# IRRIGATION STRATEGIES AND PRECIPITATION SCENARIO EFFECTS ON WILD BLUEBERRIES

By

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B.S. Kano University of Science & Technology, 2019

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Plant, Soil, and Environmental Science)

The Graduate School

The University of Maine

May 2024

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# IRRIGATION STRATEGIES AND PRECIPITATION SCENARIO EFFECTS ON WILD BLUEBERRIES

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An Abstract of the Thesis Presented
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May 2024

Wild blueberries (*Vaccinium angustifolium Ait.* and *V. myrtilloides Mitchx*.) are now under increasing variations in climate conditions (Chen et al., 2022; Fernandez et al., 2020; Tasnim et al., 2021). High temperature and changes in rainfall patterns associated with climate change have direct effects on soil moisture regimes, and therefore wild blueberry crops. Over the last century, climate change in Maine (U.S.A) has been characterized by less frequent and more intense precipitation and warming temperatures. Extreme rainfall events are increasingly affecting the structure and functions of wild blueberries. Changes in precipitation patterns are influencing plant growth, physiology and edaphic conditions of wild blueberries. Rising temperatures increase the risks of drought by increasing the rate of evaporation which reduces the soil water content.

However, the future influence of these changes on Maine wild blueberries remains unknown.

In 2022 and 2023, two experiments were conducted. The first assessed the impacts of probable future precipitation conditions on wild blueberries, while the second established the irrigation strategies for climate change risk mitigation. The experiments were conducted in a greenhouse over a period of two years (from May 2022 to October 2023). Three precipitation scenario treatments were tested on six different “parent plants” (which are likely to be different genotypes) of wild blueberries using a factorial design (2x3). This study utilized historically dry and wet years to develop a plausible future precipitation scenario. Leaf and stem morphological and functional traits, along with edaphic conditions were used to assess the performance of wild blueberries. We found that, compared to a historically dry year, the plausible future scenario increases the leaf production. However, no significant differences were observed among other treatments in 2022. In 2023, the historically wet treatment was significantly higher than the historically dry treatment, highlighting the importance of both rainfall amount and distribution in the leaf production of wild blueberries.

Furthermore, when compared to the treatment designed to simulate the future conditions, plants grown under the historically wet year treatment had significantly higher soil water content (%vwc) and soil electrical conductivity. The rainfall pattern in the historically wet treatment was more evenly distributed across the study periods compared to the historic dry and probable future conditions treatment. This suggests that the distribution of rainfall is more important than the total annual amounts.

The purpose of the second experiment is to establish the optimal amount and frequency of irrigation for wild blueberries, and to explore the effects of dry periods between precipitation or irrigation events. As wild blueberries are a biennial crop, this assessment was made to include both harvest and non-harvest years. Three different irrigation amounts and frequencies were tested, including: (a) 1-inch (2.5cm) of water per week (high irrigation frequency, or HIF), (b) 2-inch (5cm) of water every second week (medium irrigation frequency, or MIF), and (c) 3-inch (7.5cm) of water every third week (low irrigation frequency, or LIF). The effects of each treatment on crop development and soil conditions were tested at the leaf development, flowering, green fruit, and fruit ripening stages. The results show that the HIF treatment significantly increased the stem length, leaf chlorophyll concentration, soil water content, and soil electrical conductivity compared to the MIF and HIF treatments. Reduced stem length, low photosynthetic rate and soil water content were observed in plants that received the LIF treatment compared to the HIF and MIF treatments. In conclusion, our results indicate that the LIF significantly reduces the number of flowers, while the MIF produces as much flowers as HIF.

## ACKNOWLEDGEMENTS

I would like to convey my gratitude to many people who have helped me in many ways from the beginning of this research project. I would like to start by expressing my sincere gratitude to my advisor, Dr. Rachel E. Schattman, for helping me with what I needed in every single stage of this research project. Many thanks for your motivations when I was having difficulties in carrying out some tasks.

I am grateful to my committee members: Bruce Hall, Sean Birkel, and Yongjiang Zhang for their help, support and guidance during the planning, execution, analysis and writing stages of this research project. This project will not be possible without your contributions. I am also grateful to my lab mates for their feedback, support and for helping me to prepare for my oral defense.

I would also like to thank Travis Dillard and the Wyman’s team for committing their time to help us in collecting the wild blueberry transplants used to carry out this research, and for guiding our research project based on their field experiences. Lastly, I would also like to thank the Maine Wild Blueberry Advisory Committee for funding this research project.

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# CHAPTER 1: BACKGROUND

Wild blueberry growers in Maine (U.S.A.) are facing challenges imposed by change in climate conditions (Barai et al., 2021; Tasnim et al., 2021). Rainfall variability and episodic drought have greatly impacted agricultural production in the region (Fernandez et al., 2020). Over the last century, Maine's climate has warmed by an average of 3$^{o}$F (0.56$^{o}$C), with the highest temperature increases occurring along the coastal areas (Birkel & Mayewski, 2018). These regions are also where the majority of wild blueberries are grown. In addition to temperature changes, the total annual precipitation has increased by 6 inches (15.24cm) since 1895 (Fernandez et al., 2020). Higher temperatures and associated evapotranspiration in wild blueberry production areas are expected to intensify the effects of drought, potentially resulting in major economic losses (Tasnim et al., 2021). Higher precipitation intensity is directly related to warming temperatures (Frei et al., 2015). For example, the warming climate will likely increase the amount of rainfall delivered in intense storm events, along with frequent dry or drought periods between storms (Pratap and Markoni, 2022). Drought is one of the most serious environmental factors affecting the productivity of plants, as water makes up approximately 80-95% of plant biomass (Seleiman et al., 2021). It is believed that drought is the single most serious threat to global food security, and the driver of major famines in the past (Okorie et al., 2019). However, the effects of drought are dependent on several factors including the evapotranspiration and water holding capacity of soils in the crop root zone (Seleiman et al., 2021).

Drought is one major environmental stress on agricultural production. The term “drought” has several definitions. Agriculturally, drought is defined as a condition in which the soil water content is not sufficient for healthy plant growth and development, particularly in the context of climate change e.g., low rainfall amount, high temperature (Mannocchi et al., 2004). Hydrological drought is characterized by a substantial decrease in all forms of water availability in the terrestrial phase of the hydrological cycle, encompassing ground water, surface water, and snow melt (Satoh et al., 2022). Meteorological drought is defined as an increase in dry weather conditions, which results in lower precipitation and higher temperatures (Vose et al., 2015). When a drought occurs, the rate of water loss through transpiration from leaves surpasses the rate of water uptake through roots in dry settings (Goche et al., 2020). In response to drought, plants respond by limiting stomatal water loss, expanding their roots to enhance water absorption (Martínez-Vilalta & Garcia-Forner, 2017). Common signs of drought stress in plants include leaf rolling, stunting, yellowing leaves, blistering, and permanent wilting.

Wild blueberries propagate and spread through rhizomes that give rise to new roots and stems. However, drought conditions impede the spread of rhizomes, resulting in reduced growth and development of this crop (Struchtemeyer, 1956). The crop is susceptible to both drought and excess water conditions (Yarborough, 2003). Prior research suggests that, for optimal growth and development, wild blueberries require 1 inch (2.54 cm) of water per week in both crop and non-crop years. However, the probability of receiving this amount of rainfall throughout the growing season is less than 50% (Hunt et al., 2009).

A warming climate has multiple related effects on soil-water-atmospheric dynamics. For example, rising atmospheric temperatures increase the saturated vapor pressure, which has the potential to increase both precipitation amount and evaporative demand (Ficklin & Novick, 2017). Increases in evaporative demands is a key indicator of hydrological intensification, a condition characterized by faster water evaporation from soils (Ficklin et al., 2019; Huntington et al., 2006). At the same time, excessive precipitation in single rain events can lead to leaching of nutrients from root zones and contamination of ground and surface waters (Yao et al., 2021). Prior research conducted in Maine suggests that rising air temperatures will change wild blueberry development, yield, and plant health (Tasnim et al., 2022). However, it is unclear what effect changing precipitation dynamics will have on this regionally important crop. Considering this knowledge gap, the first experiment described in this thesis tested historical and probable future precipitation scenarios to determine the effects of changing rainfall patterns on the edaphic conditions and the morphological and functional traits of wild blueberries. The findings lead to important conclusions regarding the effects of a future in which annual rainfall is higher than today, but this rainfall is unevenly distributed, thus requiring broader adoption of irrigation in the wild blueberry industry of Maine.

Wild blueberries require enough soil moisture for optimum physiological and morphological growth (Gumbrewicz and Calderwood, 2022). The crop grows in well-drained gravelly/sandy soil that has a low water holding capacity. As a result, water must be supplied evenly across the season (through rainfall or irrigation) or growers may suffer severe losses. For example, drought conditions experienced in Maine in 2020 were partially responsible for a 43.7% mean crop loss among a subset of wild blueberry growers (Schattman et al., 2021). This indicates that drought presents major challenges in agricultural production areas in the United States and is projected to have significant influence on future agricultural water demand and supply (Rosenberg, 2020).

Although a lack of rainfall is usually the primary cause of drought, water loss from soils owing to high temperatures and dry wind can extend or compound dry conditions (Cohen et al., 2021). More drought stress is anticipated in areas where crop production is entirely dependent on rainfall, compared with irrigated areas. For example, in Glass et al. (2005), a distinction between irrigated and non-irrigated fields was observed, revealing a significant increase in berry yield associated with irrigation. Additionally, a study that was conducted in Maine reported that drought stress reduces the volumetric water content, stem length, stem diameter of wild blueberries (Tasnim et al., 2020). Another study reported a negative effect of droughts on various physiological traits by inducing leaf stress, reducing growth, and lowering the photosynthetic rate and yield potentials of wild blueberries (Tasnim et al., 2020; Barai et al., 2021).

Regions in Maine where wild blueberries are grown are projected to experience 12$^{o}$F (2.24$^{o}$C) increase in average annual temperature by the end of 21st century (Fernandez et al., 2020). This temperature increase is projected to bring more rainfall amount along with more frequent dry periods (IPCC, 2021), which can alter the phenology of wild blueberries (leaf development, stem density and length, floral development, and fruit development) (White et al., 2012). These changes may increase the vulnerability of wild blueberries to drought injury, thereby reducing yield and quality of harvested berries. Therefore, growers need to be able to estimate the crop water demands, and then apply irrigation water to meet those demands (Hunt, 2009). This can be achieved through regular monitoring of soil water content and crop water use.

Although wild blueberry is a relatively drought resistant crop, previous studies have shown that irrigation increases both vegetative growth and berry production (Benoit et al., 1984). Some sources predict that, in the future, wild blueberries will receive enough water from precipitation in August in one out of five years (Hunt et al., 2009). Therefore, irrigating both crop and non-crop years can significantly protect, and even increase, the growth and yield of the crop compared to no irrigation or irrigating only during the crop year. Furthermore, inadequate irrigation water or delaying irrigation until the crop stress signs are visibly noticeable can result in plant injury and significant reduction in yields (Glass et al., 2005).

Based on previous guidance from University of Maine Cooperative Extension and other advisors, Maine wild blueberry growers understand that 1 inch (2.5cm) of water per week is needed in both crop and non-crop years (Hunt et al., 2009). As a result, a common grower irrigation scheduling practice is to supply 1-inch of water per week during the growing season. However, considering the climatic variabilities such as evapotranspiration and crop coefficient, we propose that wild blueberries require different amounts of water at some growth and developmental stages, and less at others. We have tested three different irrigation frequencies, including 1-inch (2.5cm) of water per week (high irrigation frequency, or HIF), 2-inch (5cm) in every second week (medium irrigation frequency, or MIF), and 3-inch (7.5cm) per every third week (low irrigation frequency, or LIF), with the purpose of establishing optimal amount of irrigation thresholds for healthy growth and development of wild blueberries in both crop and non-crop years. By keeping the total amount of water applied to the crop consistent, but altering the frequency and duration of water applications, we sought to explore how extended dry periods between watering affect crop growth, and when water above the recommended 1-inch per week may be useful for optimizing crop development and plant health. The results of this study could provide recommendations to slightly adjust conventional irrigation recommendations and reduce the frequency of water applications during flowering.

# CHAPTER 2: EFFECTS OF HISTORICAL AND FUTURE PRECIPITATION ON WILD BLUEBERRIES

## Abstract

Historical precipitation observations from wild blueberry production areas of Maine (U.S.A) show that precipitation amounts have increased over the last several decades and are projected to increase in future as the climate continues to warm. However, it is unknown how wild blueberries will respond to changes in precipitation patterns. We evaluated the impact of projected increase in precipitation (estimated for the end of the 21st century) on the edaphic conditions and the morphological and functional traits of wild blueberries. To accomplish this, we used historical precipitation observations from the Parameter-elevation Regression on Independent Slope Model (PRISM) (PRISM dataset, 1981-present) as the basis for developing scenarios of future precipitation patterns in wild blueberry production areas of Maine. Two treatments were developed for the scenarios of observed historical precipitation: HistDry (PRISM 2001) and HistWet (PRISM 2006), as well as one plausible future scenario: Amp2.915. Our results reveal that lower average precipitation punctuated by seasonal droughts (the HistDry treatment), lead to a relatively low number of leaves, reduced leaf chlorophyll concentration and fluorescence in wild blueberries, and low soil water content. High annual precipitation with uneven distribution (as simulated through Amp2.915), leads to relatively inadequate soil water content and low soil electrical conductivity. This suggests that the future precipitation variability across the growing season may reduce the volumetric water content in the soils where wild blueberries grow. Therefore, wild blueberry growers and farm managers in Maine should consider irrigation strategies that can mitigate the

negative impacts of seasonal change in precipitation amounts on wild blueberries, in order to develop a regional plan for future food security and sustainable development.

## 2.1. Introduction

### 2.1.1. Wild blueberry production

Wild blueberries are grown commercially under natural conditions in the Northeastern part of the United States and maritime areas of Canada. The state of Maine is the leading producer of wild blueberries in the world, and accounts for up to 99% of the total production in the United States. In 2022, a total of 77.6 million pounds of wild blueberries were commercially harvested from 19,700 acres in Maine (USDA/NASS, 2023), while an additional 21,000 acres is managed in the non-crop cycle.

The crop is not planted or subjected to any breeding techniques, rather endemic genotypes are cultivated in the environments where they occur naturally. They primarily spreads by underground runners known as rhizomes, which develop near the soil surface and give rise to new roots and eventually the stems. Wild blueberries are managed and harvested on a two-year production cycle, consisting of crop and non-crop years. Following the crop harvest, the fields are pruned to ensure healthy growth and productivity in the subsequent years (Drummond, 2012). To prune the crop, growers either burn the field (thermal pruning) or mow it (Paré et al, 2020). Pruning after harvest maximizes yields in the subsequent year (the crop year).

Bees are the primary pollinators of the crop (Bell et al., 2009), and wild blueberry crops are heavily dependent on a diversity of pollination services (commercial & native) (Drummond, 2012). Fruit set is one factor that determines the yield potential, though only a portion of set fruit will be harvestable. Between fruit set and harvest, viable berries may be reduced by adverse weather conditions, weed competition, and insect pests and diseases (Drummond, 2019).

### 2.1.2. Morphological and functional characteristics of wild blueberries

Wild blueberries produce phenotypically distinct leaves that are simple, lanceolate with serrulate margins and alternate arrangement. Leaves have stomata for gaseous exchange and transpiration, and they are primary organs of photosynthesis (Vialet-Chabrand et al., 2017). The leaves store and distribute hormones, nutrients, and water in plants, which gives them a vital role in growth, development, and overall functions of wild blueberries. The number of leaves per stem increases the energy storage and survival rates of plants and is positively correlated with stomatal density (Dombroskie and Aarsen, 2012). The stomatal density is related to the growth characteristics, photosynthetic capacity and water use efficiency of plants (Xu and Zhou, 2008). Higher numbers of leaves per stem enhances the ability of plants to respond to the environmental cues and strike a balance between energy storage and fruit production (Hilty et al., 2021).

Branches provide structural support for the leaves, flowers, and fruits. The branches also determine reproductive ability, carried fruit efficiency, mechanical support, and wind resistance of wild blueberries. Prior research has shown that wild yield increases with greater numbers of branches per stem (Mathan et al., 2016). Additionally, the stems transport water from roots to the leaves, and photosynthates from leaves to the rest of plants. As a result, the number and health of branches determine the ability of plants to survive, grow and adapt to the changing environment (Meyer and Purugganan, 2013).

Stem length (also known as plant height) serves as a proxy measurement for the above ground growth and biomass of wild blueberries (Barai et al., 2022). Greater stem length enhances the light use efficiency of wild blueberries, as well as the wind and hydraulic resistance of the plants. As wild blueberries grow in dense stands, stem length is a desirable characteristic that enables taller plants to capture more light and other resources compared to shorter ones. According to Klecka et al. (2018), the overall flower visitation rates by insect pollinators increases significantly as plant height increases. Therefore, the frequency at which different pollinators visit plants is thought to be proportional to the length of stems.

Two complementary methods are often used to assess plant photosynthetic activity and physiological stress. First, leaf chlorophyll concentration is used to indicates the photosynthetic rates of mature leaves of plants (Zhang et al., 2022). The leaf nitrogen concentration of mature leaves determines the leaf chlorophyll concentration and is often used as a proxy for overall health, physiological stress, and fertilizer needs of wild blueberries. The SPAD meter provides a non-destructive method of measuring the leaf chlorophyll concentration. Lower SPAD readings indicate low chlorophyll concentrations and potentially low photosynthesis, while higher SPAD readings indicate high photosynthesis (Donnelly et al., 2020). Second, leaf chlorophyll fluorescence is used to determine the level of stress in wild blueberry leaves. Leaf chlorophyll fluorescence provides a non-destructive method of detecting changes in plant photosystems II that occur during droughts or moisture stress conditions (Kalaji et al., 2016). Leaf chlorophyll fluorescence has been used to study the physiological and photochemical efficiency of leaves and their responses to environmental conditions. According to Guanter et al. (2014), leaf chlorophyll fluorescence measurements could provide a threshold that can improve global agricultural productivity models by increasing the accuracy of model output under the climate change scenarios. In the past, leaf chlorophyll fluorescence has proven to be a useful tool in agricultural, ecological, and environmental studies (Gottardini et al. 2014).

