UC Santa Cruz

UC Santa Cruz Electronic Theses and Dissertations

Title

Crop Response Under Water Deficit is Shaped by Adjustments in Plant Structure, Function, and Fruit Yield and Quality

Permalink

https://escholarship.org/uc/item/08v330vc

ISBN

9798190915143

Author

Castro, Viridiana

Publication Date

2026-08-28

Peer reviewed|Thesis/dissertation

eScholarship.org Powered by the California Digital Library
University of California

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

CROP RESPONSE UNDER WATER DEFICIT IS SHAPED BY ADJUSTMENTS IN PLANT STRUCTURE, FUNCTION, AND FRUIT YIELD AND QUALITY

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Viridiana Castro

August 2026

The Dissertation of Viridiana Castro is approved:

_____
Professor Jarmila Pittermann, Chair

_____
Professor Ingrid Parker

_____
Professor Omar Cornejo

_____
Dr. Darryl Wong

_____
Donald Smith
Interim Vice Provost and Dean of Graduate Studies

Copyright © by
Viridiana Castro
2026

Table of Contents

List of Figures ..... *v*

List of Tables ..... *xi*

Abstract ..... *xii*

Acknowledgments ..... *xv*

Introduction *1*

Chapter 1: Physiological and yield tradeoffs among ten strawberry (Fragaria x ananassa Duch.) cultivars under reduced irrigation frequency *7*

1.1 Abstract **7**

1.2 Introduction **8**

1.2. Materials and methods **12**

1.2.1. Plant material and growing conditions 12
1.2.2 Plant water relations 15
1.2.3 Plant morphometric attributes 16
1.2.4 Leaf and petiole anatomy 16
1.2.5 Fruit Attributes 17
1.2.6 Statistics 19

1.3 Results **22**

1.3.1 Field Measurements - stomatal conductance, water potential, and LMA 22
1.3.2 Fruit Traits 26
1.3.3 Stomatal Conductance in relation to plant and fruit traits 29
1.3.4 Tradeoffs between leaves and fruit 30
1.3.5 Anatomical traits under water deficit 32
1.3.6 Berry Delight Index 33

1.4 Discussion **34**

1.5 Conclusion **39**

Chapter 2: The structure-function trade-offs of the dry-farm adapted, heirloom tomato Solanum lycopersicum L., var. Dirty Girl *40*

2.1 Abstract **40**

2.2 Introduction **41**

2.3 Methods and materials **49**

2.3.1 Study Site 49
2.3.2 Experimental design 50
2.3.3 Plant physiological attributes 51
2.3.4.Morphological measures 52
2.3.5 Foliar Carbon and Nitrogen Stable Isotopes Analysis 53
2.3.6 Plant Anatomical Measures 53
2.3.7 Stem vulnerability preparation and measures 54
2.3.8 Pressure Volume curves 56
2.3.9 Soil samples 57
2.3.10 Yields 58

2.3.11 Statistics 58
2.4 Results 61
2.4.1 Yields 63
2.4.2 Field water relations 65
2.4.3 Foliar Carbon and Nitrogen Stable Isotopes Analysis 71
2.4.4 Anatomy 74
2.4.5Pressure-volume curves 76
2.4.6 Vulnerability Curves 78
2.4.7 Soil attributes 80
2.5 Discussion 82
2.6 Conclusion 87
Chapter 3: The physiological tradeoffs of dry-farm-adapted Phaseolus vulgaris (common bean) varieties 89
3.1 Abstract 89
3.2 Introduction 90
3.3 Methods and Materials 96
3.3.1 Study Site 96
3.3.2 Experimental design for field work 98
3.3.3 Experimental design for greenhouse work 99
3.3.4 Greenhouse Watering regime 100
3.3.6 Field physiological measures 101
3.3.7 Plant growth and leaf traits 102
3.3.8 Plant anatomical measures 102
3.3.9 Pressure-Volume analysis 103
3.3.10 Yields 104
3.3.11 Statistics 104
3.4 Results 107
3.4.1 Climate 109
3.4.2 Yields 110
3.4.3 Water potential 114
3.4.4 Stomatal conductance 114
3.4.5 Height 115
3.4.6 Leaf mass per area 117
3.4.7 Anatomy 118
3.4.8 Cavicam vulnerability curves 122
3.4.10 Leaf traits 123
3.4.11 Principle component analysis 124
3.5 Discussion 125
3.6 Conclusion 128
Synthesis 129
References 135

List of Figures

Figure 1.1 Different water inputs can result in different physiological and fruiting traits. On the left is the hypothesis for a plant that is regularly irrigated. On the right is a plant that has 50% less water input. 11

Figure 1.2. A) Physiological data throughout the season. Letters represent the 10 cultivars sampled and treatments are denoted by red (reduced irrigation frequency) and blue (fully irrigated) (n=3, plants were treated as experimental unit). (a) Ψ_{leaf} (b) g_{sw} and (c) LMA. Asterisks indicate significant differences between treatments x month interactions (*= P<0.05, ** = P<0.01, *** = P<0.001). B) Physiological data during the month of August (n=3, plants were treated as experimental unit) where treatment is denoted by red (reduced irrigation frequency) and blue (fully irrigated). Box plot midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. (a) Ψ_{leaf} (b) g_{sw} and (c) LMA. Asterisks indicate significant differences between treatments (*= P<0.05, ** = P<0.01, *** = P<0.001). The order of boxplots for each cultivar are organized to highlight the largest treatment-related differences in g_{sw} (Figure 2B, panel a). All subsequent boxplots follow this order. 22

Figure 1.3. A) Fruit data collected throughout the season. Box plot midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. (a) Marketable kg per hectare (b) Marketable g per berry and (c) °Brix. n=3 for all fruit data, where plots were treated as experimental unit. Asterisks indicate significant differences between treatments (*= P<0.05, ** = P<0.01, *** = P<0.001). B) Regressions for fruit traits, where letters represent the 10 cultivars sampled and treatment is represented by red (reduced irrigation frequency) and blue (fully irrigated). (a) Marketable kg per hectare and °Brix (b) Marketable kg per hectare and Marketable g per berry and (c) Marketable g per berry and °Brix. 26

Figure 1.4. Regressions for traits paired with stomatal conductance (g_{sw}) (the predictor variable), where letters represent the 10 cultivars sampled and treatment is represented by red (reduced irrigation frequency) and blue (fully irrigated). The following traits were analyzed as response variables: (a) LMA (b) Marketable kg per hectare and (c) °Brix. 29

Figure 1.5. Regressions for traits paired with leaf mass per area (LMA) (the predictor variable), where letters represent the 10 cultivars sampled and treatment is represented by red (reduced irrigation frequency) and blue (fully irrigated). The following traits were analyzed as response variables: (a) Marketable yield (b) Marketable g per berry and (c) °Brix. 30

Figure 1.6. Graphs for phloem fraction measures. (a) Box plot midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers for 5 cultivars (n=3, plants were treated as experimental unit). (b-d) Regressions for traits paired with phloem fraction (the predictor variable), where

letters represent the 5 cultivars sampled and treatment is represented by red (reduced irrigation frequency) and blue (fully irrigated). The following traits were analyzed as response variables (b) LMA, (c) °Brix, and (d) Berry Delight Index. 31

Figure 1.7. (a) Berry Delight Index (BDI) calculated from equation 1 (n=3, plants were treated as experimental unit). Box plot midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. (b) regression for BDI (the predictor variable), and LMA (the response variable) where letters represent the 10 cultivars. 33

Figure 2.1. Plants growing in the field for each variety and treatment. A one-meter ruler is propped next to each plant for reference. Panels on the far right show the average size of fruit when dry-farmed. 49

Figure 2.2. (A)Fruit data collected for (a) average marketable kg per plant, (b) °Brix (%), and (c) average mass per fruit (kg). Data was collected for n=4 plots of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid lines) and irrigated (dashed line) conditions. Panel a, b, and c are boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Significant difference between treatment is denoted by *, where * $p<0.05$, ** $p<0.01$, and *** $p<0.001$. (B) Regression for average fruit size (kg) (the predictor variable) and the following response variables: (a) °Brix (%) and (b) fruit dry mass (%) where the colors orange (Dirty Girl) and purple (Slicer) varieties and treatment is represented by circles (dry-farmed) and triangles (irrigated). 63

Figure 2.3. (A) Seasonal data collected for (a) water potential and (b) stomatal conductance. Data was collected for n=16 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid lines) and irrigated (dashed line) conditions. Points represent mean values and vertical lines overlayed on points represent ± SD. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. Each graph has a vertical, dashed, black line indicating when water was cut-off for dry-farmed treatments and panel B has the plant phenological stages denoted at the bottom of the graph. (B) Regressions for g_{sw} (the predictor variable) and Ψ (response variable) collected on 09/23/24 (when fruits were beginning to ripen) where colors represent Dirty Girl (orange) and Slicer (purple) treatment. Panel (a) shows this relationship for the irrigated treatment and panel (b) shows this relationship for the dry-farmed treatment. 65

Figure 2.4. Seasonal data collected for (A) height and (B) LMA. Data was collected for n=16 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid lines) and irrigated (dashed line) conditions. Points represent mean values and vertical lines overlayed on points represent ± SD. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. Each graph has a vertical, dashed, black line indicating when water was cut-off for dry-farmed treatments and panel B has the plant phenological stages denoted at the bottom of the graph. 67

Figure 2.5. (A) (a) Net photosynthetic rate, (b) g_{sw} (measured with the LI 6400), and (c) WUE measured during peak productivity. Data was collected for n=16 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid lines) and irrigated (dashed line) conditions. Significant difference between treatment is denoted by *, where * p<0.05, ** p<0.01, and *** p<0.001. B) Regressions for (a) height (cm) (the predictor variable) and the response variable photosynthesis (n=64), (b) height (cm) (the predictor variable) and the response variable g_{sw} (decagon) (n=64), and (c) WUE during fruit development (the predictor variable) and the response variable fruit kg per plant (n=16). Colors represent Dirty Girl (orange) and Slicer (purple) treatment. Shapes represent dry-farmed (circle) and Irrigated (triangle) treatments. 69

Figure 2.6. (A) Boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers for (a) the foliar ratio of C:N, (b) the foliar $\delta^{13}C$ values, (c) foliar %C content (d) the foliar $\delta^{15}N$ and (e) foliar %N content. Letters indicate significant difference (P < 0.05) among groups based on Tukey's HSD tests. Significant difference between treatment is denoted by *, where * p<0.05, ** p<0.01, and *** p<0.001. Data was collected for n=16 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid lines) and irrigated (dashed line) conditions. (B) Regressions for (a) $\delta^{13}C$ (the predictor variable) and the response variable yield per plant (n=16) (b) photosynthesis (the predictor variable) and the response variable %N when irrigated (n=16), and (c) photosynthesis (the predictor variable) and the response variable %N when dry-farmed. Colors represent Dirty Girl (orange) and Slicer (purple) treatment. Shapes represent dry-farmed (circle) and Irrigated (triangle) treatments. 71

Figure 2.7. Cross sectional images of tomato (A) stems and (B) roots for plants collected during peak productivity, where (a) is dry-farmed Dirty Girl, (b) is irrigated Dirty Girl (c) is dry-farmed Slicer and (d) is irrigated Slicer. All images were taken at 20x. (C) Mean vessel diameter measures for (a) stems and (b) roots. Data was collected for n=6 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid) and irrigated (dashed) conditions. Data is represented by boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Letters indicate significant difference (P < 0.05) among groups based on Tukey's HSD tests. Significant difference between treatment is denoted by *, where * p<0.05, ** p<0.01, and *** p<0.001. 73

Figure 2.8. Regression for with stem vessel diameter (μm) (the predictor variable) with the following response variables (a) g_{sw} (b) LMA and (c) °Brix (%), where cultivar is represented by orange (Dirty Girl) and purple (Slicer), n=16. Treatment is represented by circles (dry-farm) and triangles (irrigated). 74

Figure 2.9. (A) Osmotic potential at full turgor, (B) water potential at turgor loss point, and (C) modulus of elasticity (MOE) at total relative water content measured during peak productivity. Data was collected for n=6 plants of both Dirty Girl

(orange) and Slicer (purple) varieties, grown under dry-farmed (solid) and irrigated (dashed) conditions. Data is represented by boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Letters indicate significant difference ($p < 0.05$) among groups based on Tukey's HSD tests. Significant difference between treatment is denoted by *, where * $p<0.05$, ** $p<0.01$, and *** $p<0.001$. 76

Figure 2.10. Vulnerability to embolism in stems of dry-farmed (solid) an irrigated (dashed) varieties of Dirty Girl (orange) and Slicer (purple) measured in n=6 individuals. Mean vulnerability curves of each variety and treatment group are fitted following the pfit r package with the standard error of the estimated parameters is represented by light gray areas. 78

Figure 2.11. Regressions for leaf pressure volume curve analyses (the predictor variable) with P88 (the response variable) (n=24). (A) osmotic potential at full turgor (B) water potential at turgor loss point, (C) modulus of elasticity, where variety is represented by orange (Dirty Girl) and purple (Slicer). Treatment is represented by circles (dry-farm) and triangles (irrigated). 79

Figure 2.12. (a) Seasonal data for soil moisture measured at four timepoints in the experiment: at the beginning of the season (before planting), in August (during vegetative growth), in September (during fruit development), and in October (at the end of the growing season), at four different depths in the soil column (15, 30, 60, 90 cm). Data was collected for n=4 plots of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (circles with solid lines) and irrigated (triangles with dashed line) conditions. Points represent mean values and vertical lines overlayed on points represent ± SD. (b) Seasonal data for soil moisture measured at four timepoints in the experiment for two treatments represented by blue (irrigated) and red (dry-farmed) points and lines (n=8). Points represent mean values and vertical lines overlayed on points represent ± SD. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. 80

Figure 3.1. The panels on the top half of the figure show study plants growing in the field for each variety grown under dry-farmed conditions. The bottom panels show bean yields for each variety. 96

Figure 3.2. Climate data recorded in 2024 and 2025. 97

Figure 3.3. The average maximum temperature (F°) for each month recorded in years 2024 (black) and 2025 (blue). Points represent mean values and vertical lines overlayed on points represent ± SD. The significant difference between years for each month in denoted by *, where * if $p<0.05$, ** if $p<0.01$, and *** if $p<0.001$. 109

Figure 3.4. Yield dry mass (g) per plant in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=12 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed

(solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. 110

Figure 3.5. Dry mass per pod (g) per plant in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=12 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. 112

Figure 3.6. Regression for structural investment in (A) 2024 vein density and (B) 2025 LMA (the predictor variables) with dry mass per pod (g) (the response variables). The varieties are represented by the colors purple (Hopi), dark blue (Black), and green (Green) and treatment by circles (dry-farm) and triangles (irrigated). Panel A is n=24 and panel B is n=72..... 113

Figure 3. 7. Height (cm) for plants in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=12 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. 115

Figure 3.8. Regression for height (cm) (the predictor variable) with yield (g) (the response variables) (a) black (b) Hopi and (c) Green, where treatment by circles (dry-farm) and triangles (irrigated). n=28 for Black and Hopi, n=12 for Green. 116

Figure 3.9. LMA for plants in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=12 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. 117

Figure 3.10. Vein density for plants in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=6 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both

varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference (P < 0.05) among groups based on Tukey's HSD tests. 118

Figure 3.11. Stomatal density for plants in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=6 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference (P < 0.05) among groups based on Tukey's HSD tests. 120

Figure 3.12. Stem vessel diameter for plants in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=6 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference (P < 0.05) among groups based on Tukey's HSD tests. 121

Figure 3.13. Vulnerability to embolism in leaves of dry-farmed (solid) an irrigated (dashed) varieties of Green (green) and Hopi (purple) *P. vulgaris*. This is the direct visualization of embolism spread in leaves of six individuals (black points). Mean vulnerability curves of each variety and treatment group are fitted following the pfit r package with the standard error of the estimated parameters is represented by light gray areas. Solid red lines correspond to P50. 122

Figure 3.14. Principal component analysis (PCA) of (a) physiological traits (n=12) for Black (black) and Hopi (purple), and Green (green) varieties grown under dry-farmed (circle) and irrigated (triangle) conditions Variables are centered and scaled prior to analysis. Points represent individual samples plotted along the first two principal components (PC1 and PC2). Plot (A) explains 42.00% and 16.70% of the total variance that occurred in 2024 and plot (B) explains 31.20% and 23.00% of the total variance in 2025. Arrows indicate trait loadings, with direction and magnitude reflecting their contribution to each principal component. 124

List of Tables

Table 1.1 Cultivar labels and rationale for selection for physiological testing, based on preliminary responses to water deficit. Selection was informed by early differences in yield, fruit size, plant appearance, and water drainage assessed one month after final irrigation reduction (50% relative to control)…….14

Table 2.1. Fruiting, physiological, and anatomical traits, units, and abbreviations for the two cultivars grown under dry-farmed (D) and regularly irrigated (I) conditions measured during peak productivity. Data are means with standard error in parentheses. All physiological measures were collected when fruit was ripening. 61

Table 3.1. Traits measured, units, and abbreviations for the three cultivars grown under dry-farmed (D) and regularly irrigated (I) conditions during flowering. Data are means with standard error in parentheses. Spaces with dashes are left empty because there was no measure recorded for that trait during that year. Traits that are italicized are those that have been previously reported in Hekannen *et al* 2025 (in review)… 107

Abstract

CROP RESPONSE UNDER WATER DEFICIT IS SHAPED BY ADJUSTMENTS IN PLANT STRUCTURE, FUNCTION, AND FRUIT YIELD AND QUALITY

by

Viridiana Castro

As climate conditions become warmer and drier, there is an increased threat to agricultural productivity. Increased temperatures and reduced water availability can impede crop performance and reduce yields. However, the relative effects of drought on different crops and the consequences for yield is less well understood, specifically, the physiological and structural principles that underpin crop performance under water deficit. Understanding the limits of economically important crops, especially as growers transition towards more sustainable forms of agriculture, is critical. In order for these transitions to occur, it is useful to identify the crop varieties and the suite of traits that will allow them to thrive under limited resources. To identify these suite of traits that allow crops to survive under water deficit, I studied a combination of physiological, anatomical, and morphological traits in strawberries, tomatoes, and beans, grown under well-watered and water-deficit conditions.

