. After which yields decreased through January. Another two peaks were recorded at the end of February and at the end of April. Production fluctuated for example in response to pollination efficiency and other greenhouse conditions.

Figure 10. Weekly Tomato Yield from September to April.



Yield was affected by environmental conditions, physiological disorders (blossom-end rot), and disease. Fruit quality was uniform, and fruits affected by

blossom-end rot (BER) were uncommon. Though not quantitatively measured, visual assessments during harvest hinted that overall, there were very few fruits with BER. Despite variations in weekly yield, overall production remained within the expected range for winter tomato cultivation.

## 5 Discussion and Conclusions

This chapter interprets the findings of the study and discusses their implications in the context of existing literature. It also examines how environmental and physiological factors affect tomato cultivation under hybrid lighting. The aim is to examine how changes in VPD, sap flow, and stomatal behaviour under different climatic conditions influence the occurrence of calcium-related disorders like tip-burn and blossom-end rot.

Topics discussed include transpiration, the practical application of data in cultivation, hybrid lighting in cultivation, limitations of the study, and suggestions for future research. The chapter considers the limitations of this study, reliability of the data and recommendations for future research. It also links the key findings to the theoretical framework presented earlier, interpreting how environmental and physiological factors affect calcium transport in the plant.

### 5.1 Transpiration

This study reaffirms that transpiration is critical in calcium transport within the plant, and that any factor that limits transpiration stream can lead to areas of calcium deficiencies. This was shown by a significant drop in calcium concentration during or after periods of lower transpiration rates in the upper canopy. The findings support existing literature which shows that uneven transpiration rates across the plant canopy can create differences in calcium distribution, ultimately causing disorders like blossom-end rot (Joy & Hudelson, 2024, p. 1). Results of this study confirm that vapour-pressure deficit (VPD) is the primary indicator of stomatal activity and transpiration. This finding aligns with He et al. (2024, pp. 614–618), who identified VPD as a key regulator of tomato transpiration patterns. As discussed in the theoretical background, VPD directly influences both stomatal behaviour and sap flow and was found in this study to be the most accurate factor for predicting changes in transpiration.

Heat pipes in the greenhouse were on at night for humidity control, causing the lower canopy stomata to be continuously open because of the heightened VPD. Hence the lower canopy continued to transpire, hindering sap flow in the upper canopy, limiting calcium uptake, causing tip-burn and a reduction in overall leaf size. This imbalance in transpiration stream between lower and upper canopy was concluded to have caused the tip-burn in the upper canopy, as well as the few fruits with blossom-end rot. The persistent transpiration in the lower canopy is in line with observations by Šalagovič et al. (2024, p. 1), who identified VPD-driven microclimate gradients within tomato canopies as factors influencing internal plant water and nutrient movement.

Variety selection, along with climate control, is one of the primary tools for preventing tip-burn and blossom-end rot. Proposed solution to these deficiency symptoms is to either get a dehumidification system or alternatively to increase humidity at lower canopy at night, causing stomata to close, so that sap flow can reach the upper part of the plant. By understanding how light, VPD and heating interact, growers can better mitigate calcium-related disorders.

## 5.2 Practical Application of Data in Cultivation

Growers can integrate VPD monitoring into their climate control systems, as it can be easily calculated using existing climate data, requiring only the measurements of leaf and ambient temperature and relative humidity. Even if leaf temperature readings are not available (IR-sensors required for measuring leaf temperature are expensive), VPD could be roughly estimated using just the ambient temperature and relative humidity. Sap flow sensors can be used to provide valuable information about plant stress and transpiration, and they can be easily used in commercial cultivation to identify areas of low water uptake and thus detect and predict early signs of calcium deficiencies, as well as deficiencies of other immobile nutrients which are transported via transpiration stream.

The result that is perhaps most interesting from a grower's perspective is that transpiration in the lower canopy remained consistently higher than in the upper canopy, largely due to heating pipes increasing air temperature near the base of the plants. From a cultivation perspective, this finding demonstrates how

greenhouse heating systems can unintentionally influence nutrient distribution within the plant.

### **5.3 Hybrid Lighting in Cultivation**

High-pressure sodium (HPS) lights have been the standard in greenhouse cultivation for decades. However, HPS systems are energy-intensive and produce excess heat, which can complicate greenhouse climate management. Light-emitting diode (LED) technology has increasingly replaced HPS lighting due to its higher energy efficiency and longer lifespan. Combining LED and HPS lights offers certain advantages for greenhouse tomato cultivation, as the thermal radiation from HPS lamps influences transpiration and thereby calcium transport within the plant. The increased leaf temperature observed under HPS lighting agrees with earlier studies showing that radiation intensity can influence stomatal behaviour and transpiration rates (O’Carrigan et al., 2014, pp. 68–69).

This study demonstrated that HPS lighting significantly increased leaf temperature in the upper canopy, raising VPD during the lighting period. The effect was particularly evident in the evening, when turning off the HPS lights caused a rapid decline in VPD and sap flow. These findings show how lighting strategies can directly affect growing conditions and provide a practical example of how radiant heat shapes plant responses. While hybrid lighting systems offer benefits, further research is needed to deliver clear recommendations for growers.

### **5.4 Limitations of Study and Suggestions for Future**

One limitation rose from moving and growing the tomato plants. Since the sensors were moved weekly and studied leaves differed in size and state, each week’s dataset differed from each other, and they cannot be compared to each other. Future experiments could benefit from fixed plants or movable sensors. Additionally, this study only covered a limited span of time; extending measurement period could provide more insight into transpiration under different conditions.

One of the key limitations of this study is the lack of control plants. Without control plants, it becomes impossible to determine whether the observed findings are statistically significant. As a result, conclusions about causality are speculative rather than definitive. A major limitation of this study was the reliance on a single set of sensors. Using only a single set of sensors limited the measured area and thus the reliability of the data gathered. Greenhouses have microclimatic variation within the same row or section. With only one sensor set, the data represent only a singular point in the greenhouse. Insufficient pollination may have affected yield during the experiment.

## 6 Summary

The results confirm that vapour-pressure deficit (VPD) was the most reliable indicator of stomatal activity and transpiration. VPD consistently explained changes in sap flow and transpiration rate. In this experiment, calcium deficiency did not result from reduced total water uptake, but rather from the uneven distribution of sap flow within the plant driven by increased VPD in the lower canopy. This rise in VPD was caused by heating pipes below the plants that elevated lower canopy temperature, thereby increasing VPD. This imbalance in sap flow possibly hindered calcium transport to developing leaves in the upper canopy, resulting in yellow, small leaves. High-pressure sodium (HPS) lamps raised leaf surface temperature, accelerating transpiration and sap flow especially in the upper canopy during lighting hours. Blossom-end rot was observed rarely during the experiment, while tip-burn symptoms were frequent and severe and appeared mostly in the upper canopy. Results showed that leaf calcium concentrations nearly halved during the measurement period, coinciding with observed tip-burn symptoms.

Conducting this experiment with partners from Signify and HAMK was a valuable learning experience in how climate and microclimates act under greenhouse conditions. The experiment involved multiple measurement methods which challenged me at times but also improved my knowledge and planning skills significantly. Despite limitations such as having no control group, the experiment was a resounding success. The commissioning party, Signify, also expressed satisfaction with the way the experiment was conducted and with the results obtained.

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