The physiological functions of leaves, such as respiration, photosynthesis, translocation, growth, and cell division, are influenced by leaf temperature (Still et al., 2022). Furthermore, a plant has a better chance of attaining the maximum production potential under optimal leaf temperature 77-86°F (25°C-30°C) (Yamasaki et al., 2002). Several biological and chemical reactions in leaves are temperature dependent (Yamori et al., 2014). For example, the photosynthetic acclimation to low temperatures was suggested to involve an increase in the capacity of enzymatic reactions that limit the photosynthesis at low temperatures (Yamasaki et al., 2002). Additionally, when temperatures become too high, stomata close to conserve plant water and stop transpiration. This restricts gas exchange and decreases photosynthesis, ultimately stopping the plant from growing during this period (Crawford et al., 2012).

### 2.1.3. The influence of edaphic conditions on wild blueberries

The bulk of wild blueberry soils in northeastern part of North America originated from glacial till deposited during the previous ice age. These soils include a wide range of textures, from sandy to very coarse, gravelly material, mixed with various levels of organic matter and loam (Eaton & Jensen, 1997). Due to spatial variation in soil water content in wild blueberry fields, it can be challenging to maintain soil water relationships that are conducive to plant growth and development (Gumbrewicz and Calderwood, 2022). Therefore, growers can use soil moisture monitoring to better understand soil water conditions and adjust these conditions according to the needs of wild blueberries. According to Ratshiedana et al. (2023), soil water content is associated with soil electrical conductivity. Soil electrical conductivity influences the amount of nutrients available for plant uptake, a factor critical to yield of wild blueberries (Farooque et al., 2012). The soil electrical conductivity of a nutrient solution is proportional to the total number of ions that are held onto soil particles through gravitational pull that are accessible to plants in the root zone. Low soil electrical conductivity (< 1.0mS/cm) indicates that the nutrients status of the soils is not sufficient. High soil electrical conductivity (8-20 mS/cm), on the other hand, will likely make nutrients more available to crops, but may also increase the salinity index of the soils, which may negatively affect the growth of plants (Ratshiedana et al., 2023). The ideal soil electrical conductivity is crop specific and is determined by environmental factors. Soil electrical conductivity is determined by the soil water content, salts, amount, and type of clay minerals (Eigenberg et al., 2002). Soils with high clay and organic matter content have higher soil electrical conductivity.

Soil is an important medium for energy storage and transfer, acting as a reservoir for either kinetic or potential energy. Potential energy can appear as gravitational potential energy as a result of elevation changes or as pressure potential energy as a result of soil particle compression. Soil temperature is also an important edaphic factor that affects the plant growth and is associated with abundance and diversity of beneficial soil microorganisms (Sabri et al., 2018). Most soil organisms perform better and are more abundant at temperatures ranging from 77-86$^{o}$F (25-30$^{o}$C) (Pietikäinen et al., 2005). Apart from soil microbial activity, soil temperature influences other biological processes of soils such as decomposition of soil organic matter, Nitrogen-fixation processes, and nutrient cycling (Sattari et al., 2020). Soil temperature also affects several physiological processes in plants, such as photosynthesis, transpiration, respiration, water transport, and hormonal activities (Magan et al., 2011).

### 2.1.4. Impact of climate change on wild blueberries

While there is a limited literature that attends to the effects of climate change on wild blueberries, there is a robust field of study that examines the potential effects of changing environmental conditions on most staple and some specialty crops. Changing environmental conditions have been shown to affect plant phenology and by extension their ecosystem functions (Parmesan and Yohe, 2003). Climate change has affected agricultural crops at local, regional, and global scales, and threatens the basic components of life for people and natural ecosystems (Faggian, 2021). Several studies indicate that climate change will continue to have an impact on many aspects of life, including the natural ecosystems, economies, hydrology, and agriculture. Heavy rainfall events, along with drought periods have been observed in many agricultural regions around the world (IPCC, 2021).

Increases in temperature have been linked to a 10% increase in annual precipitation in the contiguous United States (Karl and Knight, 1998). Kendon et al. (2023) used the Clausius-Clapeyron equation and predicted that the water content of the atmosphere will increase by about 7% for each degree Celsius of temperature rise under a warming climate, which may result in changes in precipitation patterns and amount. Kharin et al. (2007) found that the average precipitation amount declined in subtropical areas, while increasing in deep tropical areas under the 21st century climate scenarios. Across the globe, daily precipitation extremes are either increasing or there is insufficient data to determine the trend (IPCC, 2021). This uncertain increase has implications for both socioeconomic systems and ecosystems.

Many crop phenology changes have been understood through modeling, allowing scientists to account for a wide degree of environmental variability over a wide spatial scale. At this point, modeling studies have primarily focused on projecting the effects of rising temperatures on the phenology of temperate species, with little information available on the effects of changing precipitation (Skendžić et al., 2021). However, changes in the seasonal precipitation patterns is also likely to cause phenological variations (Henry et al., 2022). This is because precipitation and evaporation are controlled by complex, non-linear processes.

The average temperature and precipitation amount in Maine have increased by 3°F (1.66$^{o}$C) and 6 inches (15.24 cm) respectively, over the last century (Fernandez et al., 2020), with the fastest temperature increase occurring around the coastal areas where most wild blueberries are grown (Tasnim et al., 2021). Therefore, wild blueberries are exposed to warming climate and extreme precipitation events to a greater degree than crops grown in in-land production zones (Fernandez et al., 2020). The warming climate will likely intensify the hydrologic cycle and increase the frequency of extreme events like droughts and heavy rainfall in future (Huntington 2010). As temperatures increase in the future, more frequent and heavier rainfall along with drought periods will be expected (Pratap and Markoni, 2022), which are anticipated to affect the wild blueberry crops in this region. Simulation studies are needed to determine the effects of these changes on the global ecosystem and agricultural crop production in the future (Henry et al., 2022), and would be highly valued in the wild blueberry industry. However, due to non-linear relationships between the complex physical and dynamic processes, precipitation remains the most difficult part of climate to forecast. This challenge persists despite a significant advancement in data assimilation techniques, such as radar and satellites (Choi et al., 2008).

Drought conditions experienced in 2001 created economic and social challenges in Maine and the northeastern parts of the United States (Jehl, 2003). The state had its worst drought for the last 30 years, which reduced the water available for irrigation, and highlighted the needs for future management and planning. Drought is defined in agricultural crop production as when soil water content is insufficient to meet the needs of a particular crop (Rosenberg, 2020). Drought has been widely studied on various crops in many parts of the world and has been recognized as a significant challenge in agricultural production (Potop et al., 2012).

### 2.1.5. Research objectives

The overall objective of this study is to determine the impact of changing precipitation patterns on wild blueberries by the end of the 21st century. I used the Parameter-elevation Regression on Independent Slope Model (PRISM) dataset as the basis for developing three precipitation calendars representative of historical and plausible future conditions. Gaining a better understanding about how this crop will be affected by changing rainfall patterns can help wild blueberry growers and farm managers to develop climate change mitigation strategies for future food security and sustainable development. The specific objectives of the study were to:

1. Explore the effects of two historical precipitation scenarios and one probable future precipitation scenario on wild blueberry morphology.
2. Determine the effects of precipitation amount and seasonal distribution on crop development.

## 2.2. Materials and methods

### 2.2.1. Experimental design

Wild blueberry plants were harvested from Wyman’s production fields in Deblois, Washington County, Maine, United States (44°36'34.57" N, 67°55'38.40" W) on May 6, 2022, and

June 10, 2022. Deblois is in Washington county, in what is known as the Downeast region of Maine. The location experiences an average, minimum, and maximum temperature of 6.3°C, -10.6°C, and 24.2°C, respectively. Throughout the year, the average number of rainy days is 142, with an average precipitation amount of 1,298mm and a snowfall of 158cm. The region has a rocky shoreline with well-drained acidic sandy loam soils. The soils in the location where plants were harvested are classified as a Colton gravelly sandy loam, with a high-water table depth of 203cm. The location from which the wild blueberries plants were harvested is an actively managed commercial production area.

Six “parent plants” were selected based on their morphological and phenotypic differences, as observed in the field. Specifically, stem color and height, leaf color and size, and floral bud development were taken into consideration. Three of six parent plants selected (A, B, and C) were in “crop” year, while the remaining three (D, E, & F) were in “non-crop” year in 2022. The D, E, and F parent plants were pruned in the study area in 2022 which grew vegetatively and produced flowers and fruits in 2023. Ten sections (transplants) measuring approximately 10 x 10 inches (~25 x 25cm) were harvested from each parent plant and transported to the Roger Clapp Greenhouse at The University of Maine, Orono campus. An unheated high tunnel measured 5 x 10 meters was used for the experiment. The structure (Figure 2.2) was covered with plastic (6mm, clear) to exclude rainfall. The study was conducted from June to October in 2022, and from May to October in 2023.

*Figure 2.1:* Jonesboro, Maine, United States of America

***Figure 2.2**: Blueberry plants growing in a rainfall exclusion structure in the nursery section inside the Roger Clapp Greenhouse, University of Maine, Orono campus.*

The parent plants selected for this study were transplanted and randomly assigned to the experimental treatments. These transplants were placed upon ~8 inches (20cm) of gravel in 2-gallon buckets, and then watered daily for 2 weeks prior to the start of the study, in order to minimize transplant shock and ensure adequate establishment. We credit the success of the transplant process with this regular watering prior to the beginning of the experiment, as well as the amount of O and E horizons harvested with the transplants (~7-10cm for each plant). The buckets were installed on top of benches, inside the rainfall exclusion structure (Figure 2.3). The study utilized a 2x3 factorial design. In 2022, bee colonies were introduced into the tunnel on May 20, to enhance pollination; however, they were later removed on July 14.

***Figure 2.3:*** *Pots with wild blueberry transplants installed on top of greenhouse benches.*

### 2.2.2. Treatment development

Three treatments were developed for this study: Two simulated scenarios of observed historical precipitation, and one simulated a plausible precipitation calendar in Maine. Each treatment included a day-by-day watering schedule, characterized by the amount of water (in any given day and accumulated in each growing season) and the seasonal distribution of "precipitation". The daily precipitation amounts were converted from inches to seconds of water application, and delivered to the plants on a daily basis using a handheld watering can. All treatment schedules were built upon daily precipitation observations from the Parameter-elevation Regression on Independent Slope Model (PRISM) dataset for the warm season (May 1st - October 30th) for the years 2001 and 2006, from Jonesboro, Maine (Record period 1991-Present). PRISM dataset has a high spatial resolution, allowing for forecasts on a finer spatial resolution (Jeong et al., 2020). Even though regional climate models (RCMs) are widely used for future climate projection and regional climate studies, their low resolution limits their ability to account for the effects of local features such as complex topography, atmospheric circulation, and urban heat islands (Giorgi and Mearns, 1999). However, the PRISM considers the geomorphological features such as coastline proximity, topographic facet, and altitude (Daly et al., 1997; Buban et al., 2020; Jeong et al., 2020). Jonesboro is located in Washington county, in the Downeast region of Maine (Figure 2.1). The location has rocky shorelines with well-drained acidic sandy loam soils.

The three specific treatments are as follows:

1. **HistDry:** 2001 was a dry year on record in the early 21st century in Maine. It was characterized by very low and infrequent rainfall separated by prolonged periods of dryness. From May – October, 132 consecutive dry days (no rain) were recorded. The maximum amount of daily rainfall recorded was 3.51cm (1.38 inches) on 18 May, and the total May – October rainfall was 31.79cm (12.53 inches). Figure 2.4 shows precipitation accumulation across the growing season for this, and the following treatments.

2. **HistWet:** Based on 2006 observations, there were frequent and well-distributed rainfall events throughout the growing season, without any prolonged period of dryness. Within

the range of May - October, rainfall exceeding 2.54 cm (1 inch) threshold occurred on eleven (11) separate days. The total May – October rainfall was 92.62 cm (36.50 inches).

3. **Amp2.915:** Modified from the observed 2001 precipitation record (HistDry). Daily values were multiplied by a factor of 2.915 to increase the total growing season rainfall to match that observed in 2006 (HistWet). This plausible future scenario is intended to simulate Maine’s growing season precipitation patterns as they may occur by the end of the 21st century.

Plants in each group (ABC and DEF) received the same experimental treatments over two growing seasons. In other words, if a plant was included in the Amp2.915 treatment in year one (2022), it was also included in this treatment in year two (2023). Between the end of October 2022 and the middle of April 2023, no water was applied to the plants. This period was a time of winter dormancy for the crop.

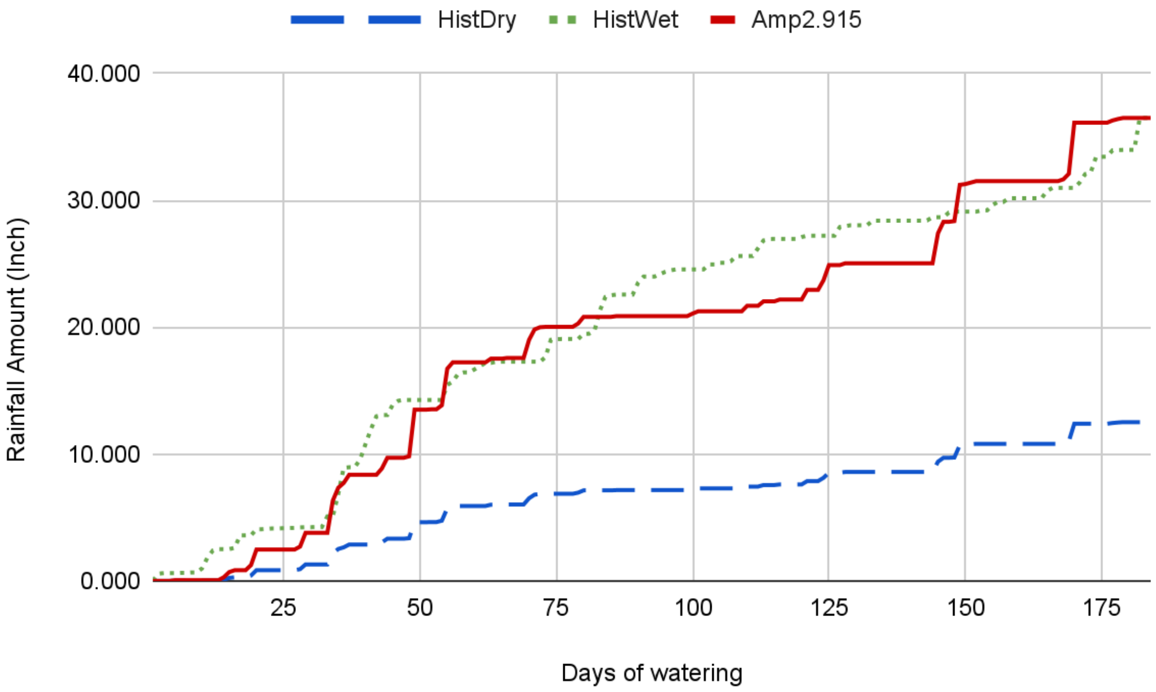


***Figure 2.4:*** *Cumulative water applications of the experimental treatments (HistDry, HistWet and AmpDry2.915). In 2022, day 0 = May 20. In 2023, day 0 = April 30.*

### 2.2.3. Assessment of morphological and functional traits

Plant morphological traits assessed in this study included number of leaves, number of branches, and stem length. A single plant from the middle of the pot was selected, tagged and maintained for data collection on morphological traits. The number of leaves per stem was recorded when leaf shoots expanded and enlarged in a whorled pattern, while the number of branches per stem was recorded when the vegetative buds turned to new branches. The number of flowers was recorded during the flowering stage, when the flower petals on the tagged plants were opened for pollination. A measuring tape (Stanley 12 ft.) was used to measure stem length from the base of the stem to the highest point of the plant.

Plant functional traits are physiological and chemical aspects of plants such as leaf chlorophyll concentration, leaf chlorophyll fluorescence, and leaf temperature. These factors affect the growth, survival, overall fitness, and reproduction of wild blueberries. Three plants from the middle of each pot were selected, tagged, and maintained for data collection on functional traits. Leaf chlorophyll concentration was measured in a SPAD unit, using a SPAD Chlorophyll Meter (SPAD MC-100, Logan, Utah, USA). Leaf temperature was measured in degrees Celsius using a Fluke 62 Max+ handheld infrared thermometer (Fluke Corporation, Everett, WA, USA). Leaf chlorophyll fluorescence was measured in Fv/Fm using a portable fluorometer (Prmyslová 470, 664 24 Drásov, Czech Republic). Edaphic conditions are directly related to the physical and chemical properties of soils. They include soil moisture content (SMC), soil temperature and soil electrical conductivity, all of which were measured with a Fieldscout TDR 150 Soil Moisture Meter once at each stage. The soil water content, soil temperature, and soil electrical conductivity were measured using a Fieldscout TDR 150 Soil Moisture Meter (Spectrum Technologies Inc., Aurora, IL, USA). Soil water content was measured in volumetric water content (%VWC), soil temperature in degree celsius (°C) and soil electrical conductivity in mS/cm.

### 2.2.4. Statistical Analysis

Prior to analysis, data were checked for normality using the Shapiro-Wilk's test, QQ-plots, and histograms. Kruskal-Wallis and Analysis of Variance (ANOVA) tests were conducted using R statistical software (Version: R-4.3.2, 2023) to test and compare the overall performance of several functional traits (leaf chlorophyll concentration, leaf fluorescence, and leaf temperature), morphological traits (stem length, number of leaves and branches per stem), and edaphic conditions (soil moisture content, soil temperature, and electrical conductivity) (see Table 2.1).