In the first chapter titled "Physiological and yield tradeoffs among ten strawberry (*Fragaria* x *ananasssa* Duch.) cultivars under reduced irrigation frequency", I hypothesized that strawberry cultivars subjected to reduced water availability would have a variety of physiological traits that would lead to tradeoffs in drought resistance and hydraulic efficiency. To test this hypothesis, I compared physiological traits among 10 different cultivars of strawberries that were

commercially grown at Driscoll's Berries facilities under regular irrigation and a 50% decline in irrigation. I found that water stress consistently increased leaf thickness and fruit soluble solids (°Brix) while reducing stomatal conductance, phloem fraction, and fruit size, revealing trade-offs between water conservation and yield.

In Chapter 2, "The structure-function tradeoffs of the dry-farm adapted, heirloom tomato *Solanum lycopersicum* L., var. Dirty Girl", I build upon the results of Chapter 1 in a different system of sustainable agriculture called dry-farming. Dry-farming is a method for growing crops under little to no irrigation. I hypothesized that dry-farm adapted varieties of tomatoes have adapted to mitigate drought stress under minimal water input through a variety of physiological traits, such as increased resistance to embolism. To test this hypothesis, I compared two popular California varieties of organic tomatoes, the dry-farm-adapted Dirty Girl and the non-adapted Cherokee Purple, under irrigated and dry-farm conditions. I observed that dry-farming conditions reduced individual plant yield by 35.32% in Dirty Girl and 59.91% in Slicer, indicating a stronger decline in Slicer, although this difference is not statically supported by significant interaction dry-farmed. This result is bolstered by enhanced carbon acquisition traits in Dirty Girls, including greater plant height, which was supported by increased leaf vein density, and root vessel diameters, two proxies pointing to greater hydraulic conductance.. Concurrently, these plants expressed drought-tolerant traits such as a safer xylem network (smaller stem vessel diameters), increased leaf thickness (leaf mass per area), increased resistance to leaf wilting (lower water potential at turgor loss point), and increased embolism resistance in stems.

To expand on the novel research of dry-farming, Chapter 3, “The physiological tradeoffs of dry-farm adapted *Phaseolus vulgaris* L. (common bean) varieties”, further investigates the traits I observed in Chapter 2. However, this study focuses on a two-year experiment with three varieties of common bean, which rely on water to form below ground associations with nitrogen-fixing bacteria. Like Chapter 2, I grew different bean varieties (Hopi, Black, and Green) under irrigated and dry-farmed conditions to test the hypothesis that dry-farm adapted varieties have adapted to mitigate drought stress through a variety of physiological traits. Across both years, dry-farming significantly reduced yield in all varieties despite shifts in anatomical traits associated with drought tolerance, with more pronounced effects in 2024, a warmer growing season. However, Hopi beans invested more carbon resources toward reproductive output, resulting in the highest dry mass per pod across all varieties, treatments, and years.

Overall, this work explores the importance of studying physiology, morphology, anatomy, and soil traits of multiple crop varieties in the context of sustainable agriculture. The information obtained in this project is essential for informing future breeding work and farming management.

Acknowledgments

I would like to thank my advisor, Dr. Jarmila Pittermann, who was involved in every step of this dissertation. Thank you for being such an incredible scientist and mentor. Your guidance was essential and your dedication is contagious.

I would also like to thank my committee members, Dr Ingrid Parker, Dr. Omar Cornejo, and Dr. Darryl Wong. They are each wonderful scientists and were committed to helping me succeed throughout my dissertation.

I would also like to thank other faculty mentors, Dr. Robin Dunkin, Dr. Stacy Philpott, Dr. Hannah Waterhouse, and Dr. Karen E. Tanner, who provided support and advice. Thank you for being excellent scientist and for encouraging me at various point of my graduate career.

I would like to thank my collaborators, Driscoll's Berries, the UCSC Center for Agroecology, and Matt Davis from Oregon State University. Without them, this work would not be possible.

I would like to thank the undergraduates that I worked with throughout my dissertation, Matt Peters, Amelia Dal Porto, Carolina Cervantes, Hanna Hekkanen, Diego Carranco, Abel Garcia-Vargas, and Shayna Graff. Their participation and dedication to this work is what made it so successful. I will always be grateful for their contributions.

I also want to thank many UCSC staff members who did everything they could to help me succeed, including Sylvie Childress, Judy Straub, Stephanie Zakarian, Nathalie Espinoza, Kirstin Yogg, and Sri Sethuratnam.

I am grateful for my lab mates in the Pittermann lab, both past and present. Particularly, Ryan Salladay, Hugh Leonard, and Alex Baer who are all wonderful scientist, colleagues, and friends.

I would also like to thank my friends for their endless support and love. Their friendship brought so much joy to my life during this experience. In particular, Allyson Salazar Sawkins (and Kiwi), Favian Ramirez, Yingyi Xi-Blazer, and Natasha Hinojosa. I will always cherish the memories I shared during my time in the program.

I want to thank my family for all their love and support. Thank you to my parents, Olga and Juan Castro, for being there for me since day one. Your strength and work ethic are truly my inspiration. Thank you to my siblings, Carlos and Stephanie, for always being there for me and for keeping my humble.

I would like to thank my partner, Aaron Roche. Thank you for being with me every step of the way. You were there to celebrate with me during my successes and you were a shoulder to lean on during the rough days. Thank you for all the love, laughs, and for growing with me. Our family (you, me, and Gypsy) has made so many special memories here in a Santa Cruz and the time I spent here will always hold a dear place in my heart. Additionally, I would like to thank his mom, Heidi, and sister Lili, for their love, support, and friendship.

Finally, I would like to acknowledge the U.S. Department of Agriculture NextGen, the UC Santa Cruz Agricultural Experiment Station funding provided by the state of California, the USDA California Department of Food and Agriculture, and the Jean H. Langenheim Graduate Fellowship for the funding this research.

The text of this dissertation includes a reprint of the following previously published material. The co-author listed in this publication directed and supervised the research which forms the basis for the dissertation.

Chapter 1:

Castro, V., C. Zavalloni, D. Liabeuf, J. Pittermann. Accepted. Physiological and yield tradeoffs among ten strawberry (*Fragaria* x *ananassa* Duch.) cultivars under reduced irrigation frequency. Frontiers in Sustainable Food Systems.

Introduction

Climate change models predict increasingly hot and dry weather conditions, and with these predictions comes the concern of how agricultural production will be affected (Calvin *et al.*, 2023; Eckardt *et al*., 2023). Many variables are influenced by a changing climate that can have adverse effects on the overall agriculture industry. Raza *et al*. 2019 group these variables into three categories that capture the types of difficulties agriculture faces on a global scale. There are direct effects that impact plant morphology and physiology, while indirect effects such as heat, drought, and soil salinity, occur externally to the plant. Lastly, there are socio-economic impacts that cause harm to society, like cost increases, policy changes, and unequal distribution of food (Raza *et al*., 2019). Agricultural systems around the globe will contend with these intertwined challenges, making sustainable and resilient crops of paramount importance.

Research shows that as climate change continues to influence these variables, many types of crops will be at peril, putting food security is at risk (IPCC, Calvin *et al*., 2023). For example, studies have estimated that rising temperatures will decrease crop production by varying levels for each one-degree Celsius increase (-2.4 % in C3 and -4.52% in C4 crops) (Tran *et al.,* 2025). Other studies show that temperature increases can lead to an elevation in soil-borne fungal plant pathogens, which impacts plant health as current chemical fungicides are mostly unsuccessful (Delgado-Baquerizo *et al.*, 2020). Climate change is of paramount concern; therefore,

researchers and farmers must continue working on solutions to improve crop security in the future. Drought-resilient crops are at the forefront of this effort.

Addressing the issue of crop vulnerability to climate change requires more information about how plants are directly affected by environmental changes such as prolonged droughts and increased temperatures. To withstand reduced water availability, plants evolved a suite of traits that make up the xylem tissue, also called the plant's water transport system (Pittermann, 2010). Within the xylem are vessels, empty dead cells that move water from the roots to the leaves. Stomata are pores in the leaves that, upon opening, gain CO_2 that is essential for photosynthesis.

Consequently, water loss through those pores is inevitable and replenishing it is vital. If plants are growing in dry soils or if there is a high vapor pressure deficit, leaf transpiration may exceed water transport capacity and result in the introduction of air into vessels. When there is enough tension from continuous transpiration and not enough water replenishment, this air may break the water column (cavitation), and lead to embolism, which describes an air-vapor blockage in the vessel. A high fraction of embolized xylem will impede water transport and may lead to the death of the plant (Tyree and Zimmermann, 2002). Breeding drought-resilient crops requires understanding their hydraulic limits (Torres-Ruiz *et al*., 2024).

In response to this risk of hydraulic failure, plants have developed physiological responses and structural features that improve transport safety. Stomatal closure prior to the onset of hydraulic failure is the first of these responses. For example, to protect the water transport system, stomata close at water potentials that

are greater than the water potential at which embolism begins to accrue (Corso *et al*., 2020; Trueba *et al.,* 2019). However, anatomical traits such as reduced vessel dimensions (length and diameter) and thicker pit membranes (perforations along the walls of vessels that also aid in the movement of water) influence resistance to embolism. In species that have adapted to survive in arid environments, smaller conduits reduce the probability of embolism spreading to neighboring vessels by decreasing inter-vessel connections. Additionally, thicker pit membranes reduce strain during high tension by minimizing the amount and size of membrane pores. (Isasa *et al*., 2023; Lens *et al*., 2022; Sperry *et al.*, 2006; Torres-Ruiz *et al.*, 2024). These adaptations convey hydraulic safety.

While increasing hydraulic safety is desirable during drought, there are costs associated with embolism resistance such as reduced transport efficiency (Gleason *et al.* 2016). Transport efficiency is often represented by hydraulic conductivity (K = flow rate / pressure gradient standardized for segment length). If plants can sustain high levels of hydraulic conductivity, then they are continuously replenishing the supply of water that is lost during transpiration and can continue to photosynthesize (Brodribb and Field, 2000). Plants that have increased resistance to embolism are often shown to have a negative relationship with transport efficiency, which results in the reduced ability to deliver water to the rest of the plant (Wheeler *et a*l 2005). This can have numerous adverse effects such as decreased CO_2 acquisition and a reduction in vital plant stores, such as reduced relative water content of leaf tissues and reduced carbohydrates that are typically accessed when photosynthetic processes are halted

(McDowell *et al* 2008). This decrease in functionality then impacts, or even stops, flower and fruit development (Pratt and Jacobsen, 2017). To this end, more studies need to examine the degree to which plants economize resources toward drought resistance over other vital functions, namely, fruit yield.

There has been much interest in agricultural crop research regarding hydraulic safety and efficiency (Anderson *et al*., 2020; Asseng *et al.*, 2015; Cantore *et al.*, 2016; Corso *et al*., 2020; Torres-Ruiz *et al.*, 2024) as high temperatures and dry soils have shown decreases in crop production (Calvin *et al*., 2023). Research in wheat for example, has found some crops to have a wide stomatal safety margin (SSM; Corso *et al*., 2020). These plants are sensitive to a changing environment and limit water loss early by closing stomata well before their turgor loss point, the point at which the leaves begin to wilt. This adaptation may lead to a loss in hydraulic conductivity and potentially reduce the overall yield of the crop, however, it can prevent embolism. In other crops, however, there seems to be a priority for fruit development before the safety of hydraulic features. In tomato crops, for example, plants prioritize fruit and seed production at the expense of their leaves, which experience xylem embolism early during drought (Harrison Day *et al*., 2022). This may be a tradeoff that only works short term, as most tomatoes are annual crops that are short lived, but may also be indeterminately growing.

While these types of studies establish the framework for plant response to drought, there is still much I do not know. Researchers predict that the success of crops in a drying climate is dependent on cultivating plants with a variety of traits that

balance relatively efficient water transport, embolism resistance, and continuous photosynthetic activity for as long as possible, all while preserving fruit production (Torres-Ruiz *et al*., 2024). This feat that will not be simple, given that plants cannot 'do it all' without incurring some kind of functional penalty. Furthermore, uncovering what traits should be selected for crop breeding may need to be accomplished on a case-by-case basis. Meaning, one suite of traits ideal for warmer and drier conditions in one crop may be a different set of traits selected in a different crop.

My research aims to uncover which traits lead to improved drought resistance and the costs that are associated with these traits. The studies I am conducting focus on the variation in physiological traits during climatic disturbance and investigate different farming techniques that can lead to a more sustainable and water-efficient farming practice. In California, the most common reasons for loss in production include damage from pests, high cost of water, and drought, which can result from climate change (Husaini and Xu, 2016; Samtani et al., 2019). It would benefit scientists and farmers to have more information behind the physiological and morphological traits that lead to drought resistance and desirable fruit production. This could alleviate problems associated with climate change and inform the types of traits that should be selected for when breeding new crops. My research aims to accomplish these goals by pursuing three chapters that evaluate three species of popular crops: strawberries, tomatoes, and dry beans . Together, these chapters integrate the impacts of drought on crop physiology and the suite of traits that allow

them to maintain yields. This research is useful for researchers and breeders as they develop more crops that can thrive under sustainable agricultural practices.

Chapter 1: Physiological and yield tradeoffs among ten strawberry (*Fragaria* x *ananassa* Duch.) cultivars under reduced irrigation frequency

1.1 Abstract

Climate change driven increases in evaporative demand and water scarcity pose significant challenges to irrigated crops, making plant water conservation a critical trait for agricultural sustainability. *Fragaria* × *ananassa* (strawberry) is an economically important but drought-sensitive crop due to its shallow root system and high transpiration demand. This study evaluated cultivar-specific physiological and anatomical tradeoffs underlying tolerance in irrigation reduction across ten commercial strawberry cultivars grown under well-watered conditions and under reduced irrigation frequency. We quantified traits such as leaf water potential (Ψ_{leaf}), stomatal conductance (g_s), and leaf mass per area (LMA), anatomy (phloem fraction, defined as the relative cross-sectional allocation to phloem tissue, stomatal density, and vessel diameter), and fruit quality (marketable grams per berry and fruit soluble solids (°Brix)). Across all ten cultivars, the reduced irrigation frequency treatment generally increased LMA and fruit soluble solids (°Brix) while reducing Ψ_{leaf}, g_s, and fruit size, revealing trade-offs between water conservation and yield. In the anatomical analysis in a subset of five of the cultivars, we observed that treatment reduced stomatal density, while two cultivars had a reduction in phloem fraction and vessel

diameter. These findings highlight a set of traits that contribute to improved water-use efficiency while elucidating the yield penalties associated with tolerance to irrigation reductions, and thus offer valuable insights for cultivar selection and breeding under water-limited conditions.

1.2 Introduction

Climate change models predict increasingly hot and dry conditions that intensify evaporative demand, raising concerns for crop water balance and agricultural production (Calvin et al., 2023; Eckardt et al., 2023). Studies indicate that extreme conditions threaten many crops, putting global food security at risk (Heino et al., 2023; Mirzabaev et al., 2023; Ristaino et al., 2021). For example, studies have estimated that rising temperatures will reduce wheat production by 6% for each 1°C increase, and while these finding are species-specific, many crop types (including maize, soybean, and rice) follow similar trends (Asseng et al., 2015; Dang et al., 2025; Hu et al., 2024). The consequences of rising temperatures underscore the urgent need for further research to protect food security. To this end, we chose to work on one of California's most economically important crops, strawberry, or *Fragaria* x *ananassa*. The goal of this study was to characterize the structural, functional and yield trade-offs associated with reduced irrigation frequency.