Additionally, Pearson's correlation test was used to establish a correlation matrix that shows the relationship among these traits and conditions. The Pearson correlation was assessed using a 0.05 level of significance.

Table 2.1: Edaphic conditions and the morphological and functional traits of wild blueberries that were used in this study, their abbreviations and units

| **Variable type** | **Variable name** | **Abbreviation** | **Unit** | **Production cycle** | **Phenophase** | **Data collection date** |
|---|---|---|---|---|---|---|
| Morphological traits | Number of leaves per stem | NLPS | no. | Crop year | Fruit ripening | August 27, 2022 & September 6, 2023 |
| | Number of branches per stem | NBPS | no. | Crop year | Fruit ripening | August 27, 2022 & September 6, 2023 |
| | Stem length | StemL | inch | Crop year | Fruit ripening | August 27, 2022 & September 6, 2023 |
| Functional traits | Leaf chlorophyll concentration | LCC | SPAD | Crop year | Fruit ripening | August 28, 2022 & September 6, 2023 |
| | Leaf chlorophyll fluorescence | Fv/Fm | Fv/Fm | Crop year | Fruit ripening | August 28, 2022 & September 6, 2023 |
| | Leaf temperature | Tleaf | ºC | Crop year | Fruit ripening | August 28, 2022 & September 6, 2023 |
| Edaphic conditions | Soil water content | SWC | %vwc | Crop year | Fruit ripening | August 26, 2022 & September 6, 2023 |
| | Soil electrical conductivity | EC | mS/cm | Crop year | Fruit ripening | August 26, 2022 & September 6, 2023 |
| | Soil temperature | SoilT | ºC | Crop year | Fruit ripening | August 26, 2022 & September 6, 2023 |

## 2.3. Results and discussion

### 2.3.1. Edaphic conditions

Edaphic conditions, or those related to soil, affect crops in many ways. The factors considered in this study were soil water content (%VWC), soil temperature (°C), and soil electrical conductivity (mS/cm). Due to spatial variation in soil water holding capacity in wild blueberry fields, maintaining an optimal soil water content is challenging (Gumbrewicz and Calderwood, 2022). Kruskal-Wallis H test was also used to determine the differences between treatment effects on soil water content (Figures 2.5A and B). Results indicate that a statistically significant difference was observed in soil water content in both 2022 ($P < 0.001$) and 2023 ($P < 0.001$). Among the treatments, HistWet had significantly higher soil water content, measured in percent volumetric water content (%vwc) of the soil. This shows that high amounts of precipitation that are evenly distributed across the growing season (as simulated through HistWet treatment) increases the soil water content more than high rates of precipitation punctuated by drought (Amp2.915), a finding that aligns with past studies of this nature (Schattman et al., 2022). This also confirms past research which shows that total rainfall amount alone has minimal effects on soil water content (Kharivha et al., 2022).

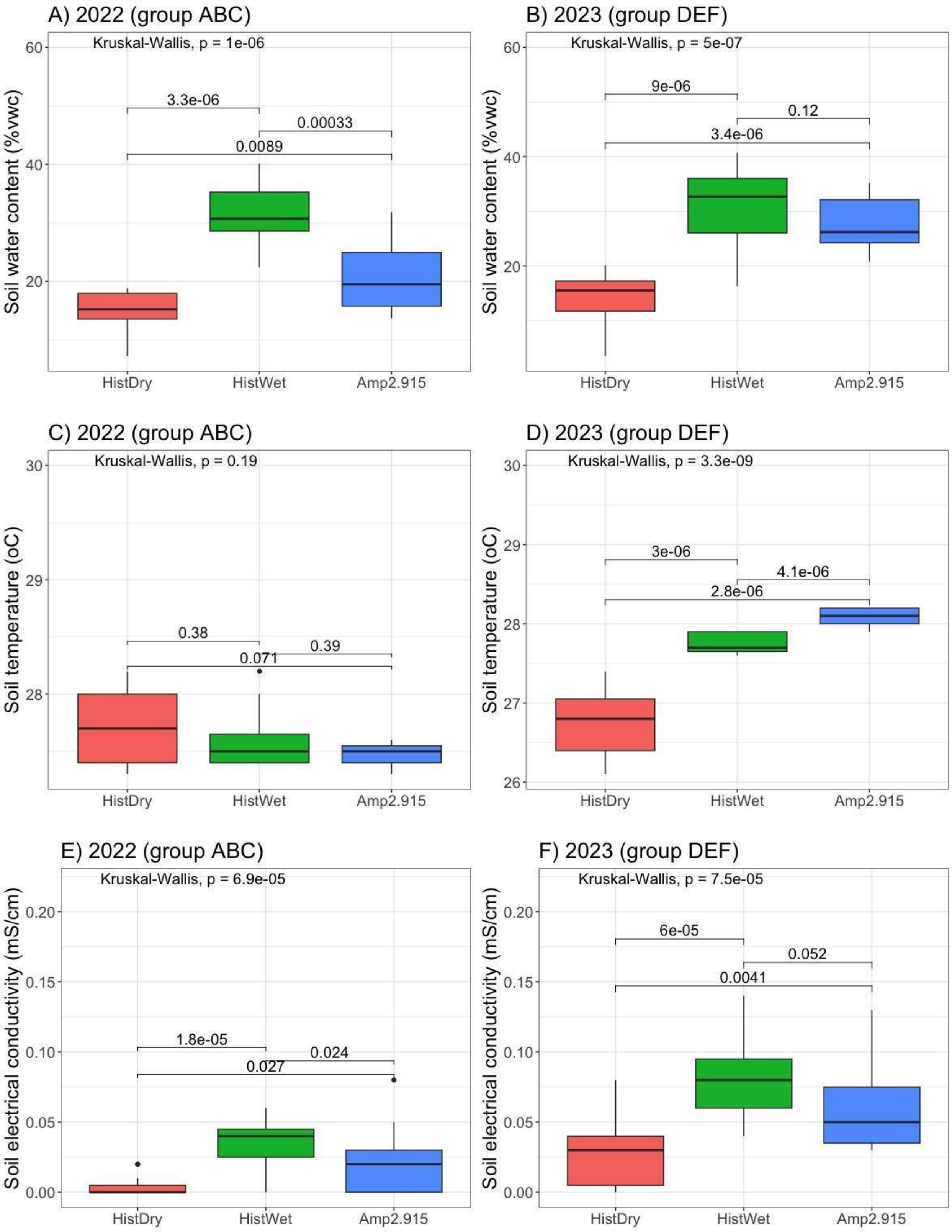

A) 2022 (group ABC)
Kruskal-Wallis, p = 1e-06
3.3e-06
0.00033
0.0089
Soil water content (%vwc)
60
40
20
HistDry
HistWet
Amp2.915
B) 2023 (group DEF)
Kruskal-Wallis, p = 5e-07
9e-06
0.12
3.4e-06
Soil water content (%vwc)
60
40
20
HistDry
HistWet
Amp2.915
C) 2022 (group ABC)
Kruskal-Wallis, p = 0.19
0.38
0.39
0.071
Soil temperature (oC)
30
29
28
HistDry
HistWet
Amp2.915
D) 2023 (group DEF)
Kruskal-Wallis, p = 3.3e-09
3e-06
4.1e-06
2.8e-06
Soil temperature (oC)
30
29
28
27
26
HistDry
HistWet
Amp2.915
E) 2022 (group ABC)
Kruskal-Wallis, p = 6.9e-05
1.8e-05
0.024
0.027
Soil electrical conductivity (mS/cm)
0.20
0.15
0.10
0.05
0.00
HistDry
HistWet
Amp2.915
F) 2023 (group DEF)
Kruskal-Wallis, p = 7.5e-05
6e-05
0.052
0.0041
Soil electrical conductivity (mS/cm)
0.20
0.15
0.10
0.05
0.00
HistDry
HistWet
Amp2.915

***Figure 2.5:*** *Kruskal-Wallis and Wilcoxon test results assessed the differences in soil water content, soil temperature and electrical conductivity in wild blueberries. Conditions are only reported for the fruit year for each group.*

Based on Kruskal-Wallis results, there was no significant difference observed between treatments in terms of soil temperature in 2022 (P = 0.19; Figure 2.5C). In 2023, however, the differences between treatments were significant. Wilcoxon tests showed that the HistDry treatment had a higher average soil temperature in 2022 (Figure 2.5D). The results in the HistDry treatment demonstrated the greatest variability in soil temperature. In 2023, HistDry was significantly cooler than both HistWet and Amp 2.915. In this year, the Amp2.915 treatment had the highest average soil temperatures across the season. In Maine, the statewide average temperature in 2022 was 3.3°F (0.6°C), compared to 4.3°F (0.8°C) in 2023. Therefore, the divergence in outcomes between 2022 and 2023 can be attributed to the higher average temperature, which resulted in higher soil temperature in Amp2.915 and HistWet treatments during the 2023 growing season.

Soil electrical conductivity is driven by a collection of factors including the presence/absence of soluble salts, percentage clay content, present/absence of minerals, soil water content, bulk density, and more. It is widely used in precision agriculture applications because of its relationship to yield in many commercially grown crops (Corwin and Lesch, 2005). A statistically significant difference was found in soil electrical conductivity ($P < 0.001$) in both 2022 and 2023, with HistDry treatment being lower while HistWet higher (Figure 2.5E and F). This suggests that evenly distributed rainfall across the growing season maintains high soil electrical conductivity in wild blueberry fields. This also suggests that rainfall that is well distributed across the growing season will enhance nutrient availability, while low rainfall amounts across the growing season reduce soil electrical conductivity. In addition, several studies have indicated a loss of soil nutrients under low rainfall conditions due to changes in soil water dynamics, which eventually affect the nutrients uptake by the plants (Kharivha et al., 2022).

### 2.3.2. Morphological traits

Kruskal-Wallis H-tests were used to determine the effects of treatments on plant morphological traits (Figure 2.6). It should be noted that this analysis was only completed during the fruit year (2022 for transplants derived from parent plants A, B, and C; 2023 for transplants derived from parent plants D, E, and F).

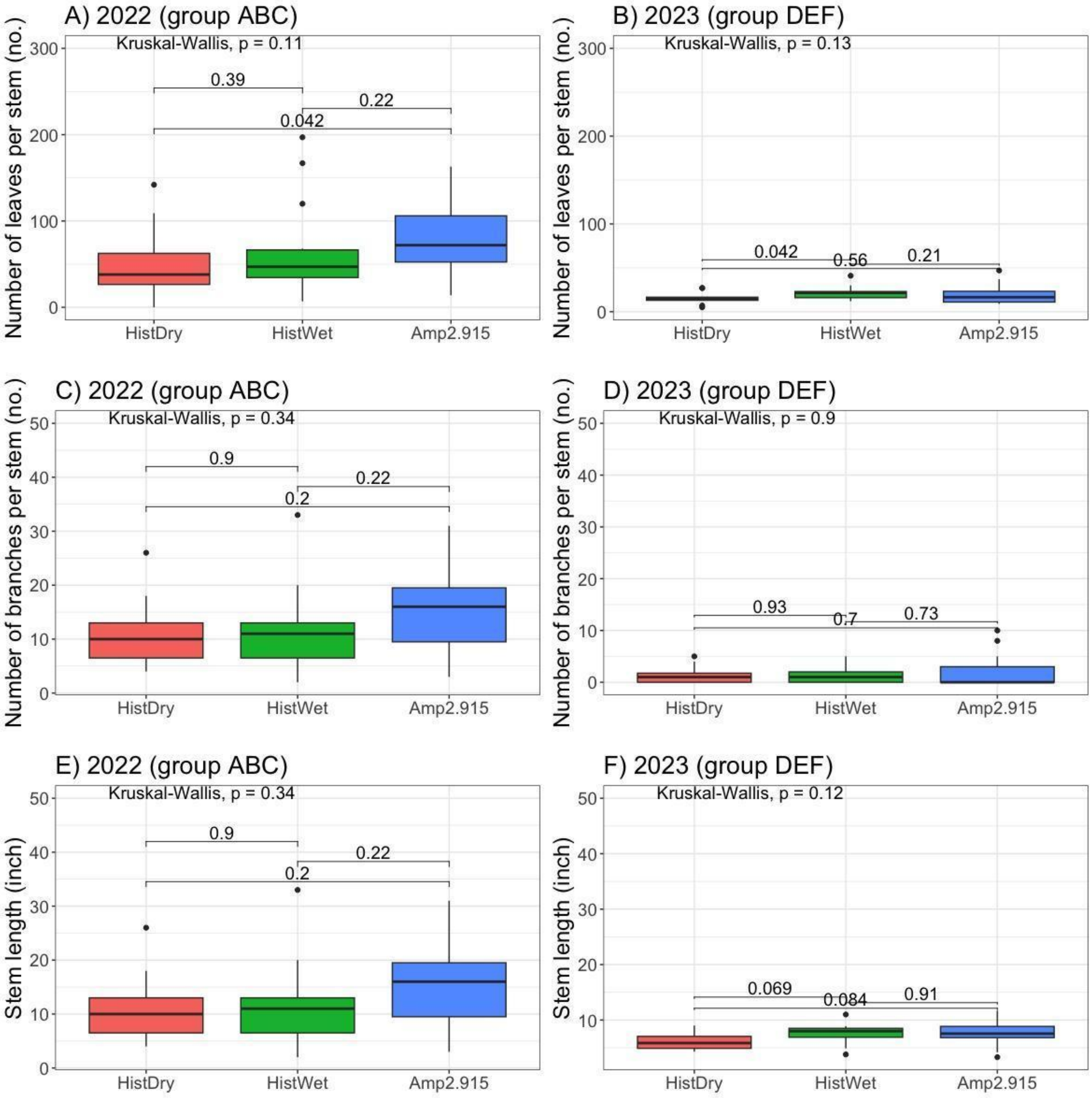


***Figure 2.6:*** *Kruskal-Wallis and Wilcoxon test results assessed the differences in the average number of leaves per stem, number of branches per stem and stem length (morphological traits) of wild blueberries.*

Kruskal-Wallis results from 2022 indicated that there was not a significant effect of treatments on stem height, number of branches, or number of leaves per stem. Although Kruskal-Wallis results were not statistically significant, one set of Wilcoxon tests revealed important differences between treatments and the number of leaves per stem. Specifically, plants watered according to Amp2.915 had significantly more leaves than HistDry in 2022 (P = 0.042). This suggests that amount of precipitation may have a greater influence on leaf development than distribution of water across the growing season. As a reminder, the Amp2.915 treatment had a relatively high annual precipitation total, but distribution was uneven with notable dry periods between days 75 and 125 of the experiment. HistDry was also characterized by uneven precipitation distribution, but the total water applied in this treatment was far less than Amp2.915 (12.53 inches, compared to 36.50 inches).

The findings from 2022 do not perfectly coincide with the findings from 2023, however. In 2023, plants subjected to the HistDry treatment (low total precipitation, unevenly distributed) had significantly fewer leaves than plants subjected to the HistWet treatment (high total precipitation, even distribution; P = 0.042). Wilcoxon tests revealed neither significant difference between HistDry and Amp2.915 (P = 0.56), nor between HistWet and Amp2.915 (P = 0.21). These results indicate that both low rainfall amounts and uneven distribution across the growing season reduces the leaf production of wild blueberries. Our 2023 results are consistent with the findings from Robinson et al. (2012), who observed that the seasonal distribution of rainfall, rather than the total amount, influences the growth characteristics and productivity of various plants in the vegetation sites in North America.

The difference in results between 2022 and 2023 can potentially be attributed to genetic variation between parent plants. Past research suggests that genetic diversity among wild blueberry plants is very high (Beers, 2019), and based on this we assume that each parent plant used in this experiment is a unique genetic individual. Previous research conducted by Barai et al. (2022) showed variation in the number of leaves among different genotypes of wild blueberries, when assessed in the same growing season. This reasoning is also aligned with findings from other crops. For example, del Chowhan et al. (2016) showed that morphological variation was observed among different genotypes of strawberry.

To more fully understand the driving mechanism behind the differences in the 2022 and 2023 results, however, further research should be conducted on a larger number of plants. It is important to note that this portion of my study did not include yield assessment due to loss of berries because of squirrels. However, the prior work of Barai et al. (2022) suggests that leaf mass is negatively correlated with wild blueberry yield. Further research should extend both the present study and the work of Barai et al. (2022) to assess the relationships more fully between wild blueberry morphology and yield.

The number of branches on a wild blueberry plant is important for several reasons. First, more branching can make mechanical harvesting more difficult (Sargent et al., 2020). Second, stems tend to have more branches if they were not adequately pruned the year before. Inadequately pruned, branching stems are likely to bear fewer berries compared to stems that have been well pruned, and which tend to have fewer branches and are taller (Eaton and Nams, 2006). I found no significant difference in the number of branches between plants managed under different treatments (2022, P = 0.34; 2023, P = 0.9) (Figure 2.6C and D). This indicates that rainfall amount and distribution have minimal effect on wild blueberry branching. This also suggests that management, specifically pruning, is a more important factor in wild blueberry branching morphology than abiotic conditions such as temperature and precipitation.

Stem length has been shown to be associated with yield in wild blueberries (Barai et al., 2022; Fournier et al., 2020), with the hypothesis being that taller plants often have larger diameter stems, higher hydraulic conductivity, higher stomatal conductance, and therefore more productive photosynthesis. It is noted that higher stems may also be more susceptible to drought and winter wind damage (Barai et al. 2022). I found no statistically significant difference in stem length in 2022 (P = 0.34) and 2023 (P = 0.12), suggesting that neither change in total amount of precipitation nor the distribution of rainfall across the season had an effect on this morphological feature (Figures 2.6E and F). This suggests that low rainfall amounts across the growing season may diminish stem growth of wild blueberries, but that total rainfall amount may have an important influence. Therefore, it is unclear whether precipitation in the current year or the preceding year is more influential on stem growth. Further research should attend to these unknowns and assess the longer-term effects of precipitation on not only stem growth, but other morphological features as well.