Fragaria x ananassa is a hybrid of *Fragaria chiloensis* and *Fragaria virginiana*, originating from Chile and North America, respectively (Ernazarova et al., 2025; Hancock et al., 2020). This species has become the foundation of today's strawberry. Over the past 30 years, strawberry global consumption has steadily increased to over 9 million tons, with the USA producing almost 20 % of the world's crop and California producing over 80% of the nation's crop (Parajuli et al., 2022; Samtani et al., 2019; Zacharaki et al., 2024). Since 2018, however, strawberry fruit yields have continuously declined due to climate change and market-driven reasons (Holmes, 2024; Unnikrishnan et al., 2024; Yeh et al., 2023) Hence, there is broad interest in cultivating strawberry cultivars that limit water use while maintaining relatively high productivity. One approach is to use a physiological framework that examines multiple drought-related traits and links them to fruit productivity.

Strawberries are herbaceous perennials with shallow root systems and a high proportion of leaf biomass, traits that, depending on climatic conditions, may limit water uptake and increase sensitivity to heat and drought (Hancock et al., 2020; Ledesma and Sugiyama, 2005; Ullah et al., 2024). If plants have access to water, they will continuously develop dense, fibrous roots that can be as deep as 40 cm and live as long as 2-3 years (Akhtar et al., 2025; May et al., 1994). However, exposure of roots to drought and temperatures above 30 °C rapidly reduces above-ground growth

(Cao et al., 2022; Papp et al., 2004). Top growth is also impeded by drought, as reduced stomatal conductance can result in decreased photosynthetic rates and reduced vegetative growth (Grant et al., 2012; Qiao et al., 2024).

Plants adopt a suite of traits to withstand drought, heat, and high vapor pressure deficits (VPD), allowing them to survive under harsh conditions. Drought-tolerant species typically exhibit lower water potentials, reduced relative water content, and thicker, smaller leaves (Mano et al., 2023; Scoffoni et al., 2011; B. Zhang & Archbold, 1993). However, this drought resistance comes at the expense of yields. Plants adjusting to water-stress exhibit a decrease in carbon storage, including leaf water content and carbohydrates (Du et al., 2020; Muller et al., 2011; Sun et al., 2023; Zhang et al., 2018). This decrease in resources can then impact, or even halt, flower and fruit development (González et al., 2023; Liu et al., 2023; Pratt and Jacobsen, 2017). While studies have investigated strawberry plants grown under drought, less is known about the tradeoffs between drought resilience and fruit production, and what shapes this relationship. We examined this across multiple strawberry cultivars of interest to growers for their response to reduced irrigation frequency. Our goal was to uncover which traits confer improved resilience under reduced irrigation frequency to *Fragaria x ananassa* and whether these traits were at the cost of yields or fruit quality. Our study addresses two questions: (1) how variable is tolerance to reduced irrigation frequency within the commercially grown cultivars of *Fragaria x*

ananassa? and (2) What are the tradeoffs in the context of the limits and constraints of reduced irrigation frequency on fruit production? We predicted that plants grown under a reduced irrigation frequency would have smaller leaves, reduced biomass, and lower rates of fruit production, whereas plants that were regularly irrigated would have higher investment in biomass that would correlate with higher fruit production. This trade-off between water conservation and yield is illustrated in Figure 1.1, which depicts how different trait combinations may emerge under varying levels of irrigation.

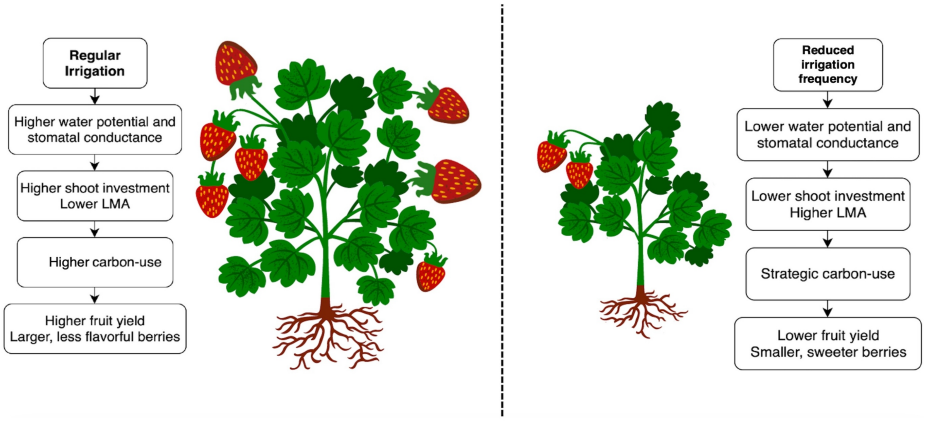

Figure 1.1 Different water inputs can result in different physiological and fruiting traits. On the left is the hypothesis for a plant that is regularly irrigated. On the right is a plant that has 50% less water input.

1.2. Materials and methods

1.2.1. Plant material and growing conditions

The experiment was designed by the physiology team at Driscoll's Berry's in Watsonville, California. This region's Mediterranean climate is characterized by dry summers and cool, moist winters. The maximum and minimum air temperatures reach 35°C and 9°C, respectively. Additionally, there are seasonal wind, rain, and fog patterns, with fog occurring in late spring and summer (Figure S1, NOAA, https://www.noaa.gov/).

The experiment was established in October 2021, using more than ten cultivars of *Fragaria* × *ananassa*, which were planted in mixed substrate bags and cultivated on table-top production systems (elevated stands with gutters connected to a drip irrigation system). The substrate was composed of 100% coco coir fiber, using a commercial strawberry growing medium. Each cultivar and treatment group had three replicates and each replicate consisted of a single plot containing two substrate bags, with each bag holding eight plants (120 bags total). Each substrate bag had a volume of 15.0 liters with the following measurements: width of 17.78 cm, length of 96.52 cm, and height of 5.08 cm. All bags were free draining, with a water holding capacity of 40-50%. For sampling, leaves were randomly selected from the 16 plants within each plot.

All plants initially received six daily irrigation cycles, between 9:00 h and 15:00 h. This drip irrigation system was regulated by installing a lysimeter in one plot per treatment group. The lysimeter served as a feed-back based, closed-loop system that monitored variables such as soil moisture, temperature and leachate to adjust irrigation. In March 2022, hoop houses were installed over the table-tops, and the reduced irrigation frequency treatment was introduced . By May 2022, water-limited plants received less than 50% of water supplied to the control group. This reduction was achieved by decreasing irrigation frequency from six cycles per day to three. On average, control plants received 12.2 liters per day whereas reduced irrigation frequency plants received 3.9 liters per day. Drainage was measured every four weeks throughout the season by collecting the drainage water in buckets and measuring the volume with a 2 L graduated cylinder. In July, 400 ml of drainage was collected from 4,500 ml applied in the reduced irrigation frequency treatment while 4,800 mL of drainage was collected from 13,300 mL applied in the control treatment. In September, 600 mL of drainage was collected from 3,900 mL applied in the reduced irrigation frequency treatment, whereas 5300 mL of drainage was collected from 13,300 mL applied in the control treatment.

Plant nutrition was managed through fertigation, supplying all macro- and micro-nutrients in accordance with best management practices. Soil electrical conductivity (EC) targets were maintained at 1.3 mS cm^{-}

^{1} during vegetative growth and increased to 1.6 mS cm^{-1} during the fruiting period. Solution pH was maintained between 5.5 and 6.5 to optimize uptake. In the reduced irrigation frequency treatment, fertilizer inputs were reduced proportionally to irrigation volume; for example, a 50% reduction in water supply corresponded to a 50% reduction in nutrient supply.

In July 2022, we selected ten cultivars for physiological testing from the established experimental population based on their preliminary responses to reduced irrigation frequency, as detailed in table 1.1 These responses were evaluated using early measurements of yield, fruit size, overall plant appearance, and water drainage. The preliminary data, collected by the Driscoll's team, were obtained in June, one month after the final irrigation adjustment, during which the reduced treatment was reduced to 50% of the control. Importantly, these observations were made prior to any physiological measurements, allowing us to use early performance differences to guide targeted trait-based analyses. Once measurements began in July 2022, we sampled from three replicate plots (n=3) of each of the 10 cultivars for both fully and partially irrigated treatments. All plots were spatially randomized within the hoop-house space. In September of 2022, the irrigation systems were flushed with pure water to remove salt accumulation, with EC levels monitored both before and after.

Table 1.1 Cultivar labels and rationale for selection for physiological testing, based on preliminary responses to water deficit. Selection was

informed by early differences in yield, fruit size, plant appearance, and water drainage assessed one month after final irrigation reduction (50% relative to control).

Cultivar	Rationale behind cultivar selection
A	Greater difference in yield and fruit size between irrigated and reduced irrigation frequency treatment
C	Both treatments had similar water intake between irrigated and reduced irrigation frequency treatment
E	No difference in yield and fruit size between irrigated and reduced irrigation frequency treatment
F	Big yield and fruit size difference between irrigated and reduced irrigation frequency treatment
G	Plant visually stressed under reduced irrigation frequency with leaf scorching
H	Small difference in yield between irrigated and reduced irrigation frequency treatment
I	Small difference in yield and fruit size between irrigated and reduced irrigation frequency treatment
J	Greater difference in yield and fruit size between irrigated and reduced irrigation frequency treatment
K	Greater difference in yield and fruit size between irrigated and reduced irrigation frequency treatment
L	No difference in yield and fruit size between irrigated and reduced irrigation frequency treatment

1.2.2 Plant water relations

During the summer of 2022, we measured stomatal conductance (g_s) for all three leaflets on a leaf and then averaged to one value per leaf (mol/m2/s; LI-600, LI-COR, Lincoln, NB, USA) for n=3 plants in both treatments for each of the 10 cultivars between the hours 10:00 h and 14:00 h, to ensure consistency. These measures were collected three times throughout the growing season in late July, late August, and late September. Samples were standardized by collecting fully expanded sun leaves. Once g_s was obtained, we measured mid-day leaf water potential (Ψ_{leaf}) on the same

leaves, with a pressure chamber (MPa; 1505D, PMS Instrument Company, Albany OR, USA). These samples were cut at the petiole and immediately placed into the pressure-chamber to avoid dehydration. A sample size of n=3 leaves per plant per cultivar limited plant defoliation to minimize the effect on other traits evaluated during the study and avoided impacting Driscoll's commercial fruit, resulting in a tradeoff between experimental rigor and commercial constraints. We acknowledge that this constrains the statistical robustness and that this is a limitation given cultivar-level comparisons.

1.2.3 Plant morphometric attributes

The leaves collected for Ψ_{leaf} were put into plastic bags, stored in a cooler with icepacks, and transported to the lab. Leaf areas, petioles included, were measured at the University of California, Santa Cruz using a leaf area meter (LI-3100, LI-COR), after which leaves were dried at 60°C in a drying oven for 72 hours, and then were immediately weighed so that leaf dry mass could be recorded. These measurements were then used to calculate leaf mass per area (LMA).

1.2.4 Leaf and petiole anatomy

Image analysis to characterize anatomical traits was analyzed in the petioles of n=3 plants of a subset of 5 cultivars, using a combination of brightfield imaging techniques (Leica DM6 B, Leica Microsystems Inc. Deerfield IL, USA). Five of the ten cultivars were selected for anatomical

measures due to limitations in time and analytical capacity. These cultivars were selected based on preliminary measurements of Ψ_{leaf} and g_s, which captured a broad range of responses.

Stomatal density was measured via impressions of the abaxial epidermis. Leaves were collected in the field and transported back to the lab where the abaxial side of all three leaflets per leaf were coated with a layer of clear nail polish, which was then carefully peeled once the polish has dried and mounted on slides with glycerin. These peels were then used to image stomata at 20x. Three random points on each leaf were sampled and stomata were counted per a selected area (the number of stomata observed per unit area, no. mm^{-2}).

Stems were collected for xylem and phloem anatomy. Stems were hand-sectioned with GEM razor blades, stained with a safranin-alcian stain, and mounted on slides with glycerin. Xylem and phloem areas were measured and then divided by total area to obtain xylem and phloem fractional area. Xylem and phloem anatomical traits reflect water and resource availability, although the direction and strength are species-specific and the relationship can vary (Awad et al., 2010; Brodribb, 2009; Guha et al., 2018; Rico et al., 2013).

1.2.5 Fruit Attributes

At the end of the growing season, fruit traits such as marketable kg per hectare (total yield per plot), grams per berry (fruit size), and °Brix (the

index of fruit sweetness), were measured for each of the 10 cultivars for both treatments. Marketable yield was obtained by measuring fruit mass (kg) per plot. These values were then scaled to kg per hectare using a row spacing of 1.38 meters, plot length of 2.00 meters, with each plot holding 16 plants. Marketable grams per berry was measured by weighing the total fruit mass per plot (g) and dividing by the number of berries. °Brix was obtained using a digital refractometer (PAL-1 Digital Refractometer, ATAGO, WA, USA) to measure the refractive index of fruit juice or the total soluble solids concentration, which indicates the concentration of sugars in the fruit juice as a percentage. This was measured in five fruits per plot.

Consumers primarily evaluate fruit quality based on size, appearance, and aroma, while flavor is a key determinant of repeat purchase (Ripoll et al., 2014; Shewfelt, 1999). As our dataset includes both marketable grams per berry (MGPB; fruit size) and °Brix values (key for flavor), we developed a composite metric to integrate these measures. Given that both variables play critical roles in marketability, they were weighted equally and compared against market benchmarks to generate a metric referred to here as the Berry Delight Index (BDI). BDI was calculated using the following formula

(Eq 1) $$BDI = \frac{MGPB}{28.5(averageliteraturevalue)} + \frac{^{\circ}Brix}{8(averageliteraturevalue)}$$

Where marketable grams per berry (MGPB) was divided by an average MGPB obtained from previously reported values (Liu et al., 2023; McAvoy, 2025; Menzel and Smith, 2014) and added to the average °Brix, which was divided by an average °Brix value for strawberries, also estimated from previous reports (Hummer et al., 2023; Keutgen and Pawelzik, 2007; Kroggel, 2014).

Because we are introducing this new metric, we want to clarify that BDI, and its equal weight of °Brix and average fruit size, has not yet been validated against consumer preference data and market standards. While this metric is limited, we felt it was useful to include because it helps draw attention to the potential benefits of reduced irrigation frequency in crop production.

1.2.6 Statistics

Seasonal variation of leaf water potential (Ψ_{leaf}), stomatal conductance (g_s), and leaf mass per area (LMA) was analyzed using a mixed-effects model with treatment, cultivar, month, and their interactions as fixed effects. Month was treated as a repeated measure by including plot as a random effect, accounting for repeated observations from the same experimental unit across the growing season. Model assumptions were assessed using Q-Q plots of residuals and residuals-versus-fitted plots. Post

hoc comparisons were performed using estimated marginal means with Tukey-adjusted p-values.

A two-way ANOVA with cultivar and treatment as fixed factors was used to analyze all physiological, anatomical, and fruit-related traits measured in August. Assumptions of normality and homogeneity of variance were assessed prior to analysis and were met. Post hoc comparisons of treatment effects within each cultivar and treatment interaction were performed using estimated marginal means with Tukey-adjusted p-values.

The lm() function in R was used to create linear regression models for reduced irrigation frequency and irrigated treatments, where treatment was included as a factor. Results were significant if $p<0.05$. Correlation matrices were calculated using Pearson's correlation coefficients with pairwise complete observations. The correlation plots in the supplemental material were created using the "corrplot" package.

Principal component analysis (PCA) was conducted to examine multivariate relationships among physiological, anatomical, and yield-related traits. PCA was preformed using the prcomp() function in R with centering and scaling applied to standardize variables to unit variance. Loadings (eigenvectors) were used to assess the contribution of each trait in principal components, while scores were used to visualize sample distribution in multivariate space. A scree plot was used to evaluate the proportion of variance explained by each principal component and to guide

component selection. This analysis is also found in the supplemental material. All statistical analyses were performed in R (version 4.2; R Core Team, 2025).

1.3 Results

1.3.1 Field Measurements - stomatal conductance, water potential, and LMA

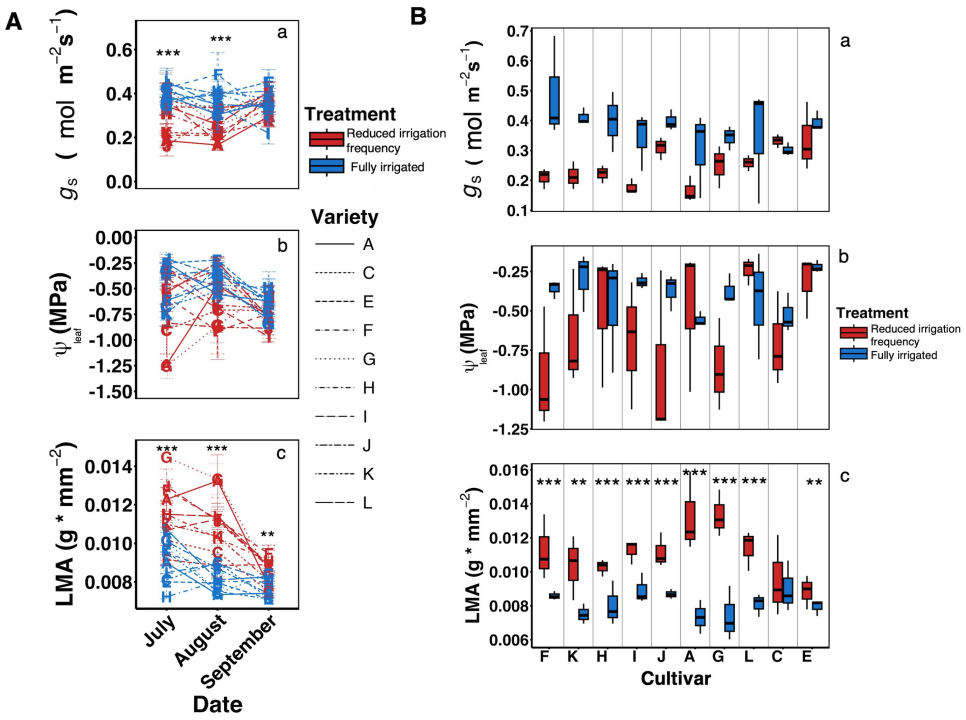

Figure 1.2. A) Physiological data throughout the season. Letters represent the 10 cultivars sampled and treatments are denoted by red (reduced irrigation frequency) and blue (fully irrigated) (n=3, plants were treated as experimental unit). (a) Ψleaf (b) gsw and (c) LMA. Asterisks indicate significant differences between treatments x month interactions (*= P<0.05, ** = P<0.01, *** = P<0.001). B) Physiological data during the month of August (n=3, plants were treated as experimental unit) where treatment is denoted by red (reduced irrigation frequency) and blue (fully irrigated). Box plot midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. (a) Ψleaf (b) gsw and (c) LMA. Asterisks indicate significant differences between treatments (*= P<0.05, ** = P<0.01, *** = P<0.001). The order of boxplots for each cultivar are organized to highlight the largest treatment-related differences in g_{sw} (Figure 2B, panel a). All subsequent boxplots follow this order.

We predicted lower water potential (Ψ_{leaf}), reduced stomatal conductance (g_s), and increased leaf mass per area (LMA) under reduced irrigation frequency. To examine this, we looked at cultivars over the summer (Figure 1.2A) and then narrowed our analyses to August (Figure 1.2B), when plants appeared most stressed due to rising air temperatures and increased VPD (supplemental Figure S1). Across all cultivars, we observed considerable separation between treatments in g_s (on average 33.05% difference), Ψ_{leaf} measures (on average 27.10%), and LMA (on average 24.95% difference) under reduced irrigation frequency (Figure 1.2B, panel a-c, table S3). This is further emphasized in the PCA. There is a clear separation between irrigated and reduced irrigation frequency treatments, with irrigated plants associated with higher stomatal conductance and yield traits, while plants under reduced irrigation frequency were associated with increased LMA and increased fruit soluble solids (ºBrix), indicating a clear tradeoff between productivity and drought-adaptive traits (Figure S5, panel a and b).

Reduced g_s was observed when plants were subjected to reduced irrigation frequency. For instance, when cultivars were pooled together, we found an interaction between treatment and month ($F_{2,120}$= 8.65, $p<0.01$), where g_s was lower when plants were exposed to reduced irrigation frequency in both July and August (Figure 1.2A, panel a). Specifically, under well-irrigated conditions, g_s was 30% higher in July and 33% higher

in August compared to water stressed conditions (Figure 1.2A, panel a). In August, g_s was significantly lower when grown under reduced irrigation frequency across all cultivars ($F_{1,40}$=33.65, p<0.001; Figure 1.2B, panel a), whereas the cultivar x treatment interaction was not significant (F = 1.53, p=0.173), indicating a generally consistent response among cultivars and no differences within cultivar due to irrigation treatment.

We observed significantly lower water potentials (Ψ_{leaf}) in the reduced irrigation frequency treatment across all three sampling months ($F_{1,120}$=20.18, p<0.001; Figure 1.2A, panel b). However, there was no significant month x cultivar interaction ($F_{2,120}$=1.35, p=0.263), indicating that cultivars responded similarly throughout the growing season despite the differences in irrigation regime. Although the reduced irrigation frequency plants exhibited lower $\Psi_{leaf,}$ the magnitude of this response was relatively consistent among cultivars, suggesting that the imposed drought treatment was sufficient to alter plant water status but not strong enough to generate cultivar-specific responses. When August was analyzed separately, Ψ_{leaf} remained significantly lower is the reduced irrigation frequency treatment when all cultivars are pooled together ($F_{1,120}$=20.18, p<0.001; Figure 1.2A, panel b), with no significant cultivar x treatment interaction.

Leaf mass per area (LMA) was significantly different between the two treatments across all months and cultivars ($F_{1,120}$=102.66, p<0.001). Additionally, there was a significant interaction between treatment and

month ($F_{2,120}$=6.53, p=0.002) with LMA values 28.57% higher than irrigated plants in July, 32% higher in August, and 25% higher in September. (Figure 1.2A, panel c). Higher LMA is associated with water conservation, and in August, we observed a significant difference between treatments across cultivars ($F_{1,40}$=74.72, p<0.001) and a significant interaction between cultivars and treatment ($F_{9,40}$=2.83, p=0.011). Specifically, this study found that nine of the ten cultivars had higher LMA when grown under reduced irrigation frequency (Figure 1.2A, panel b).

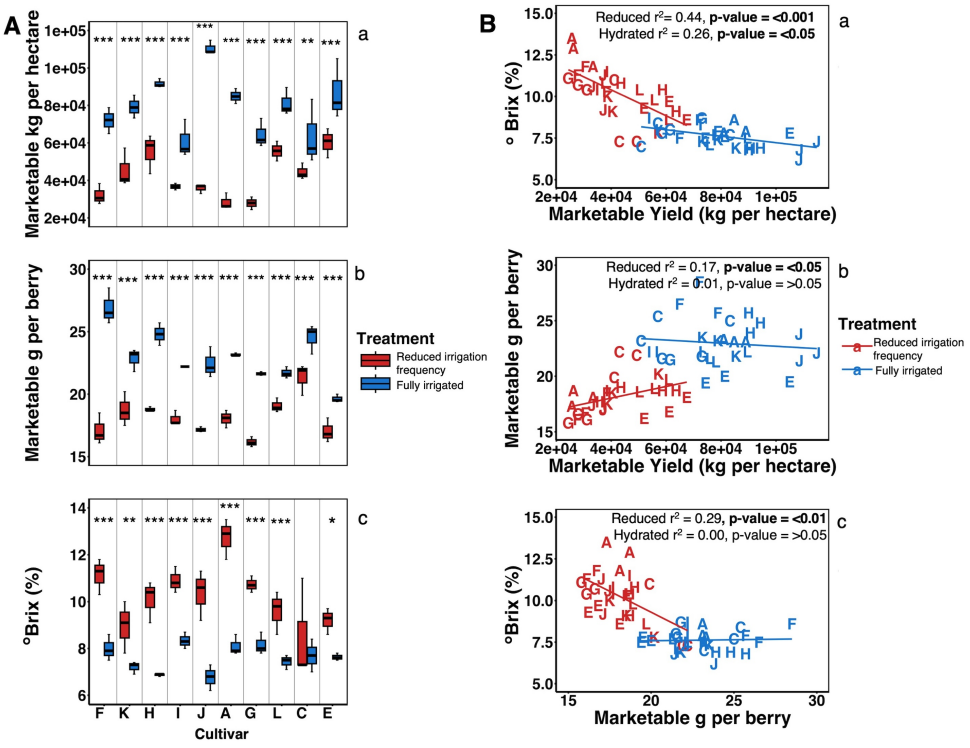

Figure 1.3. A) Fruit data collected throughout the season. Box plot midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. (a) Marketable kg per hectare (b) Marketable g per berry and (c) °Brix. n=3 for all fruit data, where plots were treated as experimental unit. Asterisks indicate significant differences between treatments (*= P<0.05, ** = P<0.01, *** = P<0.001). B) Regressions for fruit traits, where letters represent the 10 cultivars sampled and treatment is represented by red (reduced irrigation frequency) and blue (fully irrigated). (a) Marketable kg per hectare and °Brix (b) Marketable kg per hectare and Marketable g per berry and (c) Marketable g per berry and °Brix.

1.3.2 Fruit Traits

We observed a significant difference in marketable yield (kg per hectare) between the two treatments across all cultivars ($F_{1,40}$=327.46, p<0.001) and an interaction between cultivar and treatment ($F_{9,40}$=6.64, p<0.001) (Figure 1.3A, panel a). Within individual cultivars, marketable kg

per hectare was significantly lower under reduced irrigation frequency than under irrigation, with an overall production decrease across cultivars under reduced irrigation frequency. On average, reduced irrigation frequency lowered marketable yield by 46% compared to irrigated plants.

Water stress reduced fruit mass across all cultivars ($F_{1,40}$=491.57, $p<0.001$) and an interaction between cultivar and treatment ($F_{9,40}$=9.38, $p<0.001$), producing smaller berries with an average weight reduction of 21% (Figure 1.3A, panel b). Under water stress, berry size ranged from 16 g per berry (cultivar G) to 21.33 g per berry (cultivar C). Typically, average marketable values are around 28.5 g. Consequently, smaller berries had more concentrated sugars.

We observed a significant difference in °Brix between the two treatments across all cultivars ($F_{1,40}$=166.71, $p<0.001$) and an interaction between cultivar and treatment ($F_{9,40}$=2.60, $p=0.018$) (Figure 1.3A, panel c). On average, °Brix increased by 25% under reduced irrigation frequency, except for cultivar C. We observed °Brix values ranged from 6.76 (cultivar J) to 12.73 (cultivar A), whereas average marketable °Brix values tend to be around 8.0.

Reduced irrigation frequency strengthened correlations among fruit traits compared to regular irrigation. For instance, °Brix decreased as marketable yield increased under reduced irrigation frequency ($p<0.001$). This relationship was absent under irrigation (Figure 1.3B, panel a). The

same pattern is true for the relationship of marketable grams per berry and marketable yield under limited water conditions, as marketable grams per berry increased as marketable yields increased ($r^2 = 0.17$, $p<0.05$), but there was no relationship under regular irrigation (Figure 1.3B, panel b). Finally, when °Brix and marketable g per berry were compared, we found that smaller fruit also had higher °Brix values ($r^2 = 0.29$, $p<0.01$), whereas the irrigated treatment exhibited no relationship (Figure 1.3B, panel c). These data support our hypothesis that reduced irrigation frequency induces tradeoffs in fruit production.

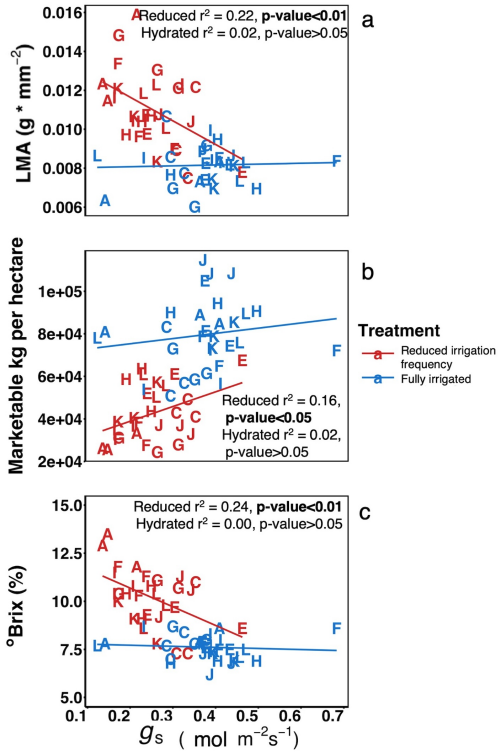

Figure 1.4. Regressions for traits paired with stomatal conductance (g_{sw}) (the predictor variable), where letters represent the 10 cultivars sampled and treatment is represented by red (reduced irrigation frequency) and blue (fully irrigated). The following traits were analyzed as response variables: (a) LMA (b) Marketable kg per hectare and (c) °Brix.

1.3.3 Stomatal Conductance in relation to plant and fruit traits

We hypothesized that stomatal conductance (g_s) would relate to both fruit traits and water tress resilience. Under reduced irrigation frequency, greater g_s improved fruit yields, but reduced fruit °Brix and leaf mass per area (Figure 1.4, panel a-c). Marketable yield positively correlated

with g_s in the reduced irrigation frequency treatment ($r^2 = 0.16$, $p<0.05$) (Figure 1.4, panel b).

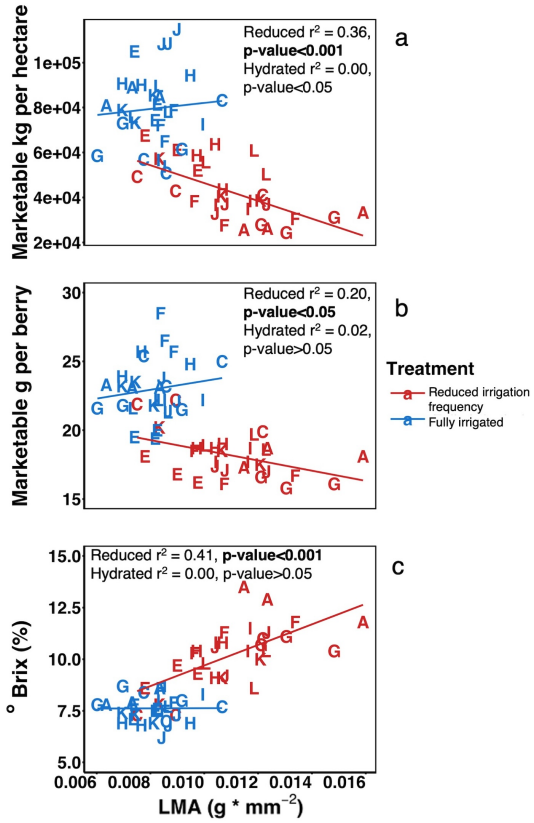

Figure 1.5. Regressions for traits paired with leaf mass per area (LMA) (the predictor variable), where letters represent the 10 cultivars sampled and treatment is represented by red (reduced irrigation frequency) and blue (fully irrigated). The following traits were analyzed as response variables: (a) Marketable yield (b) Marketable g per berry and (c) °Brix.

1.3.4 Tradeoffs between leaves and fruit

Accordingly, we observed multiple tradeoffs between LMA and fruit traits (Figure 1.5, panel a-c). Under reduced irrigation frequency , LMA increases, which we hypothesize may be due to reduced carbon availability for yield and berries. Higher LMA significantly correlated with lower yields

($r^2 = 0.36$, $p<0.001$) and smaller berry size ($r^2 = 0.20$, $p<0.05$) (Figure 1.5, panel a-b). °Brix, however, has a different relationship to LMA. Fruit °Brix increases as LMA increases in the reduced irrigation frequency treatment ($r^2 = 0.41$, $p<0.001$) (Figure 1.5, panel c). These patterns were not observed under regular irrigation.

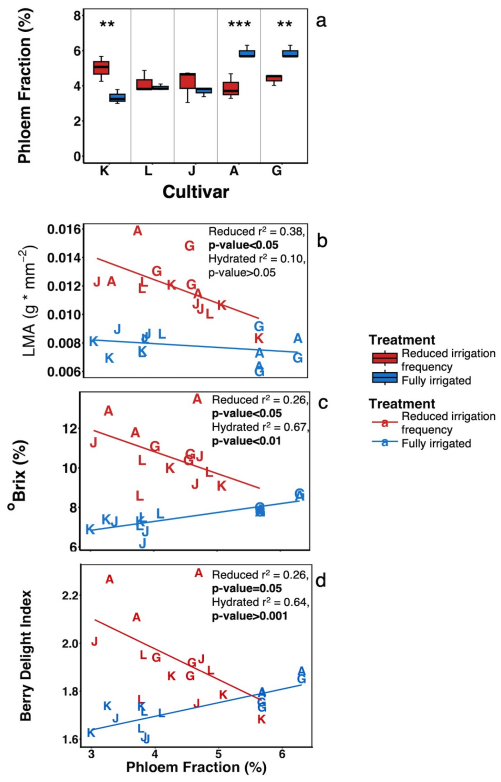

Figure 1.6. Graphs for phloem fraction measures. (a) Box plot midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers for 5 cultivars (n=3, plants were treated as experimental unit). (b-d) Regressions for traits paired with phloem fraction (the predictor variable), where letters represent the 5 cultivars sampled and treatment is represented by red (reduced irrigation frequency) and blue (fully irrigated). The following traits were analyzed as response variables (b) LMA, (c) °Brix, and (d) Berry Delight Index.

1.3.5 Anatomical traits under water deficit

There was a significant interaction between cultivar and treatment for phloem fraction ($F_{4,20}$=11.50, p<0.001) (Figure 1.6, panel a). Allocation to phloem is an indication of carbon transport capacity and another marker of the tradeoffs that occur during reduced irrigation frequency. Cultivars A and G had significantly lower phloem fraction when grown under limited irrigation. These cultivars also had higher LMA and °Brix values compared to other cultivars when grown under reduced irrigation frequency (Figure 1.6, panels b-d).