### 2.3.3. Functional traits

Plant functional traits examined in this study included leaf chlorophyll concentration (measured in *SPAD* units), leaf chlorophyll fluorescence (measured in *Fv/Fm*), and leaf temperature (°*C*). Leaf chlorophyll concentration is used to determine photosynthetic rate, and can be a proxy for disease pressure, nutritional and environmental stress in wild blueberry plants (Tasnim et al., 2020). Both Kruskal-Wallis and post hoc tests revealed no significant difference concerning the leaf chlorophyll concentration in both 2022 and 2023. This shows that the seasonal precipitation amount and distribution have minimal effect on the photosynthetic rates of wild blueberries. However, prior research suggested that an increase in rainfall will increase carbon absorption and photosynthesis of wild blueberries (Percival et al., 2012). A possible explanation for this is that low rainfall limits photosynthesis in plants by restricting water supply, resulting in stomatal closure and reduced carbon dioxide uptake.

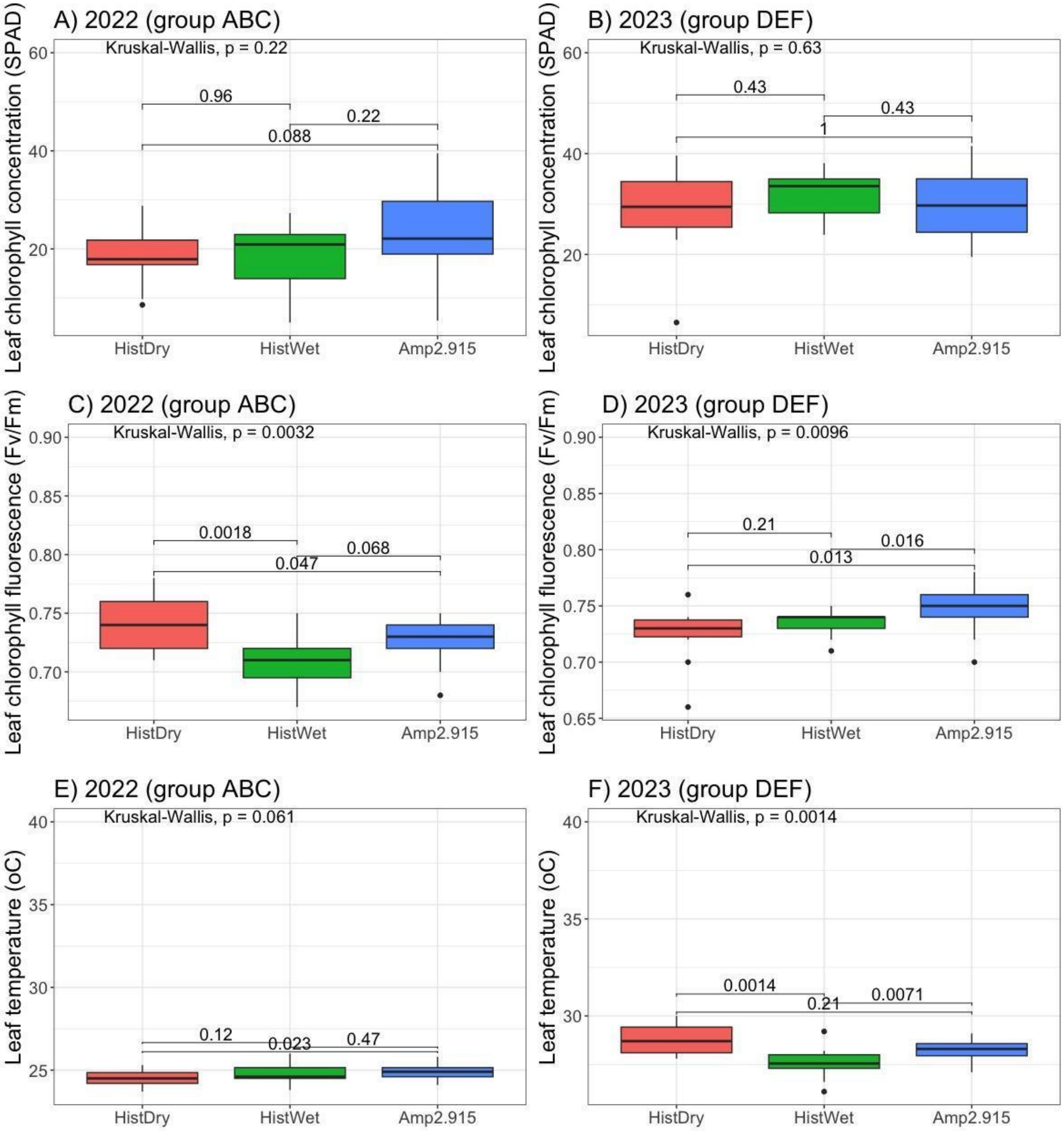


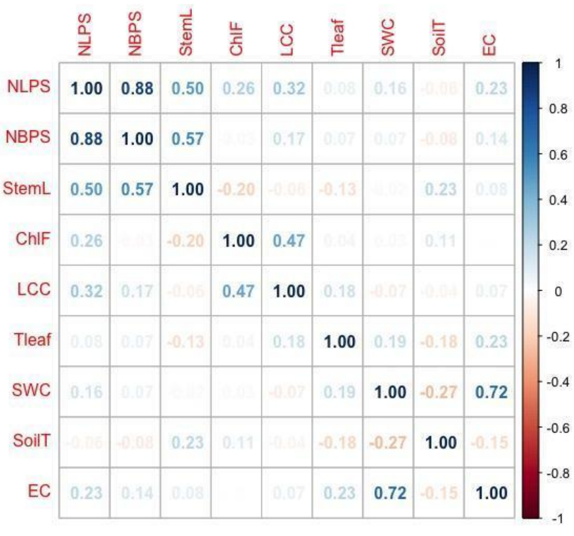
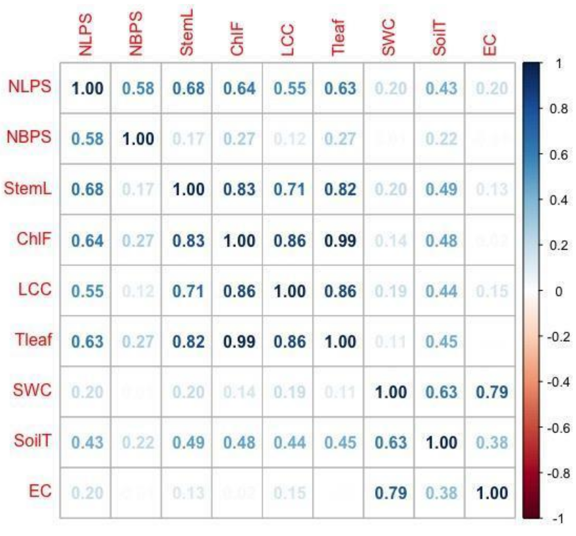
***Figure 2.7:*** *Kruskal-Wallis and Wilcoxon test results assessed the differences in leaf temperature, leaf chlorophyll concentration and fluorescence (Fv/Fm) in wild blueberries. Note that lower Fv/Fm values indicate higher levels of plant stress. Conditions are only reported for the fruit year for each group.*

Chlorophyll fluorescence, or photosynthetic potential, is measured in Fv/Fm, or the ratio of variable to maximum fluorescence. Photosynthetic potential is limited in photosystem II, the primary process through which plants produce ATP (Kawakami and Shen, 2018), is limited by thermal decay processes (Oxborough and Baker, 1997). In the present study, a statistically significant difference was observed in leaf chlorophyll fluorescence in both 2022 (P = 0.003) and 2023 (P = 0.009) (Figures 2.7C and D). This indicates the significant effects of rainfall amount and distribution on leaf water stress of wild blueberries. In 2022, significant differences were observed between HistWet and HistDry (P = 0.001) and HistDry and Amp2.915 (P = 0.047). However, low rainfall amounts induce more leaf stress in 2023 compared to 2022. This finding serves as evidence that the changes in seasonal amount of precipitation may improve the photochemical and physiological conditions of wild blueberries in future by reducing the leaf water stress. It should also be noted that excessive rainfall (as simulated through HistWet) caused greater negative effects on leaf chlorophyll fluorescence of wild blueberries than drought conditions (as simulated through HistDry). There was no statistically significant difference in Kruskal-Wallis test that assessed treatments' effect on leaf temperature in 2022 (P = 0.061). However, in 2023, a statistically significant difference was observed (p = 0.007), with HisDry leading to significantly higher leaf temperature (Figure 2.7F). This suggests that low rainfall amounts caused by seasonal change increases the leaf temperature of wild blueberries.

### 2.3.4. Relationships between morphological traits, functional traits, and soil conditions

Results from a series of Pearson's rank correlation tests (Figure 2.8) revealed that morphological traits (i.e., number of leaves per stem, number of branches per stem, and stem length) were highly correlated with one another in 2022 (all R values > 0.50). Not all traits were highly correlated in 2023, however.

Some morphological traits were highly correlated in both years. For example, there was a positive correlation between the number of leaves and branches in 2022 (R = 0.88) and 2023 (R = 0.58). This shows that a change in the number of branches is associated with greater numbers of leaves in wild blueberries. This also indicates the need of growers paying attention to management strategies that can support the growth of wild blueberry branches in order to increase the yield and productivity. Our results aligned with a finding from Kamanga et al. (2017), who observed significant and positive correlations between the number of leaves and number of branches of citrus plants. Stem length and number of leaves were positively and significantly correlated in 2022 (R = 0.50) and 2023 (R = 0.68). This indicates that the leaf production of wild blueberries is related to stem length, corroborating the findings of Paré et al. (2022).

| 1. **2022 (group ABC)** | 2. **2023 (group DEF)** |
|---|---|
|  |  |

|  | NLPS | NBPS | StemL | ChlF | LCC | Tleaf | SWC | SoilT | EC |
|---|---|---|---|---|---|---|---|---|---|
| NLPS | 1.00 | 0.88 | 0.50 | 0.26 | 0.32 | 0.08 | 0.16 | -0.06 | 0.23 |
| NBPS | 0.88 | 1.00 | 0.57 | 0.03 | 0.17 | 0.07 | 0.07 | -0.08 | 0.14 |
| StemL | 0.50 | 0.57 | 1.00 | -0.20 | -0.06 | -0.13 | 0.02 | 0.23 | 0.08 |
| ChlF | 0.26 | 0.03 | -0.20 | 1.00 | 0.47 | 0.04 | 0.03 | 0.11 |  |
| LCC | 0.32 | 0.17 | -0.06 | 0.47 | 1.00 | 0.18 | -0.07 | -0.04 | 0.07 |
| Tleaf | 0.08 | 0.07 | -0.13 | 0.04 | 0.18 | 1.00 | 0.19 | -0.18 | 0.23 |
| SWC | 0.16 | 0.07 | 0.02 | 0.03 | -0.07 | 0.19 | 1.00 | -0.27 | 0.72 |
| SoilT | -0.06 | -0.08 | 0.23 | 0.11 | -0.04 | -0.18 | -0.27 | 1.00 | -0.15 |
| EC | 0.23 | 0.14 | 0.08 |  | 0.07 | 0.23 | 0.72 | -0.15 | 1.00 |

|  | NLPS | NBPS | StemL | ChlF | LCC | Tleaf | SWC | SoilT | EC |
|---|---|---|---|---|---|---|---|---|---|
| NLPS | 1.00 | 0.58 | 0.68 | 0.64 | 0.55 | 0.63 | 0.20 | 0.43 | 0.20 |
| NBPS | 0.58 | 1.00 | 0.17 | 0.27 | 0.12 | 0.27 | 0.01 | 0.22 | [illegible] |
| StemL | 0.68 | 0.17 | 1.00 | 0.83 | 0.71 | 0.82 | 0.20 | 0.49 | 0.13 |
| ChlF | 0.64 | 0.27 | 0.83 | 1.00 | 0.86 | 0.99 | 0.14 | 0.48 | 0.02 |
| LCC | 0.55 | 0.12 | 0.71 | 0.86 | 1.00 | 0.86 | 0.19 | 0.44 | 0.15 |
| Tleaf | 0.63 | 0.27 | 0.82 | 0.99 | 0.86 | 1.00 | 0.11 | 0.45 |  |
| SWC | 0.20 | 0.01 | 0.20 | 0.14 | 0.19 | 0.11 | 1.00 | 0.63 | 0.79 |
| SoilT | 0.43 | 0.22 | 0.49 | 0.48 | 0.44 | 0.45 | 0.63 | 1.00 | 0.38 |
| EC | 0.20 | [illegible] | 0.13 | 0.02 | 0.15 |  | 0.79 | 0.38 | 1.00 |

***Figure 2.8:*** *Correlation matrix of the morphological and functional traits of wild blueberries along with edaphic conditions for 1) 2022 and 2) 2023. The vertical axis indicates the degree and direction of Pearson correlation. The definitions of trait abbreviations are listed in Table 1.1*

Functional traits were moderately to weakly correlated in 2022, and strongly correlated in 2023. In 2022, a moderate positive correlation was found between leaf chlorophyll fluorescence and leaf temperature (R = 0.47). However, a very strong positive correlation was found in 2023 (R = 0.99) (Figure 1.8). The strong correlations among dependent variables in 2023 could be attributed to genetic relatedness between the DEF parent plants (Schmidt et al., 2019). The leaf chlorophyll concentration, leaf temperature, and leaf chlorophyll fluorescence are three processes that utilize the energy absorbed by the leaf for photosynthesis, metabolic processes and temperature regulation. In 2022, a moderate positive correlation was found between leaf chlorophyll concentration and leaf chlorophyll fluorescence (measured in Fv/Fm) (R = 0.47). However, a very strong positive correlation was observed between these two traits in 2023 (R = 0.86). Leaf water stress limits ribulose bisphosphate (RuBP) synthesis and slows down the assimilation of $CO_2$ (Lawlor, 2002). This is likely because water stress in leaves destroys the ultrastructure of chloroplasts, resulting in decreased leaf chlorophyll fluorescence, leaf chlorophyll concentration, and photosynthetic activity (Sidhu et al., 2017).

The results of the Pearson's correlations also indicate a positive strong correlation between leaf temperature and leaf chlorophyll concentration (R = 0.67) which indicates that leaf temperature varies together with leaf chlorophyll concentration. Prior research shows that the photosynthetic rate of wild blueberries increases with an increase in leaf temperature but decreases substantially at a temperature higher than the optimum range (25-30°C) (Tasnim et al., 2020). Once leaf temperature surpasses this optimal range, plants will close their stomatal openings in order to conserve water.

Lastly, there were stronger correlations between edaphic conditions (soil water content, soil temperature, and soil electrical conductivity) in 2023 than in 2022. This could potentially be due to accumulated stress from two years of plants being in the study. Positive strong correlations were found between soil water content and soil electrical conductivity in 2022 ($R = 0.72$) and 2023 (0.79). This result corresponds with findings from Eigenberg et al. (2002) where a positive and significant correlation ($R = 0.896$, $P < 0.01$) was observed between the soil moisture content and soil electrical conductivity. This suggests that soil electrical conductivity varies with soil water content (Ratshiedana et al., 2023), and further explains that the sufficient soil moisture improves the soil health and fertility status by increasing the soil electrical conductivity (Turkeltaub et al., 2021; USDA, 2011). Additionally, Pearson’s correlation indicated a weak positive relationship between soil temperature and soil water content in 2022 ($R = 0.27$). However, a strong positive relationship was found between these two conditions in 2023 ($R = 0.63$). Although soil water content has a considerable influence on soil electrical conductivity, it is also affected by other factors such as air temperature and soil texture (Friedman, 2005).

### 2.3.5. Limitation of the study

This study reported findings for both the ABC and DEF group of parent plants. It is important to note that the DEF group were subjected to two years of experimental treatments, resulting in significantly higher levels of stress than the ABC group. These differences in treatment duration and subsequent stress levels between the two groups are essential factors to consider when interpreting the presented results. Additionally, the study did not include collection of yield data due to squirrel herbivory, future work could take a similar approach and carry the analysis through to its logical conclusion.

## 2.4. Conclusion and recommendations for future research

In this study, I found that relatively low annual precipitation that is unevenly distributed across the growing season, as simulated in the HistDry treatment, leads to a reduced number of leaves. Additionally, high seasonal precipitation amounts with uneven distribution (as simulated through Amp2.915) increases the leaf production of wild blueberries. This indicate that, for leaf production of wild blueberries, the distribution of rainfall is less important than its amount. Therefore, if precipitation patterns progress as expected (i.e., if higher annual rainfall is expected to arrive in heavier and more intense rain events, interspersed with droughts and dry periods), we can expect an increase in the number of leaves per stem.

Lower average precipitation amounts punctuated by seasonal drought (simulated through the HistDry treatment) lead to reduced leaf chlorophyll concentration, and by extension reduced photosynthesis. This finding reinforces past calls to improve irrigation infrastructure in wild blueberry production systems (Dalton et al. 2003). Further, our results suggests that the future precipitation variability across the wild blueberry growing season may reduce the soil water content, which in turn lowers the soil electrical conductivity. To ensure future profitability, growers should consider using irrigation strategies, which ensure that plants receive adequate water supply. Doing so will improve the soil conditions that will enable the plants to maintain the optimum photosynthetic performance, leading to improved yields and quality.

This study also found an important relationship between the soil electrical conductivity and evenness of precipitation across the growing season. Soil electrical conductivity is closely aligned with soil water conditions and is also positively correlated with yield in soils with higher proportions of clay and high levels of organic matter. Soils with high proportions of silt and sand are often characterized by low soil electrical conductivity (Farooque et al., 2012). It should be noted that, in field settings, wild blueberry soils are highly variable, which means that wild blueberry plants have heterogeneous access to nutrients and water throughout the growing season. This again points to the importance of using irrigation to supplement precipitation in coming years. By maintaining optimal soil water content, soil electrical conductivity can be held consistent across the season and by extension crop access to critical nutrients. Of course, yield is influenced by a multitude of factors (Farooque et al. 2016), but it is clear that soil properties are an important part of the equation.