Xylem fraction was significantly different between cultivars ($F_{4,20}$=2.91, p=0.048), however, treatment did not have an effect ($F_{1,20}$=0.87, p=0.362) (Figure S3, panel c). We also observed that stomatal density treatment responses were significantly different across cultivars ($F_{1,20}$=17.61, p<0.001) (Figure S3, panel a). However, there was no interaction between cultivar and treatment. Finally, we found that vessel diameter was significantly different between cultivars ($F_{4,20}$=14.38, p<0.001) and that there was an interaction between cultivar and treatment ($F_{4,20}$=21.71, p<0.001) (Figure S3, panel b)

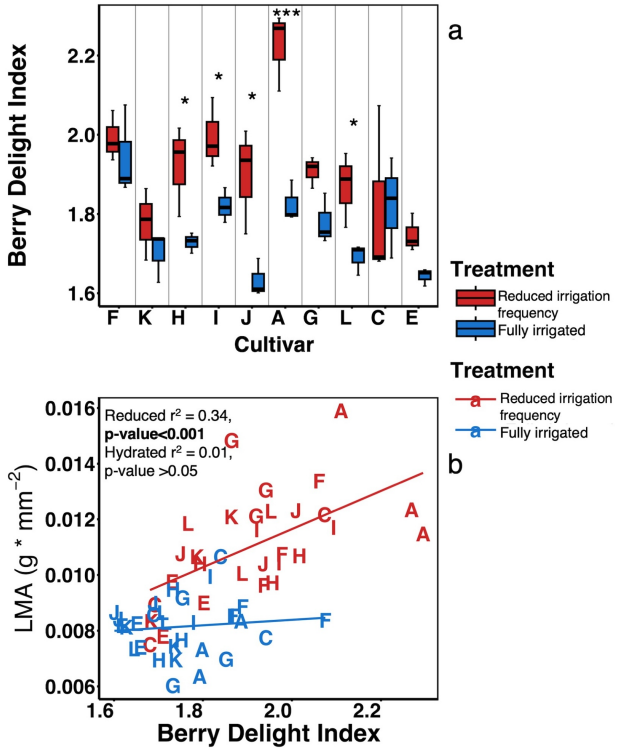

Figure 1.7. (a) Berry Delight Index (BDI) calculated from equation 1 (n=3, plants were treated as experimental unit). Box plot midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. (b) regression for BDI (the predictor variable), and LMA (the response variable) where letters represent the 10 cultivars.

1.3.6 Berry Delight Index

Although reduced irrigation frequency substantially reduced total yield and berry mass, our goal was also to evaluate how reduced irrigation frequency influences fruit market quality. To quantify this balance, we developed the Berry Delight Index (BDI; Eq. 1), integrating fruit size and sugar content based on the premise that marketability depends on °Brix

sugar content and moderate size. Overall, we observed that reduced irrigation frequency significantly increased BDI across all cultivars ($F_{1,40}$=42.90, $p<0.001$) and we found an interaction between cultivar and treatment ($F_{9,40}$=42.90, p=0.03). Cultivars that maintained high LMA exhibited strong water stress resilience (H, I, J, L, and especially A) and achieved relatively high BDI values despite yield losses.

1.4 Discussion

Many studies have examined crop physiological responses to water deficit and how reduced irrigation alters the balance between physiological function and fruit development (Van Laere et al., 2023; Zhao et al., 2020). This kind of research is critical for understanding how different strawberry cultivars respond under limited water availability and can help breeders and growers optimize both water stress resilience and yield. In our study, the physiological mechanisms we directly observed as a response to reduced irrigation frequency were increased leaf mass per area (LMA; Figure 1.2A, panel c), reduced stomatal conductance (g_s; Figure 2A, panel a), generally reduced water potentials ($\Psi_{leaf,}$ Figure 1.2A, panel b), decreased phloem fraction in two cultivars (Figure 1.6, panel a), and reduced fruit size (Figure 1.3A, panel b), while increasing fruit °Brix values (Figure 1.3A, panel c). Overall, we found that strawberries have a coordinated response to water stress, as higher LMA is associated with reduced yields and smaller berries

(Figure 1.5a and 1.5b). Two cultivars also had reduced phloem fraction, however, there was no penalty to fruit °Brix. We therefore hypothesize that phloem content does not appear to be limiting in those two cultivars. These results indicate that strawberry production under reduced irrigation frequency is feasible but is accompanied by predictable tradeoffs in fruit size and yield.

Reduced irrigation frequency may reflect a shift in carbon allocation toward greater leaf structural investment resulting in increased LMA (Figure 1.5). Under reduced irrigation frequency, plants often prioritize the development of thicker, denser leaves through adjustment in cell size, increased cell walls, higher tissue density, and greater investment in cellulose and lignin (Alonso-Forn et al., 2020; John et al., 2017). Such changes have been shown to enhance drought resilience by improving leaf longevity and water-use efficiency (Wright et al., 2004), though potentially at the cost of reduced yield. Thicker leaves with more mesophyll tissue increase the diffusion path for CO_2, reducing mesophyll conductance and limiting photosynthetic capacity (Zhang et al., 2018). Although this strategy conserves water, it may restrict carbon assimilation and consequently reduce fruit production. We would expect leaf structure and water transport to be coordinated, such that as leaves begin to grow smaller and thicker, xylem

and phloem grows smaller too. As a result, this can impact fruit and lead to reduced berry mass.

One such interaction with vascular anatomy is reduced phloem fraction in cultivars A and G under reduced irrigation frequency. Phloem fraction, which represents the relative area of phloem tissue per cross-sectional area, provides a functional link between carbon transport and fruit traits, given the central role of phloem in distributing photosynthates from leaves to developing fruit. Water stress can disrupt this process. For example, Xie et al. (2009) observed that limiting root morphology, which can occur during drought, disrupted phloem architecture and reduced grape berry growth (Xie et al., 2009). However, in our study, we observed a coordinated trait response of lower phloem fraction, higher LMA, and higher brix in varieties A and G, which suggests that there is a scaling of traits occurring between vasculature, plant size and fruit quality. While this was only observed in two of the 10 cultivars, this trait should be further investigated in future studies. In cultivars A and G, even though plants have lower phloem fraction , the delivery of sugars does not appear to be impeded given that leaves with higher LMA also have fruit with greater °Brix. It is important to note that this study does not directly test the underlying mechanisms driving these patterns, such as direct measurements of carbon flux or photosynthetic rates. More work is needed to determine how the

movement and allocation of carbon occurs in strawberries grown under reduced irrigation frequency or water deficit.

Consistent with this, we observed a negative relationship between LMA and g_s across cultivars under reduced irrigation frequency (most notably in variety A and G), suggesting that as gas exchange becomes increasingly constrained, plant growth may be reduced overall (Figure 1.3, panel a). Together, these coordinated shifts in leaf structure and growth habit highlight a strategy in which plants prioritize water conservation at the expense of efficient vasculature and fruit production.

While many plants possess adaptive drought traits that improve survival under water deficit (Torres-Ruiz et al., 2024), these adaptations can come with tradeoffs for fruit characteristics (Figure 1.3B panel a-c). Consumers primarily value fruit based on size, appearance, and aroma, while flavor strongly influences repeat purchase (Ripoll et al., 2014). Therefore, understanding the link between drought resilience and fruit market quality is critical. Previous work has shown that moderate drought can increase fruit soluble sugar concentrations and improve flavor, but often reduces size and yield (Leporino et al., 2025; Medyouni et al., 2021; Ripoll et al., 2014). Because fruit size depends on cell division and expansion, both of which rely on water and carbohydrate supply, fruit growth is particularly sensitive to water limitation.

Across cultivars, but most notably in varieties A, F, and G, we found water stress resulted in plants with smaller fruit that had higher °Brix values (Figure 1.3B, panel c), consistent with reports that sugar accumulation increases in drought-stressed fruit. For example, across cultivars, the reduced irrigation frequency treatment showed substantially reduced g_s and specifically, cultivar A had a 67% reduction in yield under reduced irrigation frequency but also higher °Brix values (Figure 1.2A, panel a and c). In contrast, a few cultivars maintained relatively fixed physiological traits under both irrigation treatments. Cultivar C, for example, exhibited similar LMA and g_s between treatments (Figure 1.2B panel a and c). Marketable yield for this cultivar was less impacted by reduced irrigation frequency when compared to other cultivars (Figure 1.3A panel a). However, even among the most resilient cultivars, fruit size declined under reduced irrigation frequency (Figure 1.3A panel b).

A comparable pattern was reported in apples, in which mild drought increased fructose accumulation and flavor quality, but severe drought significantly reduced fruit size (Tao et al., 2023). Additionally, early ABA accumulation has been found to accelerate ripening and disrupt sugar balance in plants grown under drought conditions (Sánchez-Gómez et al., 2022). Elevated ABA may also promote stomatal closure and reduce photosynthesis (Kane and McAdam, 2023), linking physiological and reproductive responses under stress. Consistent with these mechanisms, all

cultivars in our study produced smaller berries with reduced yield under reduced irrigation frequency, but most exhibited increased sugar concentration.

1.5 Conclusion

Overall, the ten cultivars displayed a range of physiological strategies, but fruit size was consistently reduced and all cultivars produced smaller fruit and lower yields when water was restricted. Our findings highlight the importance of integrating physiological and fruit-quality traits in breeding programs aimed at maintaining yield and quality under limited water availability. Future work testing these cultivars under a gradient of water deficit and in combination with additional stressors (such as high temperature and disease) will help identify genotypes best suited to increasingly variable climatic conditions (Ullah et al., 2024; Wang et al., 2024).

Chapter 2: The structure-function trade-offs of the dry-farm adapted, heirloom tomato *Solanum lycopersicum* L., var. Dirty Girl

2.1 Abstract

Dry-farming is a low-input agricultural strategy the relies on minimal or no irrigation and is most effective in regions with suitable soil and summer marine influence. Although yields are often reduced, dry-farming can enhance fruit quality, promote deep root development, limit weed production, and improve resilience to water limitation. While previous studies have described morphological traits associated with dry-farmed tomatoes (*Solanum lycopersicum)*, knowledge regarding the physiological mechanisms underlying their performance under water deficit remains limited. I investigated water- and carbon-use strategies in dry-farmed tomatoes, focusing on the adapted variety Dirty Girl compared to the non-adapted Slicer. I hypothesized that Dirty Girl would maintain productivity under drought by increasing resistance to embolism, exhibiting a more intrinsically drought adjusted response, and by accessing deeper soil resources. Dry-farming conditions reduced individual plant yield by 35.32% in Dirty Girl and 59.91% in Slicer, indicating a stronger decline in Slicer, although this difference is not statically supported by significant interaction. Dry-farmed- adapted Dirty Girls had high transpiration rates alongside reduced water potentials during fruit development. Dry-farmed Dirty Girls also exhibited enhanced traits such as greater plant height, increased leaf

vein density, and increased root vessel diameters. Concurrently, these plants expressed traits associated with drought-tolerance such as a safer xylem network (smaller stem vessel diameters), increased leaf thickness (leaf mass per area), increased resistance to leaf wilting (lower water potential at turgor loss point), and increased embolism resistance in stems. These traits resulted in reduced yields under no irrigation, with smaller fruits that had elevated soluble sugars (°Brix). While the Slicer variety also had higher resistance to embolism under dry-farming, they did not have multiple attributes associated with drought-tolerance, unlike their counterpart. Additionally, soil analysis showed increasingly limited water availability under dry-farming as the season progressed, along with differences in nutrient availability along the soil column, with nitrate and phosphorus concentrated near the surface. In conclusion, the dry-farm-adapted Dirty Girl has a unique set of attributes, distinct from the non-adapted Slicer, that promotes performance under water deficit conditions, and provides insight into traits that could inform the breeding and management of crops in water-limited environments.

2.2 Introduction

Dry-farming is a method of crop production that relies on little to no irrigation and is most effective in regions with suitable soil types and summer marine influence (Socolar et al., 2024a). In the Pacific Northwest, this includes coastal areas of California, Oregon, and Washington, where

annual rainfall is typically around 20 inches. However, dry-farming is not limited to this region as it has been practiced globally, including in Australia, China, Mediterranean climates, and parts of North and West Africa, and dates back to the earliest agricultural systems (Stewart and Thapa, 2016). Although dry-farming often results in lower yields, it can increase fruit quality, sustain production under limited water availability, promote deep root development, limit weed production, and potentially increase carbon sequestration (Farage et al., 2007).

In California, the most common reasons for loss in crop production include damage from pests and drought, which can lead to the higher cost of water, all of which can result from climate change (Husaini and Xu, 2016; Samtani et al., 2019). While drought events become more common, the use of water in crop production has also increased (Vermeulen et al., 2025). In 2015 alone, it was estimated that California used 40 billion m^3 of water for agriculture (Qin and Horvath, 2020). As policies are enacted to limit ground water usage to compensate for the limited rainfall during drought events, growers must contend with increased costs of irrigations or switching to water-saving crop types (Quandt *et al*., 2023). This highlights the need to evaluate sustainable farming practices, such as dry-farming, and identify crops capable of maintaining productivity under limited water availability.

One crop of interest is *Solanum lycopersicum,* commonly known as tomato. Tomatoes are an important, multi-functional produce that can be

cooked or consumed raw and are grown worldwide, with a global production of 189 million tons per year (Castronuovo et al., 2023). California is a favorable location to grow these fruits due to its Mediterranean climate, with production responsible for 30% of the world's processed tomatoes (Pathak et al., 2018). Due to rising temperatures and variable precipitation, however, crop production worldwide is confronted with many challenges (Calvin et al., 2023; Dang et al., 2025; Hu et al., 2024). Specifically, the tomato industry faces reduced yields due to alterations in phenology, as increased temperatures and reduced precipitation accelerate the tomato lifecycle, leading to less biomass and reduced flowering (Ventrella et al., 2012). Therefore, it is urgent that newly developed tomato varieties encompass traits that can compete with a changing climate, while still producing marketable, flavorful and nutritious fruit.

Commercial tomatoes currently offer less than 5% of the genetic diversity as their wild progenitor, which originated in Central and South America, leaving them vulnerable to these climatic issues (Bai and Lindhout, 2007). Standard hybrid tomatoes are exceptionally risky for farmers to use in monoculture, as they are susceptible to crop failure. An additional option to the standard tomato is the de-hybridized, dry-farm-adapted, tomato *Solanum lycopersicum* L., var. Dirty Girl. This is an open-pollinated tomato variety that originated as a second-year volunteer from the popular hybrid cultivar Early Girl. It has since been selectively bred for over 15 growing seasons

under dry-farmed conditions in California's central coast Santa Cruz County ("Dirty Girl," 2022). Dirty Girl tomatoes have become a popular choice among Santa Cruz County growers largely because seeds can be saved and replanted, enabling continued selection and adaptation within a specific growing environment. In addition, Dirty Girl plants have a longer growing season than many other tomato varieties and produce smaller, more condensed fruit with concentrated sugars, resulting in higher fruit quality and market value. Furthermore, dry-farmed tomatoes have been found to reach depths of 150 cm, and can be stimulated to grow deeper under dry-farming so that plants can access water and nutrients found at deeper soil horizons (Leap et al., 2017; Socolar et al., 2024b). Together, these traits make Dirty Girl an economically important bridge crop and provide incentives for growers to transition towards dry-farming systems, highlighting the importance of studying this variety

Numerous studies have characterized morphological traits associated with dry-farm tomatoes (Cantore et al., 2016; Castronuovo et al., 2023; Davis et al., 2023), but few studies have examined the water- and carbon-use strategies that allow these plants to succeed under minimal irrigation (Gill et al., 2024). While there are few studies on dry-farmed tomatoes that address the physiological tradeoffs under dry conditions, there has been research on standard tomatoes that informed our research design. Previous work suggests

trade-offs between hydraulic efficiency and safety, with reproductive structures often prioritized over vegetative tissues under drought stress (Harrison-Day *et al*., 2022).

In plant hydraulics, the safety versus efficiency tradeoff refers to the balance between maintaining an efficient xylem network that allows for continuous water transport and developing a safer xylem network that can tolerate higher tensions, with reduced risk of cavitation (Hacke and Sperry, 2001; Sperry, 2003; Gleason et al., 2016). Cavitation occurs when air seeding breaks the water column in plant conduits and eventually lead to embolism that block water transport. The more efficiently a plant can move water per xylem cross-sectional area, the higher its potential to photosynthesize, grow at faster rates, and produce more biomass and higher yields. In contrast, hydraulically safe plants that are embolism resistant can survive drier and warmer conditions. The tradeoff arises as plants with increased transport efficiency cannot have increased resistance to embolism (Pittermann, 2025).

In a study by Harrison-Day et al. (2022), for example, tomato leaves were found to wilt rapidly and exhibit high vulnerability to petiole xylem embolism at relatively high-water potentials (leaf petiole p50 = -1.39 MPa ± 0.23 *SD*), limiting water transport to leaf tissues. The study also found that while some organs were more vulnerable to embolism (leaves, petals,

petioles) other organs vital for fruit production became more resistant (stems and peduncles), supporting that standard tomatoes balance traits that offer both efficiency and safety.

Other studies have observed that increased drought resistance is often associated with the development of physiological and structural traits that enhance hydraulic safety, which may be useful to crops with limited water resources under dry-farming. Anatomical characteristics such as reduced xylem vessel diameters and lower stomatal and vein densities, play key roles in limiting vulnerability to embolism. In species adapted to arid environments, smaller xylem conduits reduce the likelihood of embolism spreading to neighboring vessels by limiting inter-vessel connectivity (Isasa et al., 2023; Lens et al., 2022; Sperry et al., 2006; Torres-Ruiz et al., 2024). Reduced stomatal and vein densities promote water conservation at the leaf level by lowering transpiration rates (Brodribb and Jordan, 2011; Zhang et al., 2022). Together, these traits enhance hydraulic resilience, but often reduce carbon gain and, consequently, yields. It remains unclear whether dry-farm–adapted tomato varieties exhibit similar trade-offs and how these strategies influence seasonal water use, drought tolerance, rooting patterns, and fruit production.

Given this, more information is needed to understand how dry-farm-adapted plants maintain high productivity during the dry summer months. Our research aims to uncover the physiological mechanisms these plants use

to flourish under harsh conditions and provide farmers with the information necessary to grow dry-farmed crops most effectively. In this study, I simultaneously assessed multiple traits in dry-farmed adapted and non-adapted varieties to understand how dry-farm crops mitigate drought through various physiological traits. I tested two varieties of tomatoes under irrigated and dry-farmed conditions: the dry-farm adapted Dirty Girl and a non-adapted Cherokee Purple (Slicer). Cherokee Purples are heirloom tomatoes that were selected for this study as a contrast to the Dirty Girl due to their large, thin-skinned fruit, which could indicate higher water consumption and greater drought-sensitivity ("Lycopersicon; Cherokee Purple Tomato," n.d.).

To characterize the traits that make dry-farm Dirty Girls successful, this study evaluated physiological, anatomical, fruit, and soil traits. Our research addressed the following questions: 1. How do dry-farm tomatoes use water throughout the season and over a day? 2. Which physiological and structural costs are associated with different water-use strategies, and how might these strategies influence drought tolerance? 3. How do different physiological traits affect crop quality and yield? and lastly, 4. Is there a relationship between varietal physiology and soil nutrient availability under dry-farmed and irrigated regimes? I hypothesized that Dirty Girl tomatoes would have greater capacity to withstand drought stress and maintain yields by increasing embolism resistance and increasing water use efficiency. I also

hypothesized that dry-farm adapted crops would have greater access to soil nutrients at deeper soil depths that enable comparable yields under dry-farmed and irrigated conditions, as well as higher yields than the non-adapted Slicer.

2.3 Methods and materials

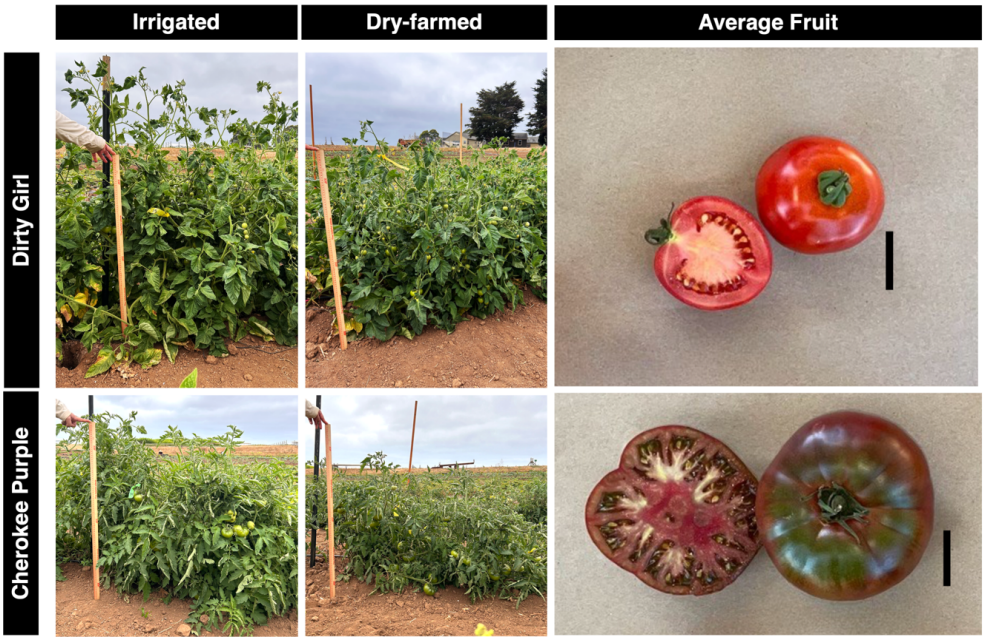

Figure 2.1. Plants growing in the field for each variety and treatment. A one-meter ruler is propped next to each plant for reference. Panels on the far right show the average size of fruit when dry-farmed.

2.3.1 Study Site

This study was performed at the University of California, Santa Cruz, Center for Agroecology (CFA). The climate is subhumid, mesothermal with moderately cool, foggy summers and cool, wet winters. Mean annual precipitation is approximately 18 inches, which mostly occurs in the winter months. During the summers, the high is 33 °C and low 10 °C. The land consists of well drained, fine-loamy soil ("Official Series Description - ELKHORN Series," n.d.). Prior to the beginning of the trial, the plots were prepared with soil amendments described by the CFA grower guide for

Organic Dry-Farmed Tomato Production on California's Central Coast (Leap et al., 2017). For the duration of the experiment, weed and pest control management were implemented per the grower guide.

2.3.2 Experimental design

Dirty Girl seeds were collected from plants that had undergone eight generations of dry-farm selection at the CFA. They were sown into a mixed substrate soil and maintained in a greenhouse for approximately two months and were transplanted after they produced significant foliage. Slicer seedlings were sourced from a local grower in Santa Cruz, California.

On June 20, 2024, seedlings were transplanted into two adjacent 37 × 37 m field blocks: one managed under dry-farm conditions and the other under irrigated conditions. Prior to planting, soil was sampled throughout field and no significant difference was observed between treatment blocks for soil moisture or soil nutrients (see section Soil Sampling for more detail). The treatment blocks were separated by a 15-foot buffer to prevent water runoff from the irrigated plots into the dry-farm plots. Each block contained four subplots of each variety, with subplot locations randomized within each block. Each subplot consisted of 20 plants, resulting in an initial total of 80 individuals per variety per treatment.

Immediately following transplanting, all plants received 1 inch of water delivered via a drip tape irrigation system, which amounts to 34.80 m^3

per 37 x37 treatment block (34,800 liters of water). Because transplanting occurred during a heatwave, supplemental irrigation of 0.25 inches (8.7 m^3 or 8,700 L of water) per week was applied to all plots for three weeks to facilitate root establishment. Irrigation was discontinued on July 15 for plants assigned to the dry-farm treatment. Thereafter, only the irrigated plots received weekly watering to replace evaporative transpiration losses. Data were collected throughout the tomato growing season, from June to October 2024.

2.3.3 Plant physiological attributes

Throughout the summer, measures of leaf stomatal conductance (g_s; µmol m^{-2} s^{-1}) were collected every other week with a Decagon Porometer (SC-1, METER Group, WA, USA). I randomly selected and measured 16 irrigated and dry-farmed plants from each of the two varieties between 10:00 h and 14:00 h, to ensure consistency during sampling period. Leaves that were sampled were those that were fully expanded, apical growth that were sun-exposed and south facing.

Concurrently, leaves that were used for g_s measures were then used to measure leaf water potential (Ψ_{leaf}; MPa) using a Scholander-type Pressure Chamber (1505D, PMS Instrument Company, Albany OR, USA). Leaves were cut at the petiole, immediately put into the pressure chamber head to avoid dehydration, and pressurized until water was seen at the surface of the excision.

On September 29, 2024, net carbon assimilation (Anet; μmol CO2 m^{-2} s^{-1}) was measured on n=16 fully expanded sun leaves. Photosynthetic rates were measured using a Li-Cor 6400 instrument (Li-Cor, Lincoln, Nebraska, USA), with cuvette conditions set to and maintained at 400 ppm CO_2, temperature of 25 °C, PAR at 2,000 μmol m^{-2} s^{-1}, and a leaf to air vapor pressure deficit of 1-3 kPa. Additionally, with this instrument I collected g_s and calculated instantaneous water use efficiency (WUE; maximum A_{net} g_{sw}^{-1}).

2.3.4.Morphological measures

As an estimate of plant productivity, plant heights were recorded for plants every two weeks over the growing season. Height was measured starting at the base of the plant, where it met the soil, to the apical leaf (cm).

Leaf mass per area (LMA), a trait closely associated with carbon allocation and water-use strategies, was included in our study. Leaf areas, including leaf petioles, were measured every two weeks using a leaf area meter (LI-3100, LI-COR), after which leaves were dried at 60°C in a drying oven for 72 hours. Once dry, leaf dry mass was immediately recorded. These measurements were then used to calculate LMA.

2.3.5 Foliar Carbon and Nitrogen Stable Isotopes Analysis

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic compositions reveal how carbon and nitrogen isotopes are incorporated into leaf tissues (Gouveia et al., 2019). Under low water availability, lower $\delta^{15}N$ generally indicates that there is less enrichment of nitrogen isotopes, which is attributed to lower soil microbial activity in drier environments, while higher $\delta^{13}C$ indicates the plant's high water use efficiency. To quantify these traits, four leaves were collected from n=16 plants of each variety and treatment, put into paper bags, and taken back to the lab to be dried at 60 °C in a drying oven for 72 hours. After drying, leaves were ground with a mortar and pestle until the material became a fine powder. Approximately 2.500 mg each were analyzed for percent nitrogen weight (%N), percent carbon weight (%C), $\delta^{15}N$, $\delta^{13}C$ and carbon to nitrogen ratio (C:N) by combustion in a CN-EA-iRMS ECS 4010-Delta Plus XP. These analyses were carried out in the Stable Isotope Laboratory, at the University of California, Santa Cruz.

2.3.6 Plant Anatomical Measures

Quantitative image analysis was used to characterize the xylem anatomy in stems and roots of n=6 plants, along with measures of leaf stomatal and vein density, using a combination of brightfield and fluorescence imaging techniques (Leica DM6 B, Leica Microsystems Inc. Deerfield IL, USA). Stems were sectioned with a microtome (Lab-Microtome, Swiss Federal Research Institute, Switzerland) and stained with

a safranin-alcian blue mixture, which contains 0.35 g of safranin in 35ml of 50% EtOH and 0.65g of alcian blue in 65 ml of distilled water. The stained samples were then mounted onto slides with glycerin. The images were photographed at 100x and 20x. Lumen diameter and lumen area was measured for all vessels in a section using ImageJ (Rueden et al., 2017). I followed the same protocol to prepare and image root samples. I standardized root cross sections by sampling 20 cm below the root:shoot junction at the end of the season.

The leaves I used for stomata and vein density measures were cleared using 1M KOH. After leaves were cleared, they were stained with the safranin-alcian stain and mounted onto a slide. These prepared samples were used to image veins and stomata at 100-200x using a combination of brightfield and fluorescence imaging techniques (as described in previous paragraph). Three random points on each leaf were sampled to measure vein density (vein length divided by lamina area; mm mm^{-2}). Similarly, three random points on each leaf were sampled and stomata was counted per a selected area (the number of stomata observed per unit area, no. mm^{-2}). Both measures were performed on the abaxial side of the leaves.

2.3.7 Stem vulnerability preparation and measures

Embolism resistance of vascular tissue was assessed in six individuals per variety and treatment (n = 6). Stems were collected before

sunrise, to minimize xylem tension. Prior to excision, target stems were enclosed in black plastic bags and allowed to equilibrate for approximately 30 minutes. Stems were then cut underwater and maintained submerged during transport to the lab to prevent the introduction of air into the xylem.

In the lab, stems were recut underwater to an initial length of 50 cm. Native hydraulic conductivity (K_{native}) was recorded by measuring flow rate through the stems gravimetrically with a hydraulic apparatus containing a 20 mM KCl solution under a pressure head of ~5 kPa following the methods of Sperry et al (1988). Stems were then flushed using a 20 mM KCl solution at 10kPa for 1 h to remove native embolism, after which maximum hydraulic conductivity (K_{max}) was measured using the same hydraulic apparatus. These values were used to calculate the precent loss in hydraulic conductivity ($PLC_{native)}$. The results from PLC_{native} were inconclusive, as stems would not consistently refill for either variety under both treatments.

Following measurements of $K_{native\ and}$ $K_{max,}$ stems were used to construct xylem vulnerability curves using the centrifuge method following Hacke et al. (2000). Stem segments were recut under water to 14.2 cm and spun in a modified super speed centrifuge (Sorvall RC5C) at progressively increasing rotational speeds to generate increasingly negative xylem water potentials. Hydraulic conductivity ($K_{spin,}$) was measured after each centrifugation spin used to calculate the progressive loss of hydraulic conductivity with decreasing xylem water potential. Vulnerability curves

were constructed from these measurements and used to estimate the xylem water potentials corresponding to 12%, 50%, and 88% loss of hydraulic conductivity (P12, P50, and P88, respectively). Vulnerability curves were relativized to a starting xylem water potential of -0.25 MPa rather than 0 MPa to reduce the potential influence of open-vessel artifacts on the initial portion of the curve.

Maximum vessel length was determined independently using additional stems and was measured as 50 cm for Dirty Girls and 45 cm for Slicers. I recognize that our longest vessels exceed the 14.2 cm length of the rotor, however, the vulnerability curves provide valuable comparative information on the relative differences in embolism resistance in one species between the two treatments that were sampled using the same methods.

2.3.8 Pressure Volume curves

I performed pressure-volume curves analyses to resolve how different leaf-water-use strategies influence plant function. Pressure-volume curves quantify the response of plant tissue to drought limitations by progressively drying leaves on a benchtop and measuring leaf water potentials and mass (g) at progressive intervals. These measures are then used to compute multiple parameters of leaf function, including water potential turgor loss point (Ψ_{TLP}), osmotic potential at full turgor (π), and modulus of elasticity (ε).

These measurements were performed on leaves that were fully expanded sun leaves. During the peak of the growing season, leaves were collected early in the morning before they were exposed to sun and put into humidified bags while they were transferred to the lab. Once in the lab, the petioles were cut under water and kept in water to rehydrate for at least 2 hours, when water potential was at or close to zero. Leaf turgor loss point and other metrics of leaf drought resistance were then measured on n=6 plants for both varieties and both treatments using the pressure-volume approach of Sack *et al*. 2003.

2.3.9 Soil samples

At the beginning of the season, soil moisture probes (Meter Terros 1, METER Group, WA, USA) were installed in the plots at three different depths: 30, 60 and 90 cm, for each variety and treatment (n=4). The probes were left in the ground for the duration of the experiment.

Additionally, soil physical and chemical properties were measured at four timepoints in the experiment – in June (before planting), August (during vegetative growth), September (during fruit development), and October (at the end of the growing season). Soil samples were collected using open bucket augers from four different depths in the soil column (15, 30, 60, 90 cm). These samples were collected from 2-3 random points located within each plot and were then homogenized so that there was one representative sample per soil depth, per plot, per variety and treatment (n=4). The soil

attributes I collected were soil moisture, nitrate (NO_3^-), ammonium (NH_4^+), and phosphorus (P).

2.3.10 Yields

Fruit data was recorded per plot and was collected weekly from September 23 - October 28. Fruit was harvested once ripened, and immediately sorted by fruit quality, which was classified into the following categories: marketable and unmarketable (fruit that was damaged by insects, sun damaged, or blossom end rot). After sorting, total fresh weight was recorded per plot (kg). Kg per plant was calculated by taking total plot mass and dividing by the number of plants within each plot. Data was also collected for fruit water content (fresh mass - dry mass; g) and °Brix soluble sugar content (%). °Brix was obtained using an analog refractometer (MASTER-10M, ATAGO, WA, USA).

2.3.11 Statistics

Traits that were measured across the growing season (Ψl_{eaf}, g_{sw}, LMA, and height) for Dirty Girl and Slicers were analyzed using a three-way ANOVA with variety, treatment, and stage (date) as fixed effects, including interaction terms. Prior to analysis, data was checked for normality and homogeneity of variance using Shapiro-Wilk tests and visual inspection of residual plots. Post hoc comparisons were conducted using estimated marginal means (emmeans) with pairwise contrasts to evaluate treatment effects within each variety and year.

Differences among treatments, varieties, and their interaction were assessed using a two-way ANOVA for all traits measured at one time point. Prior to analysis, model assumptions were assessed by testing normality of residuals and homogeneity of variance. Where necessary, variables were transformed using log transformations to meet model assumptions. When significant main or interaction effects were detected, post hoc comparisons were conducted using Tukey's HSD test to control. Statistical significance was determined at $p = 0.05$.