Lastly, the correlation matrix results indicate a significant relationship between number of leaves and branches, leaf chlorophyll concentration and fluorescence, and soil water content and soil electrical conductivity. This indicates the appropriate next step in data analysis would be a factor analysis and regression of factors on the response variables. This would allow us to better understand the relationships between morphological traits, functional traits, and edaphic conditions, and provide wild blueberry growers with better information for understanding annual and long-term crop development and performance.

# CHAPTER 3: ASSESSMENT OF WATER NEEDS OF WILD BLUEBERRIES AT FOUR PHENOLOGICAL STAGES

## Abstract

Establishing effective irrigation amount and frequency for agricultural crops is necessary for water resource management and ensuring that water is used efficiently. Irrigation scheduling refers to when and how much water is applied to a crop in order to support healthy growth and development. In this study, I examined different irrigation schedules for wild blueberries during a typical growing season in the Northeast United States. Previous studies on the plant-water needs of wild blueberries only examined weekly water applications and have not tested irrigation frequency. In fact, a large number of commercial wild blueberry growers do not irrigate at all, relying on precipitation to meet crop water needs. When irrigation does take place, the common irrigation schedule is to supply 1 inch (2.5 cm) of water per week in both crop and non-crop years. The purpose of this study is to establish recommendations for wild blueberry irrigation schedules that consider optimal amounts, frequency, and crop developmental stages. This study utilized a factorial design approach, using three different irrigation scheduling treatments including (a) 1-inch of water per week (high irrigation frequency or HIF), (b) 2-inch (5cm) of water every other week (medium irrigation frequency or MIF), and (c) 3-inch (7.5cm) of water every third week (low irrigation frequency or LIF). The performance of wild blueberries was evaluated at crop and non-crop years, including the leaf development, flowering, green fruits and fruit ripening stages. Our results indicate that the HIF had a favorable impact on wild blueberry plants during the leaf development, flowering, green fruit, and fruit ripening stages. Additionally, applying 2-inch (5cm) of water every other week has the potential to produce as many flowers as applying 1-inch (2.5cm)

per week. Notably, the LIF irrigation schedule proved detrimental to crop performance at each growth and developmental stage. These findings suggest that growers should supplement ambient precipitation when rainfall is below 1 inch (2.5cm) per week during leaf development, green fruit and ripening stages. Future research should further investigate the relationship between flowering, irrigation, and the ability of wild blueberries to retain fruits through to harvest.

## 3.1. Introduction

For the past several decades in Maine, wild blueberries have been cultivated with and without the use of irrigation (Glass et al., 2005; Struchtemeyer, 1956). However, in recent years, the variability of rainfall has necessitated an increased use of irrigation (Dalton and Yarborough, 2004). Although wild blueberries are considered drought resistant crops, several studies have indicated that the application of supplemental water during the dry periods can reduce crop failure, by improving the yields and quality of harvested berries (Hunt, 2009; Dalton et al., 2002). Long-term weather patterns in wild blueberry production regions in Maine and maritime Canada indicate that wild blueberries will receive enough water (in the form of rainfall) in one of every five years in August (Hunt, 2009). Rather than relying on rainfall alone, irrigating wild blueberries in both crop and non-crop years can significantly increase vegetative growth and yield. In addition, although several research projects on plant-water needs of wild blueberry have been conducted, a simple technique to determine plant water demand at various stages of the developmental and production cycles is yet to be developed (Percival et al., 2003).

Like many other crops, wild blueberries take most of the water they use through their roots (Hunt, 2009). Plant water uptake in the root zone is influenced by root architecture, soil type, and water availability (Lobet et al., 2014). For example, low soil water availability not only limits the development of the crop, but impairs physiological functions, thereby reducing the growth and production of berries (Bryla et al., 2012). Excess soil water content, on the other hand, can damage the root hairs and cause poor aeration in the root zone, thereby reducing plant water uptake (Duddek et al., 2023). Wild blueberries, like most members of the *Ericaceae* family, are more susceptible to overly wet or dry conditions at some stages of development than others (Hunt, 2009). This implies that an effective irrigation scheduling should take into consideration the sensitivity of crops to water stress at various growth and developmental stages. Water stress has adverse effects on the morphological and physiological response of wild blueberries (Benoit et al., 1984; Glass et al., 2005). As a result, in order to establish irrigation thresholds, it is important to understand the phenological responses at different phases of growth.

### 3.1.1. Phenology, phenological stages, and variation

Plant phenology is the study of plant life-cycle events in response to changes in climate conditions (Stucky et al., 2018). Phenology is a science that touches all aspects of ecosystem, community, and evolutionary processes (Forrest and Miller-Rushing, 2010). It is directly and indirectly connected to climate conditions and plays an important role in ecosystem processes such as nitrogen and carbon cycling (Katal et al., 2022). Climate-driven phenological changes affect the fitness of plants through changes in resource availability (Henry et al., 2022). This is because the overall abundance of resources has a significant influence on availability and should not be overlooked while studying phenological synchrony. Over the last several decades, much effort has been put in place to quantify the level at which plant phenophases respond to local variations in temperature and precipitation (Fitchett et al., 2015). Despite an increase in attention to this important topic, specialty crops such as wild blueberries have so far been overlooked.

Phenological events in plant communities are being studied using both satellite remote sensing and direct, or ground-based phenological observations (Fitchett et al., 2015). Even though the shifts in plant phenology have major consequences for ecosystem functions such as competition, nutrient cycling, and food webs, some phenological changes could have a positive impact. For example, some species and genotypes adapt to changing environmental conditions (Parmesan and Yohe, 2003), and their performance is enhanced. Therefore, phenological stages can be thought of as bioindicators that can be used for detecting the ecological impacts of climate change on plants (Schwartz et al., 2013).

Furthermore, it has been observed that plant allometry influences bud phenology in two different *Vaccinium* species studied (*Vaccinium angustifolium* and *Vaccinium myrtilloides*) (Fournier et al., 2020). *Plant allometry* is the relationship between the size of an organism and components of its morphology, physiology, and life cycle. Understanding plant phenology and allometry, provides important information about how plants partition resources, including features that are useful in process-based ecosystem models (Rudgers et al., 2019).

Phenological observations are opening new windows for research in the areas of ecology and environmental science due to an increasing concern about forecasting and documenting the effects of climate change (Forrest and Miller-Rushing, 2010). Advances in the areas of ecology, phylogenetics, quantitative genetics, molecular and developmental biology have also contributed to advancement of phenological research (Forrest and Miller-Rushing, 2010). As phenology encompasses all aspects of plant life cycles, monitoring phenological stages is also important for farmers who want to employ certain management strategies (e.g., irrigation, pollination, harvesting, fertilizer or pesticides applications) at different phases of the crop production cycle.

Still, there is much work to be done to understand how a changing climate will or will not influence plant phenology, and by extension, food production and food security.

### 3.1.2. Environmental factors (E), genetic factors (G), and their interaction

Environmental factors such as temperature, precipitation, and photoperiod have been used in phenological studies to estimate phenological and morphological shifts that could manifest in the future, considering the dramatic environmental changes that climate change will likely bring (Miller-Struttmann et al., 2015). This is because adverse climatic conditions (e.g., drought, excess rainfall, excess heat) may lead to abnormal phenological cycles which could in turn result in prolonged dormancy, mismatched synchrony with pollinator species, and yield loss (Henry et al., 2022). The timing of plant phenological stages may also change as a result of shifting environmental factors, especially temperature, and precipitation (Piao et al., 2019), as different species of plant respond differently to different cues (Murphy et al., 2007).

Genotypes lead to both heritable variation and local adaptations to the local environment, which are often manifested phenologically and morphologically. Thus, shifts in phenological development affect the reproduction and fitness of individual plants, as well as the fitness of other organisms (e.g., bees and other insect pollinators) that are dependent on them. Interpreting these changes is challenging in many crops, including wild blueberries, given the high degree of genetic diversity (Barai et al., 2022), and lack of an understanding about how this diversity interacts with environmental stresses to affect plant development and performance. The genes inherited from the parents and expressed by each individual can result in phenological variations among the individuals of a common species. Wild blueberry is a highly genetically diverse crop where thousands of genetically distinct individuals can exist in a single field (Beers et al., 2019). This diversity is credited to the fact that wild blueberries are commercially cultivated in the absence of breeding and planting. Rather, endemic wild blueberry plants spread via rhizomes when conditions are favorable (i.e., highly acidic well-drained soils, overstory vegetation, and competitive weeds removed) wild blueberries establish themselves and can be commercially cultivated.

The interaction of environmental and genetic factors contributes to variations in the timing of phenological stages (Henry et al., 2022). This leads to early or late emergence of leaves, flowers, or fruits, and can influence the susceptibility of plants to drought, frost, or mechanical injury. Simultaneously, changes in environmental conditions can alter plant phenotype and genetic expression, leading to spatial clusters of plant individuals with genetic similarities (Albecker et al., 2022). The local adaptation of an organism via genetic responses along climatic gradients can be co-gradient (when both environmental and genetic effects on a phenotypic character act in the same way), counter-gradient (when they act on the plants in opposite ways), or have no relationship with the climatic gradient (Conover & Schultz, 1995). Wild blueberry production is confronted with challenges imposed by climate change, thus, understanding these interactions and how they affect wild blueberry development is critical for developing an irrigation plan that will mitigate the negative effects of climate change.

### 3.1.3. Estimation of crop water requirements

Several methods and technologies are used to establish optimal irrigation amount and frequency. These often incorporate soil type and weather conditions, primarily evapotranspiration (Bryla, 2015). For efficient irrigation management in the wild blueberry industry, growers should be able to precisely estimate the crop water requirements. Therefore, weather-based factors such as crop evapotranspiration, rainfall amount and developmental stage of a crop have to be taken into consideration (Hanson et al., 2003). Doing so ensures the provision of adequate water to plants while preventing both overwatering and underwatering. Crop water requirement is defined as the water depth needed to compensate for evapotranspiration for growing disease-free crops, and to achieve the optimum production yield (Gabr and Fattouh, 2021). Plant transpiration accounts for about 90% of total evapotranspiration, while evaporation accounts for the remaining 10%. To derive crop water requirements from reference evapotranspiration, the specific crop coefficient must be determined.

$$ETc = ETo \times Kc$$

*ETc = Crop water requirements; ETo = Reference evapotranspiration; Kc = Crop coefficient*

The crop coefficient is determined by the prevailing weather conditions, growth stages of a crop, and the growing season. It is employed to estimate the crop water requirements, incorporating the impacts of different weather conditions into reference evapotranspiration and crop factors as integral components of the crop coefficient. For example, irrigation scheduled using crop coefficient, according to the FAO56 guidelines resulted in an annual water savings of 0.8 ML/ha, compared to 3.6 ML/ha using a traditional approach typically employed by highbush blueberry growers in Australia, without reducing berry yield or quality (Keen and Slavich, 2012). Several methods and technologies have been developed to address increasing water scarcity challenges in different agricultural production regions in the world (Friedman et al., 2023). The FAO56 approach, which uses the Penman-Monteith equation for crop coefficient and reference crop potential evapotranspiration, has been adopted as a global standard for farmers, researchers and extension workers to determine potential and actual crop evapotranspiration rates.

According to FAO56 guidelines, the Penman-Monteith approach is still the most commonly used method for estimating crop reference evapotranspiration from meteorological data. Not only that, the Penman-Monteith equation is widely used to estimate vegetation transpiration or soil evaporation (Allen, 1996). The purpose of utilizing the actual evapotranspiration rate of a crop, as opposed to a reference, is to obtain more precise information about crop irrigation needs (Steduto et al., 2012; Gabr and Fattouh, 2021). In an era of climate change, where users increasingly compete for water resources, irrigation approaches aimed at maximizing water use efficiency will become even more crucial than in the past (Hunt et al., 2009). Crop water requirements are influenced by the amount of water evaporating from plants and soil surfaces through evaporation and transpiration (i.e., evapotranspiration). Assuming all other environmental factors remain constant, the evapotranspiration rate will be higher on drier, hotter, or windier days than in humid or cooler conditions.

Ambient precipitation and soil water content in temperate humid regions, like the Northeast United States, are often adequate to satisfy the water demand of agricultural crops. The need to supplement crop water needs with irrigation varies year-to-year. In this setting, irrigation is best used to ensure that the short-term water deficits do not reduce the yield of agricultural crops (Dalton et al., 2002).

The irrigation requirements of a crop change over the course of the growing season, based on amount and frequency of rainfall, evapotranspiration rates, and crop phenological stage (Hunt, 2009; Zhang et al., 2023). These are important factors that determine the irrigation needs of wild blueberries. Maine has a continental climate with relatively high humidity (Fernandez et al., 2020). In arid and semi-arid regions of the world, for example, irrigation is unquestionably necessary. However, in humid regions where there is enough rainfall to cover crop water demands in some or most years, the situation is more challenging (Wilson, 1898). This is because rainfall conditions in these regions change every year, and yield reductions occur when evapotranspiration demand of a crop is not satisfied.

### 3.1.4. Irrigation scheduling and irrigation for shallow rooted crops

The net irrigation water requirement is defined as the amount of water that must be supplied through an irrigation system to ensure that the agricultural crops receive the required amount of water for healthy and successful growth (Pereira and Alves, 2005). When irrigation water is the only water source for the plant, the irrigation requirement must be higher than the crop water requirement for an efficient irrigation system. This is because there may be losses due to evaporation, runoff, and infiltration beyond the root zone, during the irrigation process. Also, if the crop receives some part of the water from alternative sources (e.g. deep seepage, rainfall, etc.), the crop water requirement will be slightly higher than the demand for irrigation water (Gabr and Fattouh, 2021). As a result, the net irrigation water requirement is calculated as follows:

$$\text{NIWR} = \text{CWR} - \text{Effective rain}$$

*NIWR = Net irrigation water requirement; CWR = Crop water requirements*

Irrigation schedules take into account the net irrigation water requirement, and are used to guide the timing, amount, and spatial distribution of water in agricultural crop production. Each crop has several stages of growth and development. Because irrigation needs are variable at each stage, irrigation planning must incorporate scheduling for optimal use of water resources (Solangi et al. 2022). When developing an irrigation schedule, the following variables must be considered: (a) the daily crop water requirement, (b) the effective depth of the crop root zone, and (c) the soil type (Gabr, 2018). In addition, other significant factors include optimum water use, crop tolerance, and crop sensitivity to water stress at different growth stages (FAO, 2007).

Irrigation water is applied based on crop water requirements and soil water conditions. The use of irrigation in agricultural systems has different effects depending on the amount, frequency, and annual precipitation in the growing area. Irrigation frequency is one of the important factors that have a significant effect on crop yields (FAO, 2007). This could translate into short frequency irrigation events, or watering in differentiated blocks based on topography, soil type, or other environmental conditions. Fare et al. (1994) found that increasing irrigation frequency while reducing the volume can be used to reduce the nutrients leaching.

The timing of irrigation and precipitation holds significance. For instance, water applied to cropland through irrigation or precipitation at night tends to flow downward, influenced by capillary and gravitational forces (Friedman, 2023; Gul et al., 2023). Conversely, during the day, when transpiration and water uptake resume, only a small portion of water will move upward against gravity, primarily due to capillary action (Friedman, 2023). Elevating the irrigation amount is likely to increase the rates of evapotranspiration during the daytime hours. However, the ratio of evapotranspiration to irrigation rate will also rise with an increased irrigation rate. This highlights the pivotal role that the irrigation amount plays in regulating the actual evapotranspiration rate.

### 3.1.5. Research objectives

The purpose of this study is to establish recommendations for wild blueberry irrigation schedules that consider optimal amounts, frequency, and crop developmental stages. Inefficient irrigation management leads to either excessive or inadequate water application, resulting in the leaching of nutrients (Schattman et al., 2023). This nutrient leaching poses a significant threat to the yield potential and profitability of wild blueberries (Gumbrewicz and Calderwood, 2022). Therefore, the adoption of optimal irrigation scheduling is crucial to maintain the appropriate soil water content and nutrient levels within the crop root zone. The specific objectives of the study were to:

1. Assess the effects of irrigation treatments with different frequencies on morphological traits, functional traits, and edaphic conditions.
2. Segment findings by phenological stages to better understand when irrigation is more, or less, important for ensuring crop health and productivity.

## 3.2. Materials and methods

### 3.2.1. Study sites and plant materials

The study utilized a 2x3 factorial design (two factors, each with three levels). The treatment schedule consisted of three different irrigation frequencies, including 1-inch (2.5cm) of water per week (high irrigation frequency, HIF), 2-inch (5cm) of water every other week (medium irrigation frequency, MIF), and 3-inch (7.5cm) of water every third week (low irrigation frequency, LIF). In each of these three treatments, the total volume of water used over the simulated growing season was equal to 27 inches (68.58cm). Individual plants were handled under the same treatment for both years of the study (2022, 2023).

Wild blueberry plants were harvested from Wyman’s production fields in Deblois, Washington Co., Maine, United States (44°53'51.00" N, 68°40'07.93" W), on May 6, 2022 and June 10, 2022. The location experiences an average, minimum, and maximum temperature of

6.3°C, -10.6°C, and 24.2°C, respectively. Throughout the year, there are, on average, 142 rainy days, with precipitation reaching an average of 1,298mm and snowfall measuring 158cm. The region features a rocky shoreline and well-drained acidic sandy loam soils. The specific soils in the harvested plant location are categorized as Colton gravelly sandy loam, with a high-water table depth of 203cm. The location from which the wild blueberry plants were harvested is an actively managed commercial production area.