Soil data was analyzed using linear mixed-effects model fitted with the lme3 package in R. Soil depth, month, treatment, and variety, along with all possible interactions among these factors, were specified as fixed effects. Plot was included as a random intercept to account for repeated measurements within sampling units. The significance of fixed effects was assessed using Type III ANOVA. Model assumptions of normality and homogeneity of variance were evaluated through visual inspection of residual plots. Where necessary, response variables were transformed using log transformations to meet model assumptions, as was the case for NO_3^-, NH_4^+, and P. Post hoc pairwise comparisons were conducted using estimated marginal means with Tukey adjustments.

The lm() function in R was used to genrate linear regression models for trait interactions. Results were significant if $p<0.05$. Correlation matrices

were calculated using Pearson's correlation coefficients with pairwise complete observations. The correlation plots in the supplemental material were created using the "corrplot" package.

Principal component analysis (PCA) was conducted to examine multivariate relationships among physiological, anatomical, and yield-related traits. PCA was performed using the prcomp() function in R with centering and scaling applied to standardize variables to unit variance. Loadings (eigenvectors) were used to assess the contribution of each trait in principal components, while scores were used to visualize sample distribution in multivariate space. A scree plot was used to evaluate the proportion of variance explained by each principal component and to guide component selection. All statistical analyses were performed in R (version 4.2).

2.4 Results

Table 2.1. Fruiting, physiological, and anatomical traits, units, and abbreviations for the two cultivars grown under dry-farmed (D) and regularly irrigated (I) conditions measured during peak productivity. Data are means with standard error in parentheses. All physiological measures were collected when fruit was ripening.

Trait	Units; Abbreviation	Dirty Girl		Slicer	
		D	**I**	**D**	**I**
Average kg per plant	kg	3.17 (0.96)	4.53 (2.05)	2.42 (0.46)	4.49 (1.38)
°Brix	%	6.65 (0.25)	5.87 (0.18)	5.48 (0.14)	4.69 (0.49)
Mass per fruit (kg)	kg	0.053 (0.010)	0.089 (0.008)	0.151 (0.035)	0.216 (0.044)
Fruit dry mass (%)	%	8.79 (1.74)	7.47 (1.35)	6.87 (0.91)	6.17 (1.97)
Leaf water potential	MPa; Ψl_{eaf}	-0.97 (0.15)	-0.74 (0.16)	-0.72 (0.24)	-0.76 (0.13)
Stomatal Conductance (Decagon)	µmol m^{-2} s^{-1}; g_{sw}	479.63 (125.95)	543.51 (146.09)	306.24 (141.22)	535.33 (142.84)
Height (cm)	cm	118.25 (8.62)	133.06 (20.91)	74.44 (14.24)	91.07 (18.30)
Leaf mass per area	g mm^{-2}; LMA	7.60 E-03 (1.10 E-03)	6.80 E-03 (1.00 E-03)	6.40 E-03 (1.00 E-03)	5.60 E-03 (8.00 E-04)
Photosynthesis	µmol CO_2 m^{-2} s^{-1}; A_{net}	23.10 (4.53)	24.21 (3.92)	14.10 (5.36)	20.13 (6.60)
Stomatal Conductance (Li-Cor 6400)	µmol m^{-2} s^{-1}; g_{sw}	0.70 (0.23)	1.01 (0.47)	0.41 (0.19)	0.87 (0.46)
Water use efficiency	A_{net} g_{sw}^{-1}; WUE	35.51 (9.39)	27.78[a] (9.80)	36.61 (10.68)	26.41 (7.29)
Carbon:Nitrogen ratio	C:N	12.92 (1.97)	11.36 (1.26)	9.88 (1.90)	10.12 (1.52)
Carbon Wt %	%C	40.29 (1.52)	41.56 (1.23)	40.87 (1.87)	40.58 (1.89)

Nitrogen Wt %	%N	3.71 (0.56)	4.32 (0.51)	4.98 (0.88)	4.77 (0.71)
Carbon isotopic composition	$\delta^{13}C$	-27.69 (0.72)	-28.44 (0.40)	-27.86 (0.85)	-28.52 (1.20)
Nitrogen isotopic composition	$\delta^{15}N$	5.93 (0.78)	5.89 (0.75)	4.64 (0.81)	5.49 (0.97)
Vein density	mm mm^{-2}	9.10 E-03 (9.00 E-04)	9.10 E-03 (8.00 E-04)	8.30 E-03 (1.00 E-03)	8.30 E-03 (1.10 E-03)
Stomatal density	no. mm^{-2}	230.89 (41.75)	211.09 (28.51)	244.27 (52.43)	223.48 (72.53)
Stem vessel diameter	µm	35.94 (1.93)	41.69 (7.44)	36.02 (2.39)	44.92 (3.05)
Stem hydraulic vessel diameter	µm	53.87 (7.15)	64.84 (11.29)	58.58 (7.61)	74.49 (6.60)
Total stem lumen area	μm^2	3.53 E+05 (3.13 E+05)	4.72 E+05 (3.50 E+05)	4.34 E+05 (3.25 E+05)	8.35 E+05 (4.96 E+05)
Root vessel diameter	µm	114.03 (40.02)	78.48 (2.47)	71.11 (9.69)	87.76 (14.98)
Osmotic potential at full turgor	MPa; π_{TLP}	-0.58 (0.08)	-0.28 (0.06)	-0.38 (0.12)	-0.33 (0.10)
Water potential at turgor loss point	MPa; Ψ_{TLP}	-0.83 (0.07)	-0.49 (0.13)	-0.62 (0.03)	-0.66 (0.08)
Modulus of elasticity at total relative water content	Mpa; ε	7.05 (2.17)	2.25 (0.50)	2.24 (0.68)	2.46 (0.87)

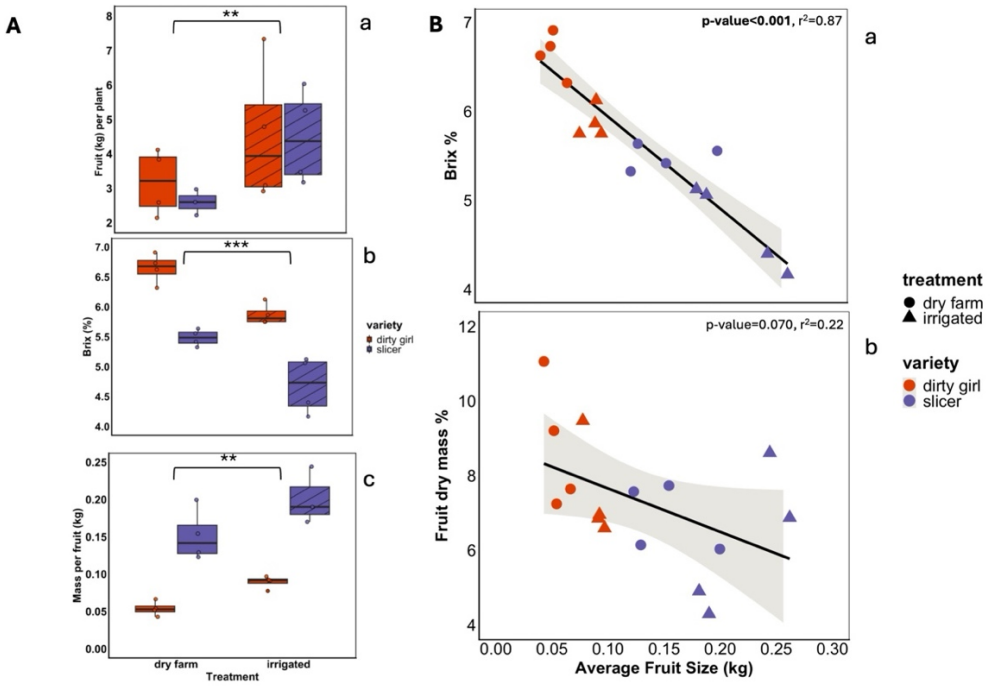

Figure 2.2. (A)Fruit data collected for (a) average marketable kg per plant, (b) °Brix (%), and (c) average mass per fruit (kg). Data was collected for n=4 plots of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid lines) and irrigated (dashed line) conditions. Panel a, b, and c are boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Significant difference between treatment is denoted by *, where * $p<0.05$, ** $p<0.01$, and *** $p<0.001$. (B) Regression for average fruit size (kg) (the predictor variable) and the following response variables: (a) °Brix (%) and (b) fruit dry mass (%) where the colors orange (Dirty Girl) and purple (Slicer) varieties and treatment is represented by circles (dry-farmed) and triangles (irrigated).

2.4.1 Yields

By the end of the growing season, dry-farming strongly depressed marketable yield per plant ($F_{1,12}=6.47$, $p=0.026$, Figure 2.2). There was no significant effect of variety ($p=0.057$) or treatment x variety interaction

(p=0.612), although dry-farming reduced individual plant yield by 35.32% in Dirty girls and 59.9% in Slicers (Figure 2.2A panel a; table 1).

The Brix° results support increased flavor in dry-farmed tomatoes. Again, I observed a significant difference between treatment ($F_{1,12}$=28.88, p<0.001). Additionally, Dirty Girl tomatoes had 20.7% higher soluble solids content (°Brix) compared to Slicers ($F_{1,12}$=64.66, p<0.0001, Figure 2.2A panel b).

Another yield parameter I measured was mass (kg) per fruit. I again observed that dry-farming tomatoes were significantly lower in mass than irrigated tomatoes ($F_{1,12}$=12.41, p=0.004). Here I found that Dirty Girls had significantly lower mass when compared to Slicers (88.4% difference, $F_{1,12}$=61.73, p<0.001) (Figure 2.2A panel c). While fruits were smaller, they also had higher °Brix values (p<0.01 for both Dirty Girls and Slicers, Figure 2.2B panel a).

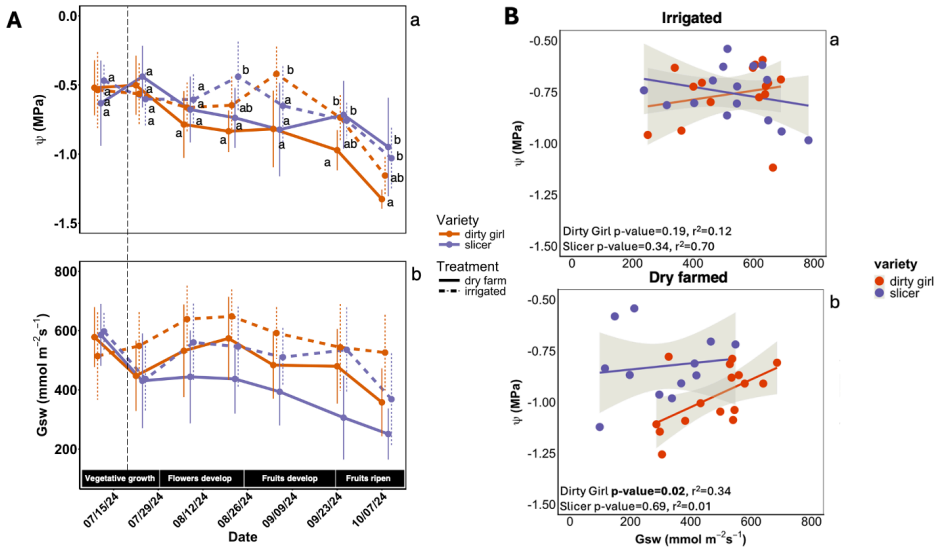

Figure 2.3. (A) Seasonal data collected for (a) water potential and (b) stomatal conductance. Data was collected for n=16 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid lines) and irrigated (dashed line) conditions. Points represent mean values and vertical lines overlayed on points represent ± SD. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. Each graph has a vertical, dashed, black line indicating when water was cut-off for dry-farmed treatments and panel B has the plant phenological stages denoted at the bottom of the graph. (B) Regressions for g_{sw} (the predictor variable) and Ψ (response variable) collected on 09/23/24 (when fruits were beginning to ripen) where colors represent Dirty Girl (orange) and Slicer (purple) treatment. Panel (a) shows this relationship for the irrigated treatment and panel (b) shows this relationship for the dry-farmed treatment.

2.4.2 Field water relations

I expected dry-farming practices to lead to decreases in plant physiological response throughout the season. Specifically, I expected lower water potential, reduced stomatal conductance, decreased biomass, and increased leaf mass per area from both varieties under dry-farming, with a slight advantage for dry-farm-adapted Dirty Girls.

Regardless of irrigation, all groups had decreasing water potential values as the season became warmer and drier ($F_{6,419}$=15.96, $p<0.001$; Figure 2.3A panel, Figure S1). However, during the peak growing period, when plants had reached their maximum height and tomatoes were beginning to ripen, dry-farmed Dirty Girls had 26.9% lower water potentials than all other treatment groups (Table 1).

Contrary to our predictions, this occurred concurrently with increased gas exchange measures (Figure 2.3A panel b). On average, Dirty Girls had higher stomatal conductance than Slicers ($F_{1,419}$=20.05, $p<0.001$). Under dry-farming, Dirty Girls had lower water potentials later in the season ($p=0.018$ for dry-farmed dirty girls, Figure 2.3B panel b).

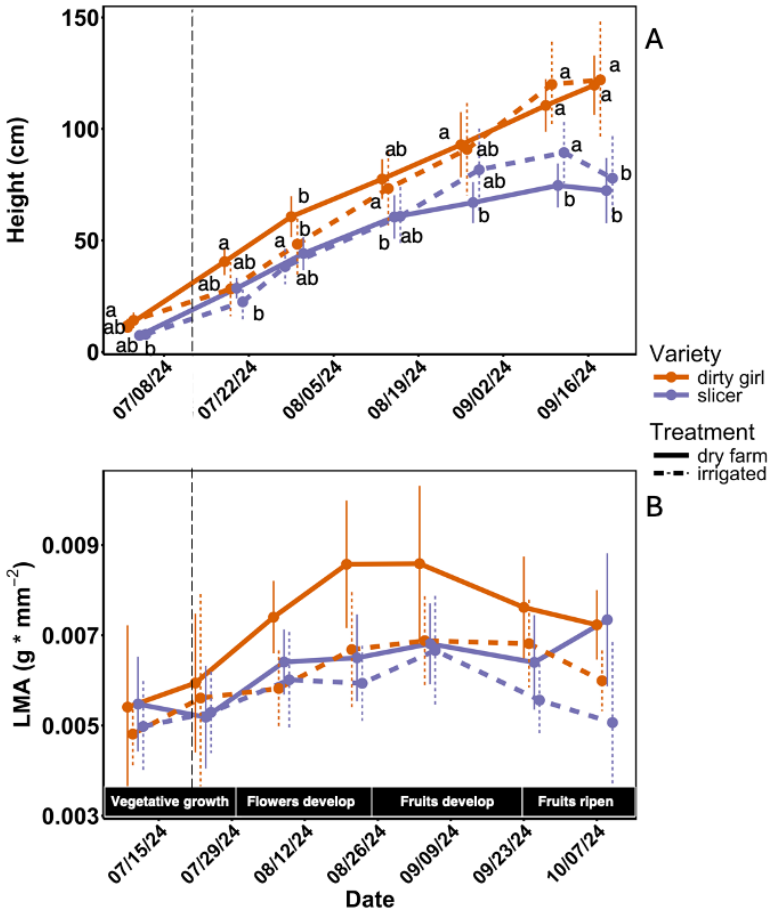

Figure 2.4. Seasonal data collected for (A) height and (B) LMA. Data was collected for n=16 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid lines) and irrigated (dashed line) conditions. Points represent mean values and vertical lines overlayed on points represent ± SD. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. Each graph has a vertical, dashed, black line indicating when water was cut-off for dry-farmed treatments and panel B has the plant phenological stages denoted at the bottom of the graph.

High g_{sw} was beneficial to Dirty Girls as it led to high productivity. Early in the growing season, Dirty Girls were fast growing and had greater heights in comparison to Slicer varieties (Figure 2.4A). Both dry-farm and

irrigated Dirty Girls had similar heights throughout the growing season (Table 1) while dry-farm slicers plateaued as the season progressed. This resulted in a 20.10% difference in height between varieties as plants began to fruit. While I did not measure biomass, I are using height as an indicator of plant productivity because in the field I observed that taller plants also produced more foliage. Additionally, Dirty Girls developed leaves with greater mass per unit area ($F_{1,379}$=18.70, $p<0.001$), with LMA increasing by 19.23% as fruits began to ripen (Figure 2.4B).