Wild blueberry plants from 90 pots were selected, tagged and maintained for data collection and measurements. Three of the six “parent plants” chosen (A, B, and C) were in “crop” year in 2022, while the remaining three (D, E, and F) were in "prune" year, which grew vegetatively and produced flowers and fruits in 2023. This determination was made based on prior research showing the high degree of genetic diversity in wild blueberry fields (Beers et al., 2019; Barai et al., 2022), and by visual observation of plant phenological differences. In future project phases, we will assess the genetic similarities and differences among the plants utilized in this study.

### 3.2.2. Data collection

In 2022, data were collected for leaf development, flowering, green fruit, and fruit ripening stages. Consequently, plant characteristics were documented at these four phenological stages: leaf development, flowering, green fruit, and fruit ripening. Additionally, we monitored the phenological stages of six distinct genotypes of wild blueberry in two years. Throughout the experimental period, 15 plants were observed for each parent plant, totaling 90 plant pots. At each phenological stage, we measured both the morphological and functional traits of individual plants, along with edaphic conditions. It should be noted that wild blueberries are considered to have reached a particular phenological stage when more than 70% of the total number of individual plants in the field have reached that stage (UMaine Extension, 2021). Currently, the University of Maine Cooperative Extension has established an online wild blueberry phenology tracker that can assist growers and researchers to understand and keep track of the phenological stages of this important crop. A crop specific tracker of this type is highly useful to growers, as plant phenology, physiology, and architecture are species-specific and strongly related to the allometric traits of plants (Fournier et al., 2020).

**Table 3.1:** Leaf and stem morphological and functional traits of wild blueberries, along with edaphic conditions that were evaluated in this study.

| Type of variable | Variable name | Units | Production cycle | Phenophase | Data collection date |
|---|---|---|---|---|---|
| Morphological traits | Number of leaves per stem | no. | Crop and non-crop year | LD, F, GF, FR | LD: June 28, 2022 & May 24, 2023<br>F: Data was not collected<br>GF: July 30, 2022 & June 24, 2023<br>FR: August 22, 2022 & September 2, 2023 |
| | Number of flowers per stem | no. | Crop year | F | F: July 22, 2022 & June 1, 2023 |
| | Number of branches per stem | no. | Crop and non-crop year | LD, F, GF, FR | LD: June 28, 2022 & May 24, 2023<br>F: July 22, 2022 & June 1, 2023<br>GF: July 30, 2022 & June 24, 2023<br>FR: August 22, 2022 & September 2, 2023 |
| | Stem length | inch | Crop and non-crop year | LD, F, GF, FR | LD: June 28, 2022 & May 24, 2023<br>F: July 22, 2022 & June 1, 2023<br>GF: July 30, 2022 & June 24, 2023<br>FR: August 22, 2022 & September 2, 2023 |

*Table 3.1 Continued*

| | | | | | |
|---|---|---|---|---|---|
| Functional traits | Leaf chlorophyll concentration | SPAD | Crop and non-crop year | LD, F, GF, FR | LD: June 28, 2022 & May 25, 2023<br>F: July 23, 2022 & June 9, 2023<br>GF: July 31, 2022 & June 25, 2023<br>FR: August 23, 2022 & September 5, 2023 |
| | Leaf chlorophyll fluorescence | Fv/Fm | Crop and non-crop year | LD, F, GF, FR | LD: June 28, 2022 & May 26, 2023<br>F: July 23, 2022 & June 9, 2023<br>GF: July 31, 2022 & June 27, 2023<br>FR: August 23, 2022 & September 6, 2023 |
| | Leaf temperature | °C | Crop and non-crop year | LD, F, GF, FR | LD: June 28, 2022 & May 25, 2023<br>F: July 23, 2022 & June 9, 2023<br>GF: July 31, 2022 & June 25, 2023<br>FR: August 23, 2022 & September 5, 2023 |
| Edaphic conditions | Soil water content | %vwc | Crop and non-crop year | LD, F, GF, FR | LD: June 29, 2022 & May 23, 2023<br>F: July 23, 2022 & June 9, 2023<br>GF: July 31, 2022 & June 26, 2023<br>FR: August 24, 2022 & September 5, 2023 |
| | Soil temperature | °C | Crop and non-crop year | LD, F, GF, FR | LD: June 29, 2022 & May 23, 2023<br>F: July 23, 2022 & June 9, 2023<br>GF: July 31, 2022 & June 26, 2023<br>FR: August 24, 2022 & September 5, 2023 |
| | Soil electrical conductivity | mS/cm | Crop and non-crop year | LD, F, GF, FR | LD: June 29, 2022 & May 23, 2023<br>F: July 23, 2022 & June 9, 2023<br>GF: July 31, 2022 & June 26, 2023<br>FR: August 24, 2022 & September 5, 2023 |

*LD = Leaf development; F = Flowering; GF = Green fruit; FR = Fruit ripening*

A single stem from the middle of the pot was selected, tagged and maintained for repetitive data collection on morphological traits. The number of leaves per stem were measured at each phenological stage, when leaf shoots were extended and enlarged in a whorled pattern. The number of branches per stem was measured when vegetative buds developed into new branches. The stem length was measured from the base of the stem to the highest point of the plant using a measuring tape (Stanley 12 ft.). The number of flowers was recorded during the flowering stage, when the flower petals on the tagged plants were opened for pollination.

Three stems from the middle of each pot, totaling 270 stems, were randomly selected, tagged, and maintained for data collection on functional traits. The leaf chlorophyll concentration was measured in a SPAD unit using a SPAD Chlorophyll Meter (SPAD MC-100, Logan, Utah, USA). A Fluke 62 Max+ handheld infrared thermometer (Fluke Corporation, Everett, WA, USA) was used to measure the temperature of the leaves. At the time of data collection for the leaf chlorophyll fluorescence and leaf temperature, a single stem from the middle of the pot was chosen at random. Leaf chlorophyll fluorescence was measured in Fv/Fm using a portable fluorometer (Prmyslová 470, 664 24 Drásov, Czech Republic). The average of three readings was reported and the data collection dates for 2022 were August 26 and 27; and September 2, and 5 for 2023.

Edaphic conditions assessed in this study included soil water content, soil temperature, and soil electrical conductivity, all of which were measured using a Fieldscout TDR 150 Soil Moisture Meter (Spectrum Technologies Inc., Aurora, IL, USA). The soil water content was measured in volumetric water content (%vwc), while the soil temperature in degree Celsius (°C), and soil electrical conductivity in mS/cm. In 2022, data was collected on June 12, July 23, August 3, and August 14. In 2023, the collection dates were May 23, June 6, June 26, and September 5 at the leaf development, flowering, green fruit and fruit ripening stages.

### 3.2.3. Statistical analysis

A series of Kruskal-Wallis H-tests were used to determine trait variation (i.e., leaf, floral and fruit phenology) between treatments at four phenological stages. Wilcoxon post hoc tests were used to determine differences between treatments. 0.05 level of significance was used in this study. The effects of irrigation treatments on morphological traits, functional traits, and edaphic conditions were analyzed using R statistical software (Version 4.3.2, 2023) with the packages such as ggplot2 (V3.4.4; Wickham, 2016) to create box and bar plots, and ggpubr (Kassmbara, 2023) for visualizations of paired comparisons.

## 3.3. Results

Although the effects differed depending on treatment group (ABC versus DEF, Figure 3.1), our results indicated that irrigation frequency affected the average number of leaves per stem during the leaf development and fruit ripening stage. Specifically, HIF recorded a larger number of leaves at the leaf development and fruit ripening stages, compared to LIF. This suggests that extended periods between waterings increases the loss of leaves later in the growing season, especially when plants have produced high numbers of leaves early in the growing season. In 2023, no significant difference was observed between treatments in either leaf development, green fruit, or fruit ripening stages.

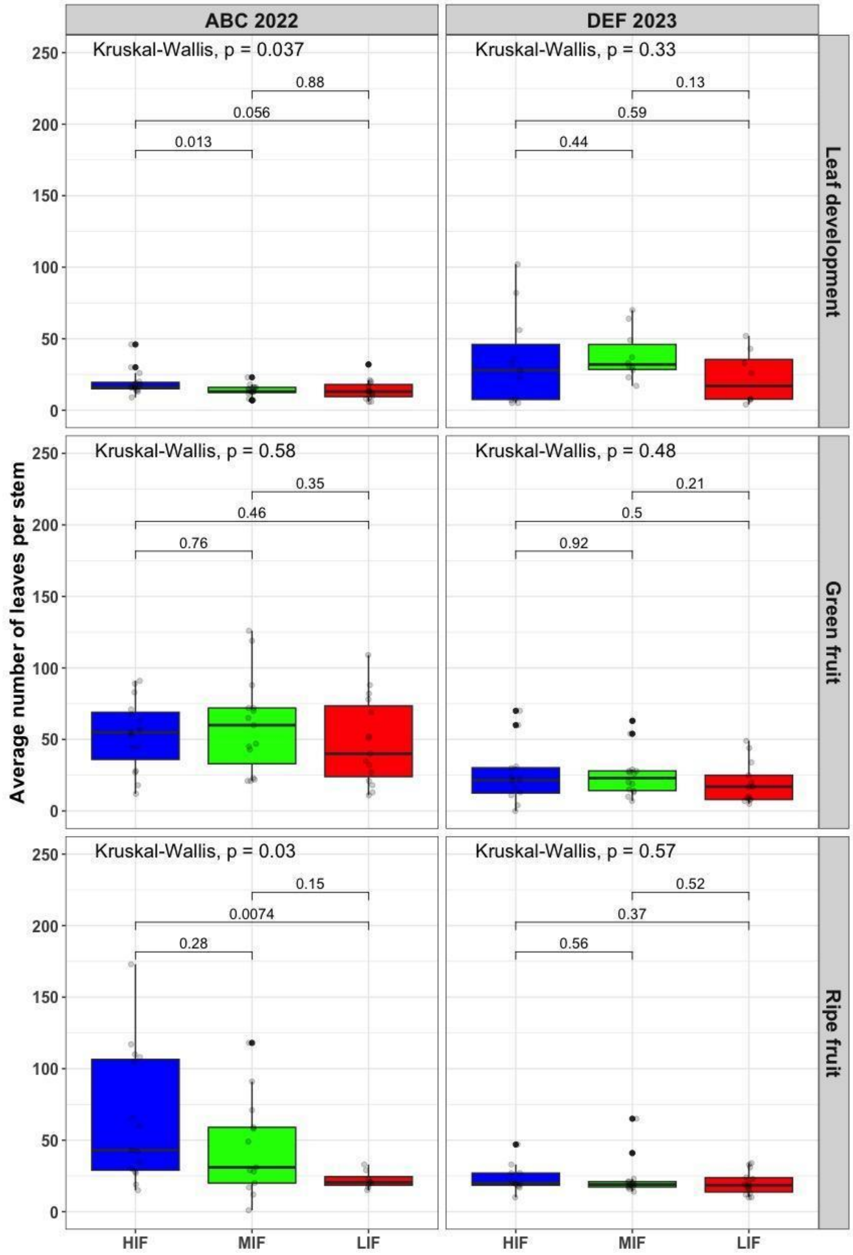


***Figure 3.1:*** *Average number of leaves by treatment at leaf development stage, green fruit, and fruit ripening stages. Error bars show standard deviation. HIF = high irrigation frequency, HIF; MIF = medium irrigation frequency; LIF = low irrigation frequency.*

In both 2022 and 2023, there were no significant differences observed among the treatments regarding the average number of branches per stem (Figure 3.2). This observation leads to the conclusion that the irrigation frequency does not have any noticeable impact on the growth of branches in wild blueberries across the four major phenological stages, including the leaf development, flowering, green fruit, and fruit ripening stages.

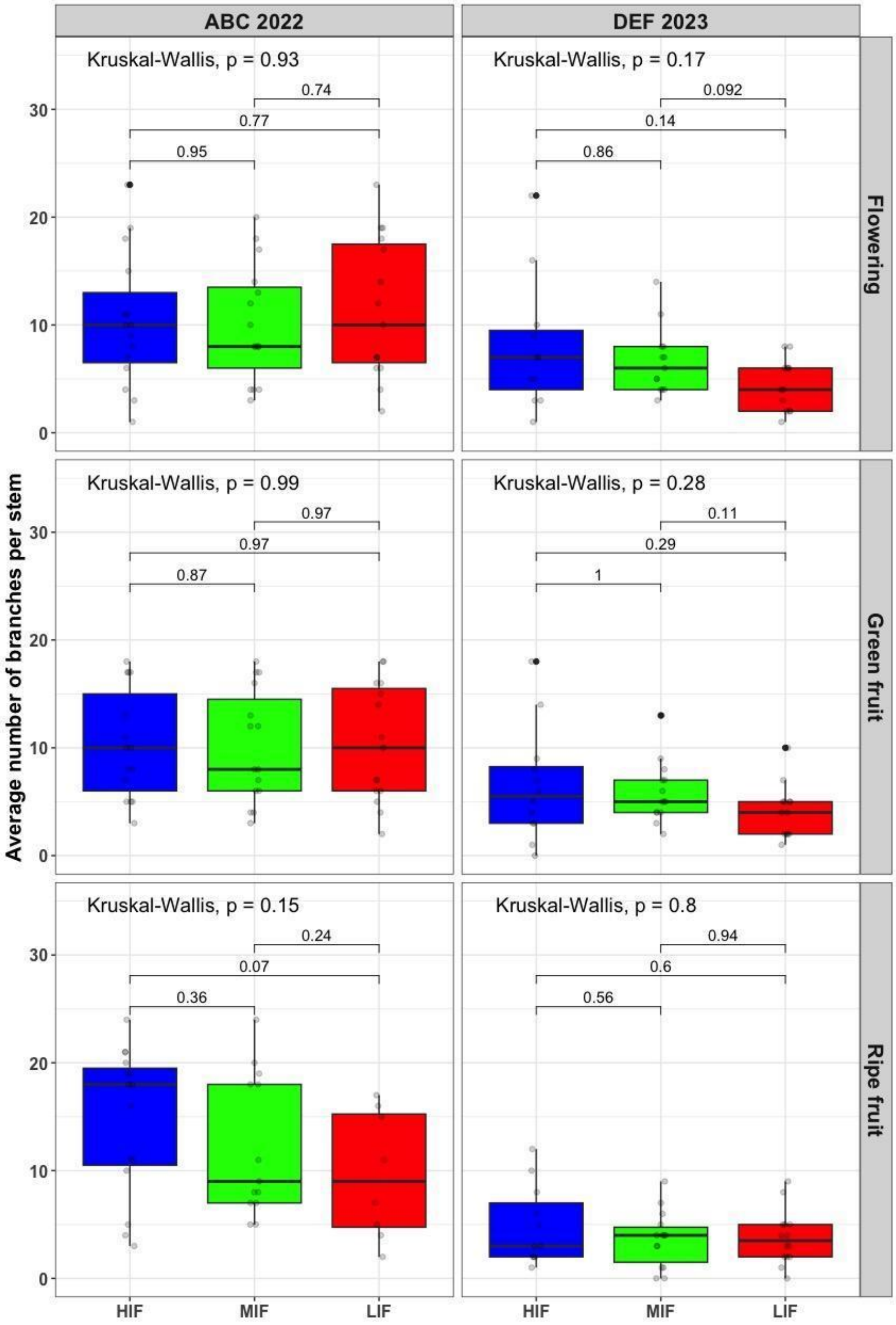


***Figure 3.2:*** *Average number of branches by treatment at flowering, green fruit, and fruit ripening stages. Error bars show standard deviation. HIF = high irrigation frequency, HIF; MIF = medium irrigation frequency; LIF = low irrigation frequency.*

Significant differences in stem length were observed among treatments during various growth and developmental stages (Figure 3.3). Notably, the plants under HIF had significantly longer stem length than MIF during the leaf development and flowering stages in 2023, and significantly longer than LIF during the green fruit (2023) and fruit ripening (2022) stages. The LIF treatment within the ABC group, on the other hand, resulted in the shortest stem length. This finding reveals a link between irrigation frequency and stem elongation in wild blueberries, which implies that dry periods between waterings may slow down the stem elongation.

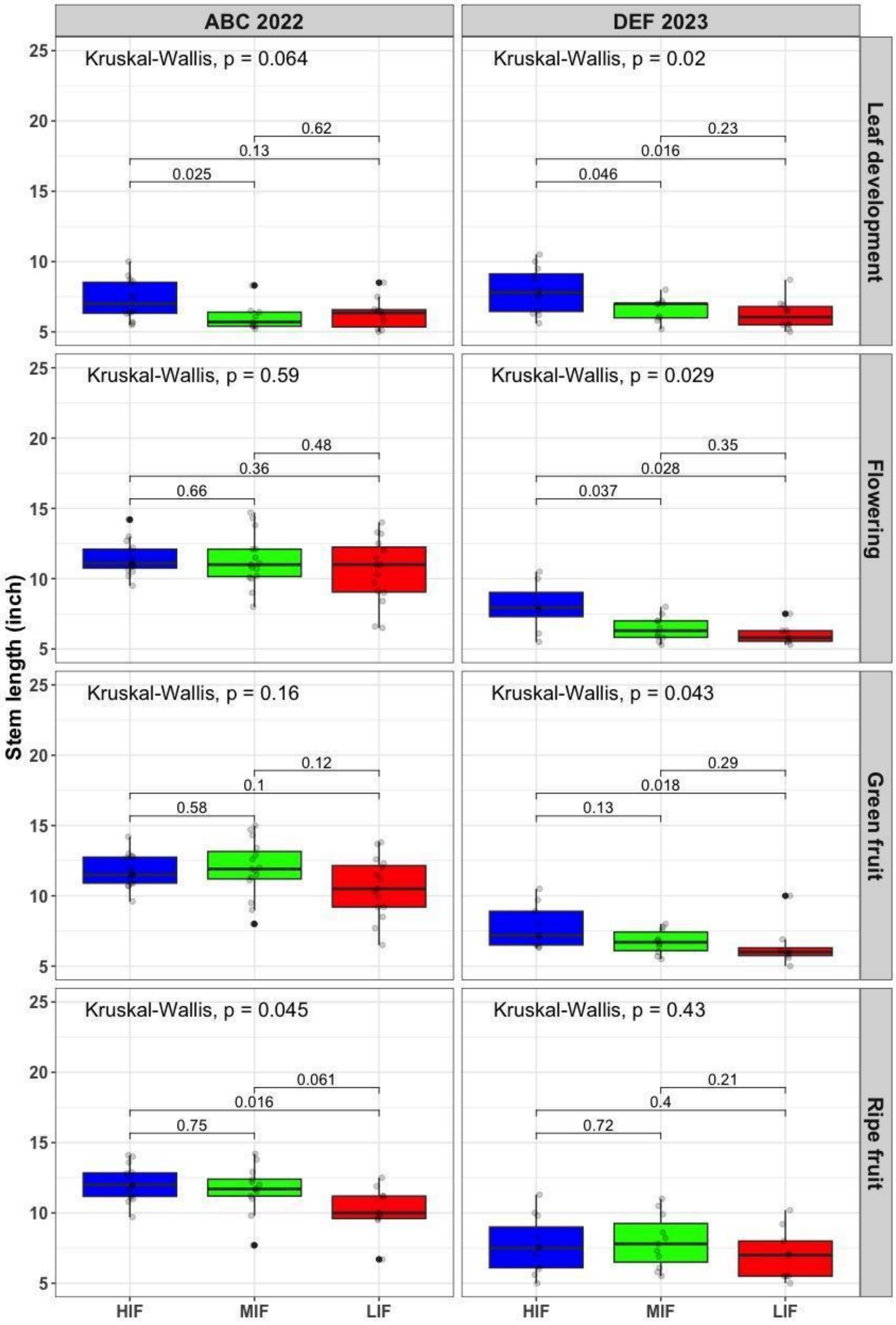


***Figure 3.3:*** *Stem length by treatment at flowering, green fruit, and fruit ripening stages. Error bars show standard deviation. HIF = high irrigation frequency, HIF; MIF = medium irrigation frequency; LIF = low irrigation frequency.*

The irrigation frequency had a minimal effect on the average number of flowers per stem of wild blueberries (Figure 3.4). In 2022, the plants in group ABC that were irrigated under the HIF and MIF treatments had significantly more flowers than plants watered under the LIF treatment. However, there were no significant differences among the treatments in 2023. This suggests that, at flowering stage, reduced frequency of watering may not have severe negative effects on crop potential of wild blueberries. In addition, in the year 2022, the application of LIF resulted in the lowest mean number of flowers per stem, signifying that LIF may have a negative effect by reducing the number of flowers of wild blueberries.

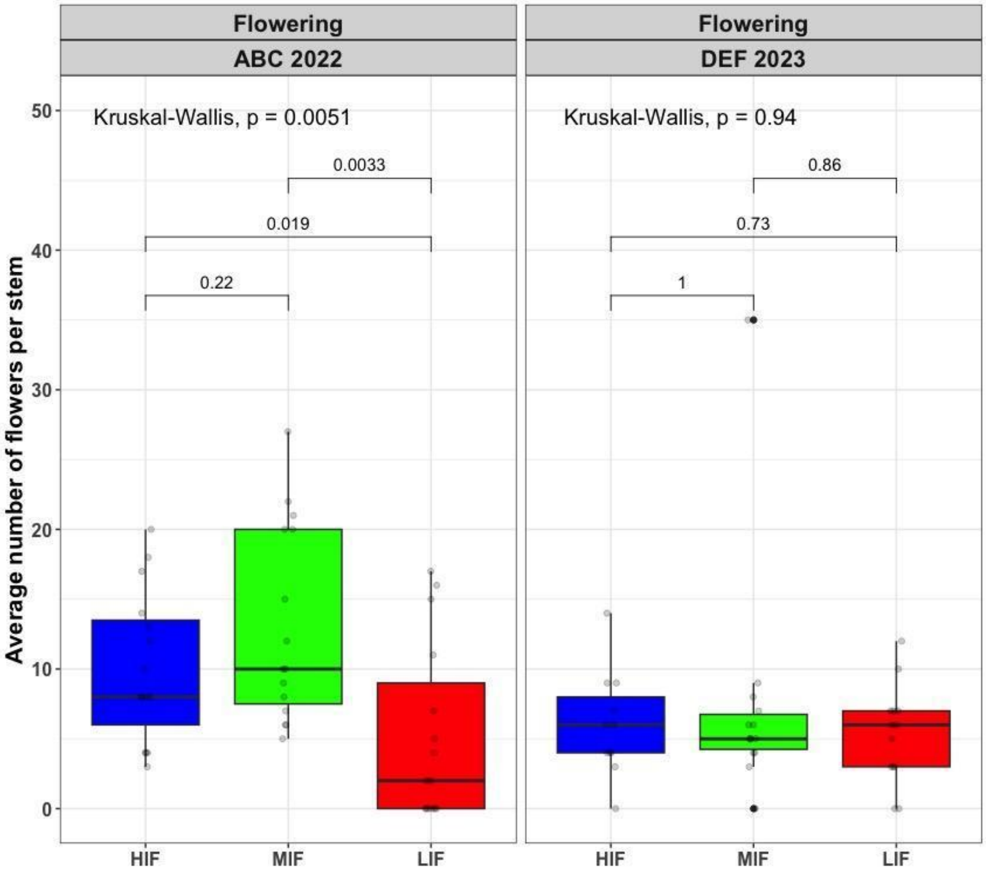


***Figure 3.4:*** *Number of flowers by treatment at flowering stage. Error bars show standard deviation. HIF = high irrigation frequency, HIF; MIF = medium irrigation frequency; LIF = low irrigation frequency.*

Irrigation frequency had a significant impact on the leaf chlorophyll concentration of the ABC group during the leaf development (2022) and green fruit (2023) stages (Figure 3.5), though these differences were not consistently observed in both years. Our results suggest that plants that were irrigated under the HIF treatment had significantly higher photosynthetic rates than plants irrigated under other treatments at the leaf development stage only, and only in 2022. In addition, our results suggest that irrigation spaced multiple weeks apart (LIF) can reduce the photosynthetic rate of wild blueberries at the leaf development stage. The chlorophyll concentration of plants in the DEF group was not significantly affected by irrigation frequency at any phenological stage, except for the green fruit stage. At this stage, plants watered under the LIF treatment had leaves that had significantly lower SPAD readings than plants watered under MIF treatments.

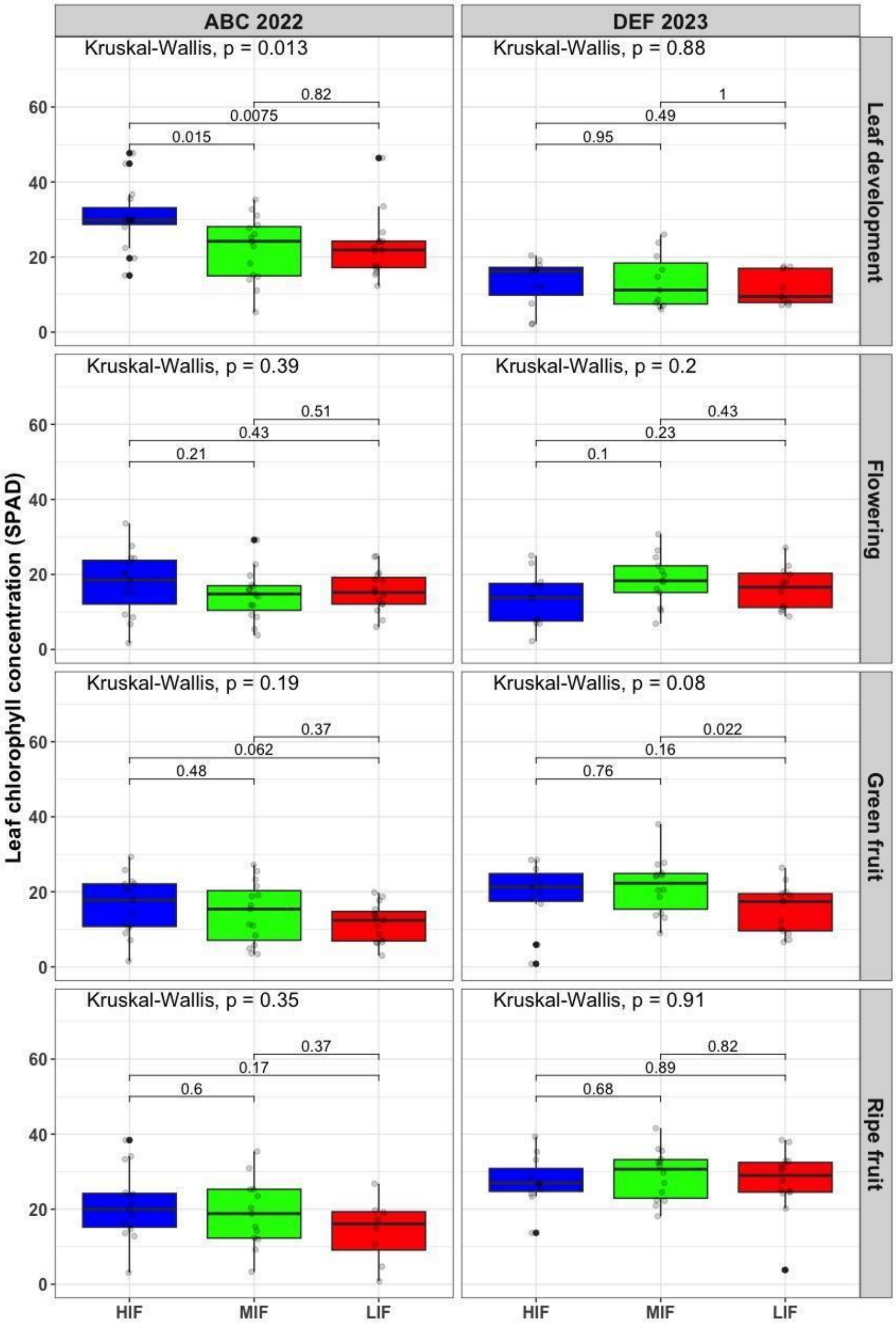


***Figure 3.5:*** *Leaf chlorophyll concentration (SPAD) by treatment at leaf development stage, flowering stage, green fruit, and fruit ripening stages. Error bars show standard deviation. HIF =*

*high irrigation frequency, HIF; MIF = medium irrigation frequency; LIF = low irrigation frequency.*

Maximum quantum efficiency of Photosystem II (measured in Fv/Fm) is often used as a proxy for assessing the crop stress. Chlorophyll fluorescence, or photosynthetic potential, is the ratio of variable to maximum fluorescence. It should be noted that the lower Fv/Fm values indicate higher levels of stress in leaves. Higher readings are therefore desirable. While there was no significant difference in this metric among the treatments at the leaf development stage, there was a statistically significant difference at the flowering, green fruit, and fruit ripening stages in both 2022 and 2023. Specifically, plants subjected to the LIF treatment demonstrated higher levels of stress (Figure 3.6).

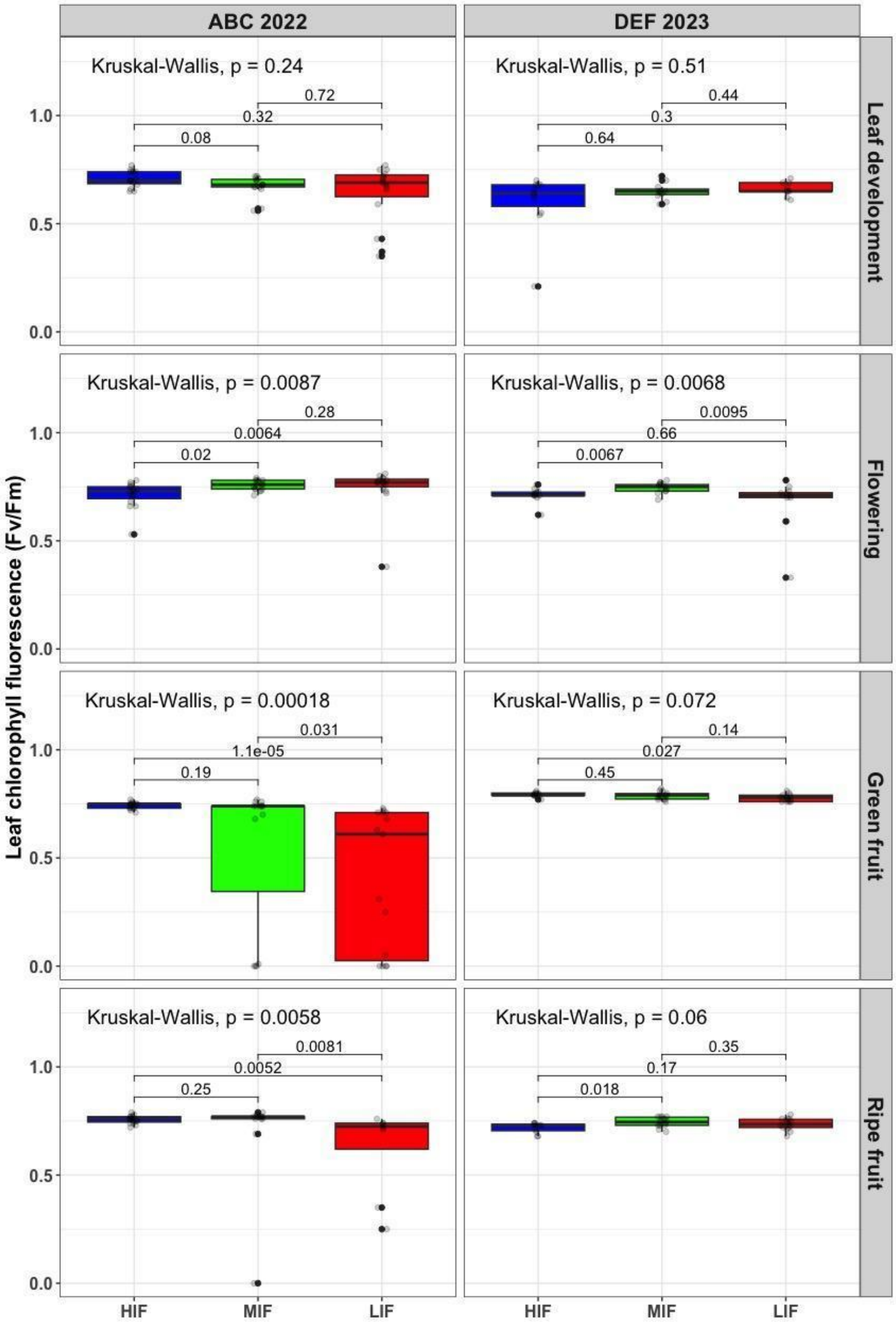


***Figure 3.6:*** *Maximum quantum efficiency of Photosystem II (Fv/Fm) by treatment at leaf development stage, flowering stage, green fruit, and fruit ripening stages. Error bars show*

*standard deviation. HIF = high irrigation frequency, HIF; MIF = medium irrigation frequency; LIF = low irrigation frequency.*

Irrigation frequency showed a considerable impact on the soil water content (SWC). In 2022 and 2023, the soils managed under HIF and MIF treatments had significantly higher soil water content ($P < 0.001$) when compared to soil managed under the LIF treatment, specifically at leaf development stage (Figure 3.7). This trend was also evident in the ripe fruit stage. In most cases, soil water content did not differ significantly between the HIF and MIF treatment. The exception to this was at flowering stage (in both 2022 and 2023), where the HIF treatment had significantly higher soil water content than MIF. This was also true at the fruit ripening stage in 2023. Thus, the soil water content of wild blueberry soils increases with an increase in irrigation frequency.

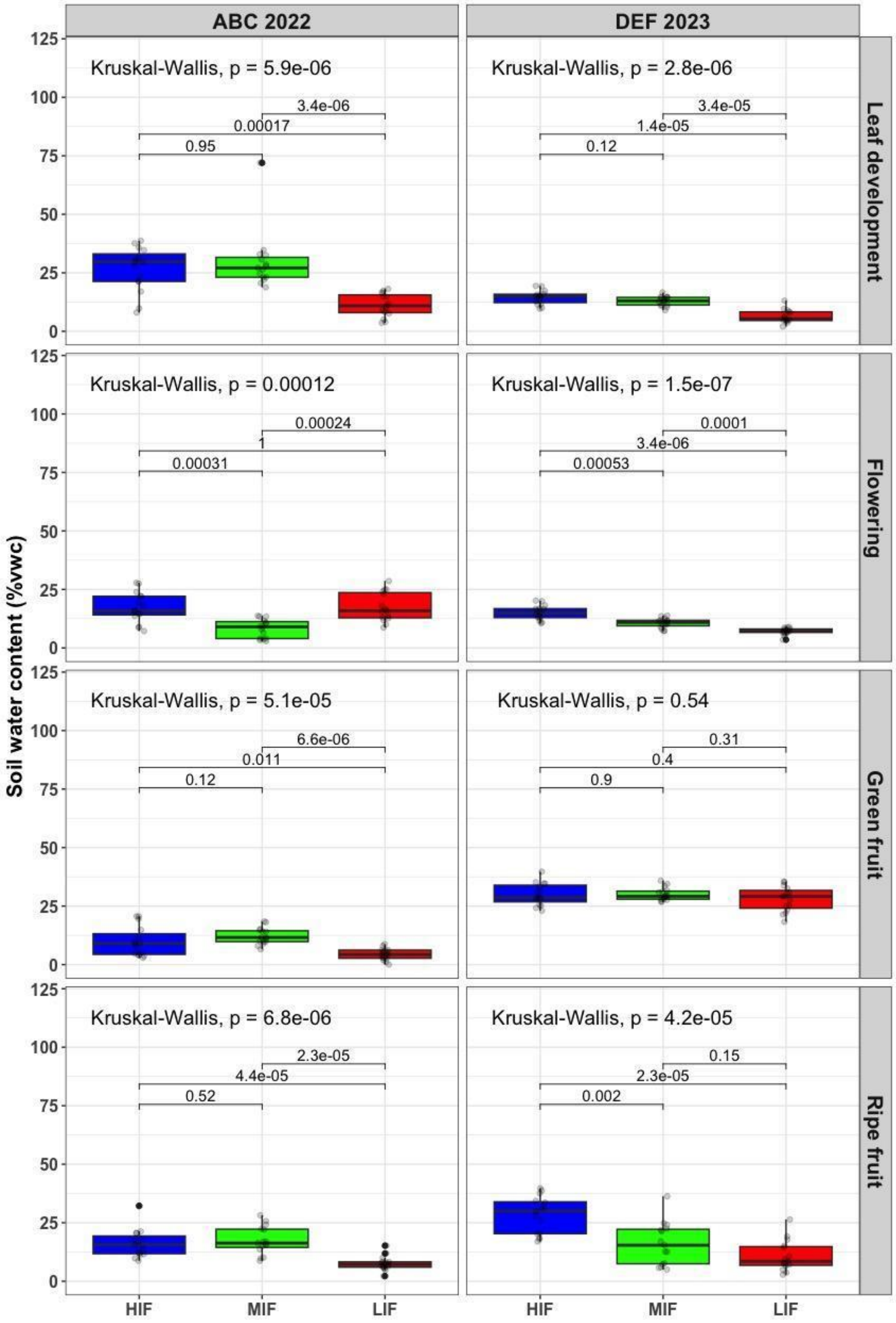


***Figure 3.7:*** *Soil water content (%VWC) by treatment at leaf development stage, flowering stage, green fruit, and fruit ripening stages. Error bars show standard deviation. HIF = high irrigation frequency; MIF = medium irrigation frequency; LIF = low irrigation frequency.*

We also assessed the effect of irrigation frequency on soil electrical conductivity, an example of an edaphic condition that affects crop nutrient access. Soil electrical conductivity is driven by a collection of factors including the presence/absence of soluble salts, percentage clay content, present/absence of minerals, soil water content, bulk density, and more (Eigenberg et al., 2002; Ratshiedana et al., 2023). In 2023, a statistically significant difference was observed among treatments at all four phenological stages, while in 2022, differences were noted at the leaf development and fruit ripening stages, as illustrated in Figure 3.8. This indicated that the irrigation frequency has a significant effect on the soil electrical conductivity of wild blueberry soils. It should be noted that while soil electrical conductivity is related to soil water content, interpreting soil electrical conductivity values requires an understanding of local soil conditions, particularly the soil water content. In keeping with this, our study confirms that the soil electrical conductivity increases with soil water content, especially in gravelly sandy and well-drained soils typically present in wild blueberry production.

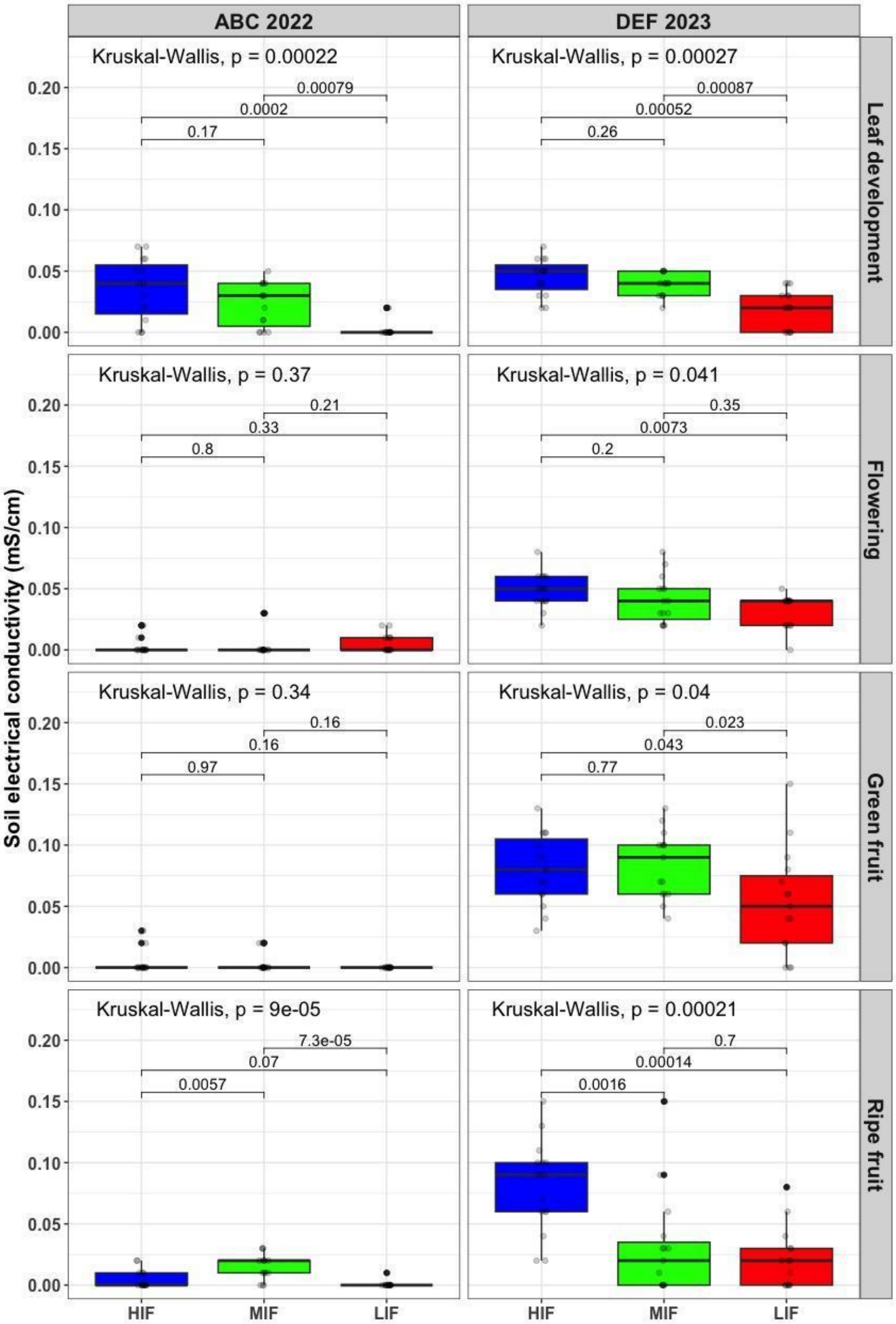


***Figure 3.8:*** *Soil electrical conductivity by treatment at leaf development stage, flowering stage, green fruit, and fruit ripening stages. Error bars show standard deviation. HIF = high irrigation frequency; MIF = medium irrigation frequency; LIF = low irrigation frequency.*

Significant differences in soil temperature among treatments were observed at each phenological stage in both 2022 and 2023, as illustrated in Figure 3.9. Specifically, the LIF treatment was associated with higher soil temperatures in 2022, indicating that the extended intervals between irrigations led to drier conditions and subsequently elevated soil temperatures. However, the unexpected observation in 2023 revealed that LIF was significantly cooler than both HIF and MIF. In this year, the HIF treatment had the highest average soil temperatures across the season. This divergence in results between 2022 and 2023 may be attributed to the fact that the statewide average temperature in 2022 was 3.3°F (0.6°C), compared to 4.3°F (0.4°C) in 2023.

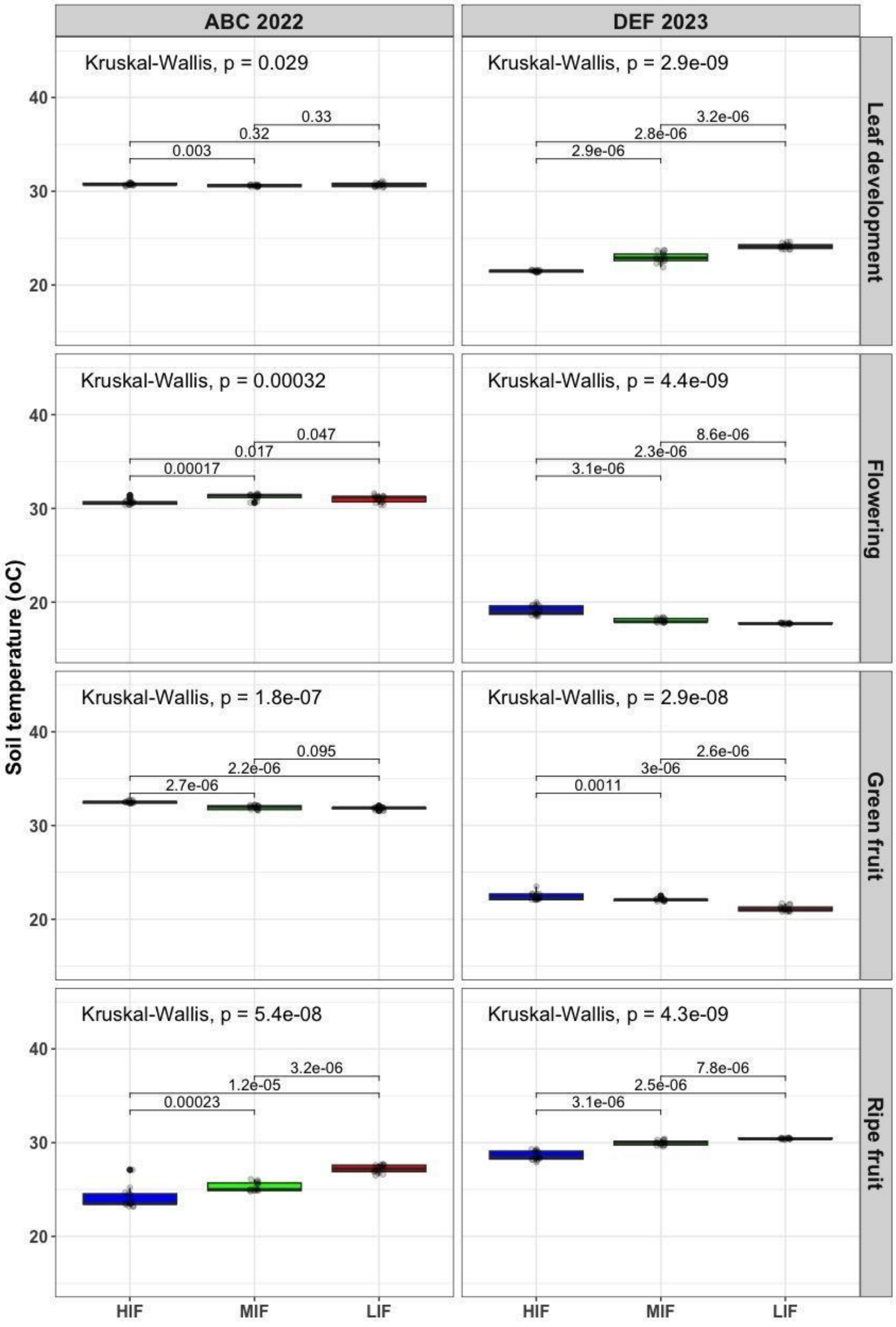


***Figure 3.9:*** *Soil temperature by treatment at leaf development stage, flowering stage, green fruit, and fruit ripening stages. Error bars show standard deviation. HIF = high irrigation frequency; MIF = medium irrigation frequency; LIF = low irrigation frequency.*

## 3.4. Discussion

### 3.4.1. Leaf development stage

The number of leaves per plant is a visual key trait (phenotype) that determines the growth rate and health status of plants. A statistically significant difference was observed in the average number of leaves per stem at leaf development stage in 2022. In this year, plants irrigated with HIF produced significantly more leaves compared to other treatments. In addition, plants watered under the HIF treatment had higher leaf chlorophyll concentration and soil water content compared to LIF and MIF, though this trend did not extend consistently beyond leaf development stage. This points to the importance of consistent rainfall or irrigation during the early stages of crop development (in Spring). The even distribution of rainfall at this point in the season is critical for development of healthy and robust plants with good photosynthetic capacity.

Our results align with irrigation recommendations from the UMaine Cooperative Extension, which emphasizes the importance of providing wild blueberry plants with one inch (2.5cm) of water per week during both crop and non-crop years (Hunt, 2009). Wild blueberries thrive in sandy-loam soils, making them susceptible to rapid drying. The low water holding capacity of these soils highlights the need for understanding the soil-water and plant-water relations of the crop. This knowledge is essential for understanding the needs for irrigation before observable indicators of water stress develop in the plants. Notably, HIF recorded significantly higher soil water content, indicating its efficacy in maintaining sufficient soil water content. Additionally, HIF had significantly higher soil electrical conductivity, in contrast to the lowest values recorded under Low LIF. This finding aligns with previous research in cranberries by Samson et al. (2016).

### 3.4.2. Flowering stage

At the flowering stage, no significant differences were observed in the number of branches per stem and leaf chlorophyll concentration (SPAD) among the treatments. However, post hoc test results revealed that, in certain years, plants subjected to MIF were more likely to have a higher mean number of flowers per stem compared to those irrigated under LIF treatment.

Notably, the HIF and MIF demonstrated the potential to produce a higher average number of flowers compared to the LIF. Given that flowers serve as the reproductive organs of wild blueberries, stress-induced alterations in their structure can have profound implications for both plant and pollinator functions (Lawson and Rands, 2018). Pollination success depends on the successful transfer of pollen from one flower to another. However, several studies have indicated that the high rainfall frequency can disrupt the transfer of pollen, thereby interfering with pollination causing a significant reproductive disadvantage to wild blueberry plants (Jacquemart, 1996). The major floral reward for the vast majority of pollinators is nectar, which consists of glucose, sucrose and fructose dissolved in water (Baker and Baker 1983). Flowers that are subjected to excess rainfall amount and frequency risk diluting their nectar (Lawson and Rands, 2018). Consequently, there is a possibility that soil water content (%vwc) in wild blueberry soils subjected to LIF is reduced.

### 3.4.3. Green fruit stage

Our results indicate that, at the green fruit stage, no significant differences were observed in morphological traits except for stem length in 2023. This trend aligns with findings from the leaf development stage, suggesting that water stress does not induce senescence or leaf drop at this stage of growth. Furthermore, our study suggests that increasing irrigation frequency had no effect on the growth of stem length or the production of new branches. Additionally, functional traits at the green fruit stage showed significant differences in leaf chlorophyll fluorescence with LIF inducing more leaf stress compared to other treatments. Additionally, the significant differences that were observed among the treatments for the soil water content, soil electrical conductivity and soil temperature indicates that the irrigation frequency has a major impact on the edaphic conditions of wild blueberry soils. These findings are consistent with those reported in Caron et al. (2016), who found that edaphic conditions change when soil water content changes in cranberries production.

### 3.4.4. Fruit ripening stage

At the fruit ripening stage, data on the number of mature berries per stem was not collected due to squirrel herbivory. Our findings revealed a significant difference in stem length and the number of branches per stem. Specifically, HIF was associated with increased stem length and the formation of new branches, suggesting a positive influence. As LIF was significantly lower at leaf development and fruit ripening stage, the findings suggested that the extended periods between waterings increases the loss of leaves at the end of growing season, which was also the case in cranberry production (Binet and Laperriere, 1997).

Our results also indicated that irrigation frequency had no effects on the performance of leaf chlorophyll concentration of wild blueberries. However, the results for the leaf chlorophyll fluorescence indicated a statistically significant difference among the treatments. LIF recorded the lowest Fv/Fm, indicating a potential increase in drought stress for wild blueberries under LIF conditions. Furthermore, our study highlighted that HIF positively influences soil water content and enhances soil nutrient availability, as reflected in increased soil electrical conductivity.

Additionally, a statistically significant difference in soil temperature was observed, with LIF recording higher temperatures. This implies that soil temperature tends to increase with a decrease in irrigation frequency at the end of growing season (Dong et al., 2016).

### 3.4.5. Limitation of the study

The study acknowledges potential bias, as soil water content data was collected at different times for each treatment. Specifically, data on soil water content was collected a day before watering for each treatment. As a result, the average three weeks volumetric water content was reported for the HIF treatment. In this study, results were reported for both the ABC and DEF groups of plants. It's noteworthy that the DEF group underwent two years of experimental treatments, leading to a notably higher level of stress in comparison to the ABC group. This distinction in treatment duration and resulting stress levels between the two groups is an important factor to consider when interpreting the reported outcomes.

## 3.5. Conclusion

In this experiment, three different irrigation frequencies were tested on the edaphic features and the morphological and functional traits of wild blueberries. Our results revealed that HIF promotes the growth of leaves, branches, stem length of wild blueberries during the leaf development and fruit ripening stages. Therefore, whether wild blueberry growers are relying on ambient precipitation or supplemental irrigation, ensuring an adequate water supply, with at least one inch per week, throughout the growing season holds significant importance. As expected, HIF demonstrated a higher soil water content at each growth and developmental stage, positively influencing soil nutrients availability by increasing the soil electrical conductivity.

Additionally, many of our functional trait measures were not statistically different between the HIF and MIF treatments, including leaf chlorophyll concentrations (SPAD) at flowering, green fruit, and fruit ripening stages. Our results further indicate that reducing irrigation frequency increases water stress in wild blueberry soils. Therefore, LIF should be avoided as plants were faced with drought stress as demonstrated by the soil water content and soil electrical conductivity. It is of great importance that the crop has sufficient water (at least 1 inch per week) during the growing season when leaves and flower buds are developing. Our results indicate that the MIF produces as much flowers as HIF. Therefore, irrigation frequency can be extended to applying 2 inches every two weeks, in order to reduce the labor and costs of irrigation. Growers with available labor may find this information valuable, as irrigation demands attention and effort, especially during the busiest periods of the growing season. Our final step in this project is to conduct further statistical analysis to assess trends across the season. This study will also inform future research studies starting at the Wyman's Wild Blueberry Research and Innovation Center, located in Old Town, Maine.

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