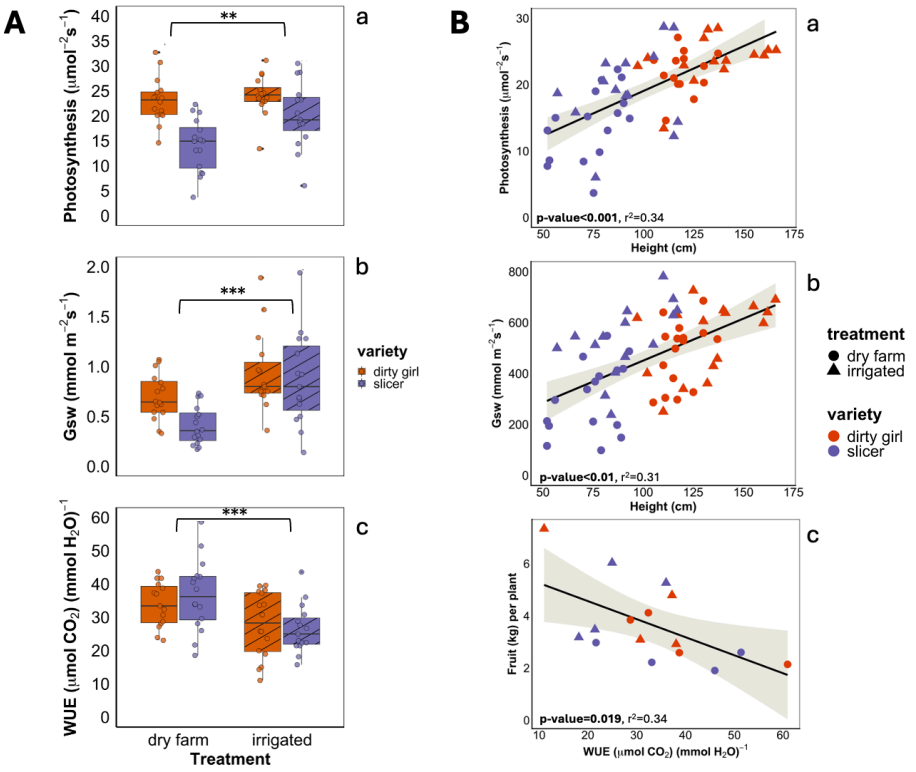

Figure 2.5. (A) (a) Net photosynthetic rate, (b) g_{sw} (measured with the LI 6400), and (c) WUE measured during peak productivity. Data was collected for n=16 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid lines) and irrigated (dashed line) conditions. Significant difference between treatment is denoted by *, where * $p<0.05$, ** $p<0.01$, and *** $p<0.001$. B) Regressions for (a) height (cm) (the predictor variable) and the response variable photosynthesis (n=64), (b) height (cm) (the predictor variable) and the response variable g_{sw} (decagon) (n=64), and (c) WUE during fruit development (the predictor variable) and the response variable fruit kg per plant (n=16). Colors represent Dirty Girl (orange) and Slicer (purple) treatment. Shapes represent dry-farmed (circle) and Irrigated (triangle) treatments.

Plant photosynthetic rates and stomatal conductance that were measured in mid September supported the prediction that dry-farming would decrease crop productivity. While overall I found that Dirty Girls had higher photosynthetic rates than Slicers ($F_{1,59}=25.90$, $p<0.001$), there is a penalty to

dry-farming. The dry-farmed treatment had significantly lower rates of photosynthesis than the irrigated treatment ($F_{1,59}$=7.32, p=0.009).

The stomatal conductance Li-Cor 6400 data demonstrates this same pattern, as Dirty Girls had higher stomatal conductance than Slicers ($F_{1,59}$=8.09, p=0.006). Again, however, the dry-farmed treatment had significantly lower stomatal conductance than the irrigated treatment ($F_{1,59}$=19.16, p<0.001). Both photosynthesis and stomatal conductance were used to calculate WUE (Figure 2.5A panel c), a value that is typically higher when plants take in more CO_2 than they lose water. Here I observed that dry-farmed varieties had significantly higher WUE than irrigated crops ($F_{1,59}$=14.24, p<0.001). This may be the result of the tradeoffs that occur between safety and efficiency. For example, I observed that plants that had more vegetative growth also had higher photosynthetic capacity (p<0.001, Figure 2.5B panel a). However, this resulted in higher transpirational demands with greater water loss (p<0.01, Figure 2.5B panel b). When plants had lower vegetative growth and lower photosynthetic rates, they exhibited increase WUE. As a result, dry-farming leads to a tradeoff in the form of lower yields (p<0.01, Figure 2.5B panel c).

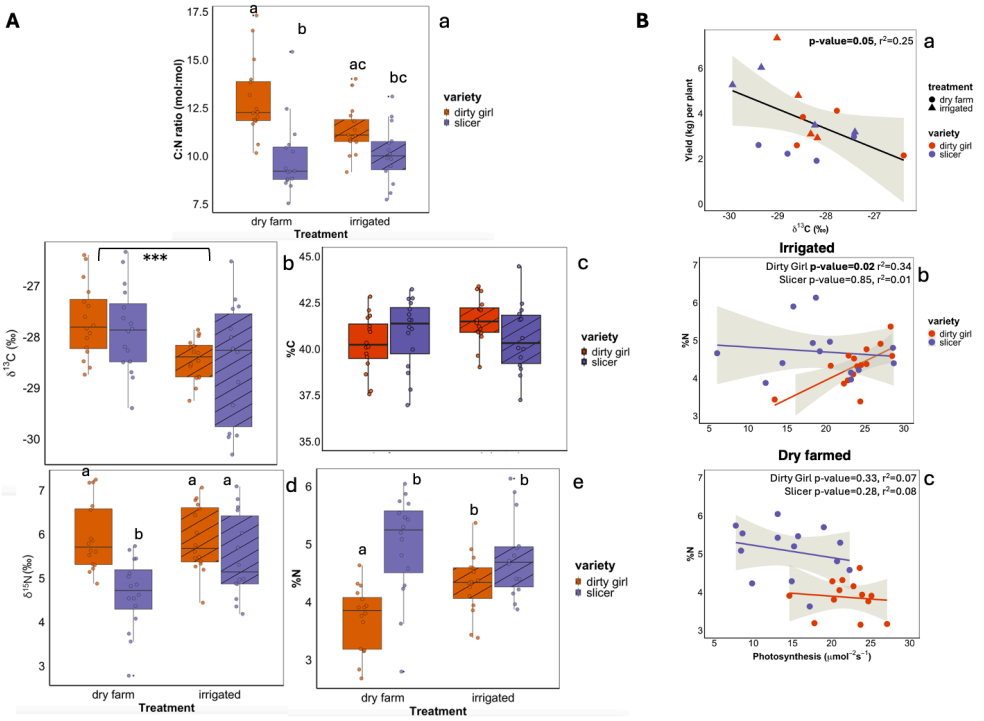

Figure 2.6. (A) Boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers for (a) the foliar ratio of C:N, (b) the foliar $\delta^{13}C$ values, (c) foliar %C content (d) the foliar $\delta^{15}N$ and (e) foliar %N content. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. Significant difference between treatment is denoted by *, where * $p<0.05$, ** $p<0.01$, and *** $p<0.001$. Data was collected for n=16 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid lines) and irrigated (dashed line) conditions. (B) Regressions for (a) $\delta^{13}C$ (the predictor variable) and the response variable yield per plant (n=16) (b) photosynthesis (the predictor variable) and the response variable %N when irrigated (n=16), and (c) photosynthesis (the predictor variable) and the response variable %N when dry-farmed. Colors represent Dirty Girl (orange) and Slicer (purple) treatment. Shapes represent dry-farmed (circle) and Irrigated (triangle) treatments.

2.4.3 Foliar Carbon and Nitrogen Stable Isotopes Analysis

Within treatment, dry-farmed Dirty Girls had a significantly higher C:N ratio compared to Slicers, with a 26.67% difference between the two

varieties within the treatment. Dry-farm Dirty Girl showed no difference compared to its irrigated counterpart (Figure 2.6A panel a).

I found that in $\delta^{13}C$ was significantly higher in the dry-farmed treatment than in the irrigated treatment ($F_{1,58}$=11.37, p=0.001). There was no difference in $\delta^{13}C$ between varieties (Figure 2.6A panel b). This aligns with the data WUE, as $\delta^{13}C$ has been found to be tightly coupled to WUE.

In contrast, dry-farmed Slicers had a lower $\delta^{15}N$ combined with a higher foliar nitrogen content (%; Figure 2.6A panel d).

While there was no difference in foliar carbon content (%) between any groups (Figure 2.6A, panel c), dry-farmed Dirty Girls were found to have the lowest foliar nitrogen content (%) across both varieties and treatments (Figure 2.6A panel e).

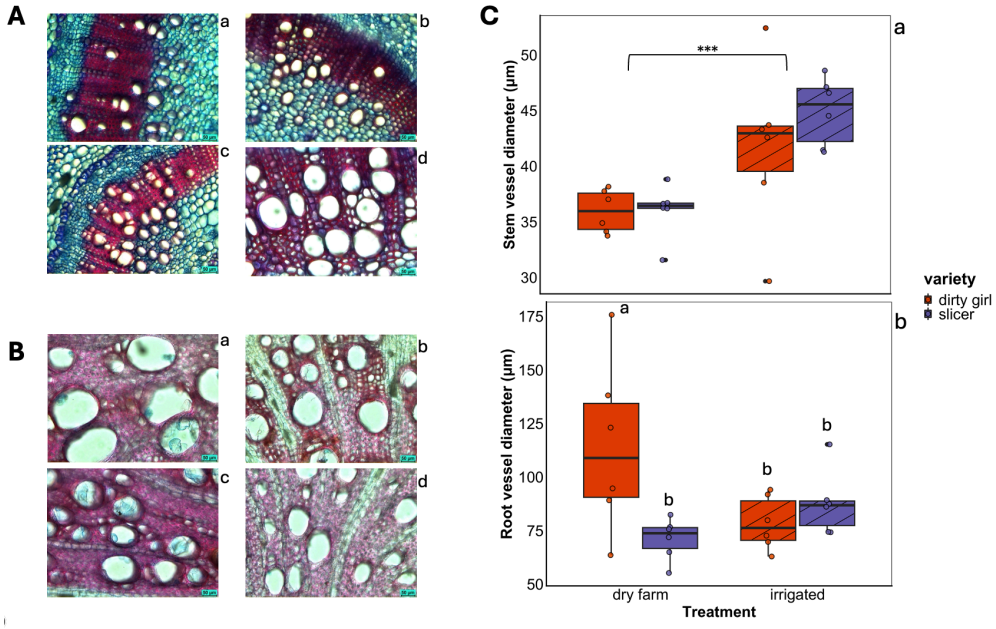

Figure 2.7. Cross sectional images of tomato (A) stems and (B) roots for plants collected during peak productivity, where (a) is dry-farmed Dirty Girl, (b) is irrigated Dirty Girl (c) is dry-farmed Slicer and (d) is irrigated Slicer. All images were taken at 20x. (C) Mean vessel diameter measures for (a) stems and (b) roots. Data was collected for n=6 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid) and irrigated (dashed) conditions. Data is represented by boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. Significant difference between treatment is denoted by *, where * $p<0.05$, ** $p<0.01$, and *** $p<0.001$.

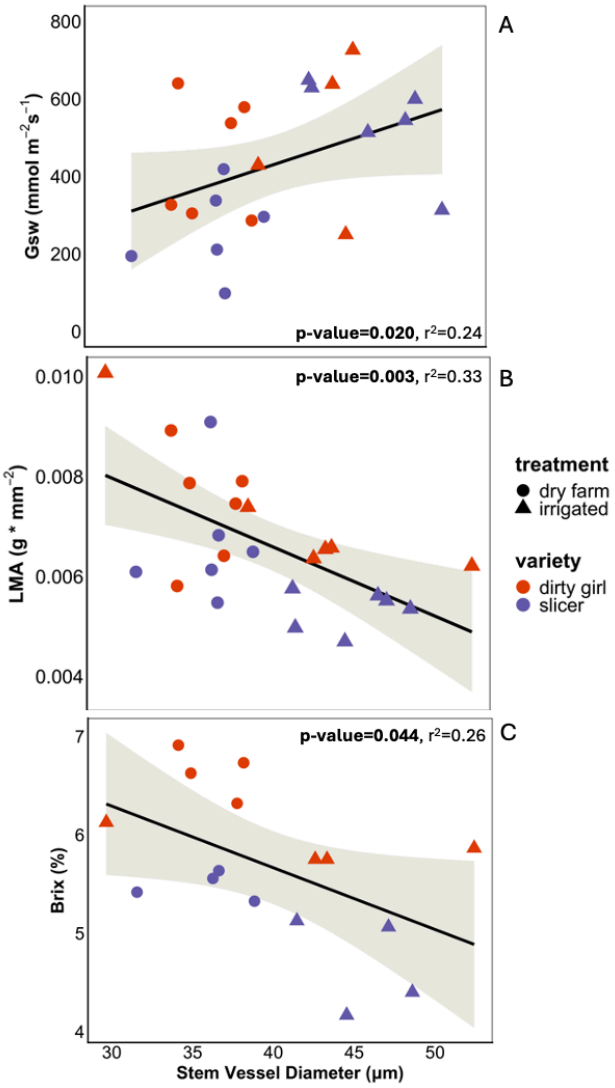

Figure 2.8. Regression for with stem vessel diameter (µm) (the predictor variable) with the following response variables (a) g_{sw} (b) LMA and (c) °Brix (%), where cultivar is represented by orange (Dirty Girl) and purple (Slicer), n=16. Treatment is represented by circles (dry-farm) and triangles (irrigated).

2.4.4 Anatomy

Dirty Girls had higher leaf vein density as compared to Slicers, regardless of treatment, however there was no difference between treatments. This

indicates that leaf vein density may not be adaptive to dry-farming, but instead be a fixed trait in some tomato varieties (Table 2.1). Interestingly, there was no difference in stomatal density in any of our treatment groups, which contradicts the typical correlation between vein and stomatal density.

Xylem anatomy is often a proxy of hydraulic function and in this study, I found that the varieties had differences in vessel diameter measures in both stems and roots. In stems, I found dry-farmed varieties had significantly lower vessel diameters than irrigated varieties ($F_{1,20}$=17.36, $p<0.001$). I observed larger vessel diameters were correlated to higher stomatal conductance ($p=0.020$, Figure 2.8A), however that also resulted in lower LMA ($p=0.003$, Figure 2.8B). While smaller vessel diameters result in a penalty to plant productivity, I observed that smaller diameters were correlated to higher °Brix values, indicating that smaller vessels may increase fruit quality ($p=0.044$, Figure 2.8C).

In contrast, I found dry-farm Dirty Girls had significantly larger roots, with an average of 36% wider vessel diameters as compared to all other groups (Figure 2.7C panel b). This indicates that under dry-farming, Dirty Girls invest more carbon resources into root functionality.

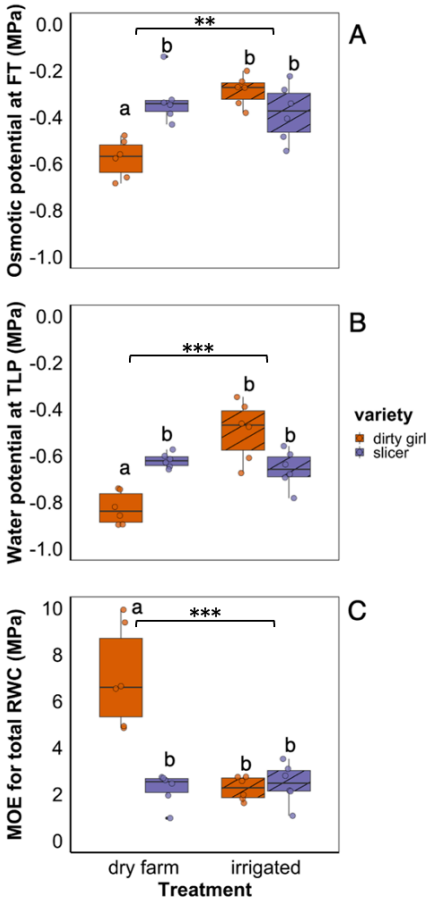

Figure 2.9. (A) Osmotic potential at full turgor, (B) water potential at turgor loss point, and (C) modulus of elasticity (MOE) at total relative water content measured during peak productivity. Data was collected for n=6 plants of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (solid) and irrigated (dashed) conditions. Data is represented by boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Letters indicate significant difference ($p < 0.05$) among groups based on Tukey's HSD tests. Significant difference between treatment is denoted by *, where * $p<0.05$, ** $p<0.01$, and *** $p<0.001$.

2.4.5Pressure-volume curves

The resilience of Dirty Girls grown in dry-farmed conditions may be

partially attributed to leaf-water-use strategies that limit dehydration during

water deficit conditions, which I measured using pressure-volume curves. I found that dry-farmed Dirty Girls had a 33.8% decrease in water potential at turgor loss point ($\Psi_{TLP)}$ when compared to all other groups (table 2.1, Figure 2.9B), which is indicative of the ability to tolerate lower water potentials before wilting occurs.

I also found dry-farmed Dirty Girls to have 55.0% decrease in osmotic potential at full turgor ($\pi_{FT;}$ table 2.1; Figure 2.9A), indicating that these plants allocate more solutes to their leaves, which is what allows plants to retain turgor at lower water potentials. Finally, another water-use strategy that confers an advantage to dry-farmed Dirty Girls is a 101.7 % higher modulus of elasticity at total relative water content (ε; table 2.1; Figure 2.9C). This is useful because petioles that contain more flexible, less lignified tissues can withstand higher tensions that occur at lower water potentials, which may be beneficial as I observed that field water potentials were lower for dry-farmed Dirty Girls (Niklas, 1991; Figure 2.10a, p=0.050).

2.4.6 Vulnerability Curves

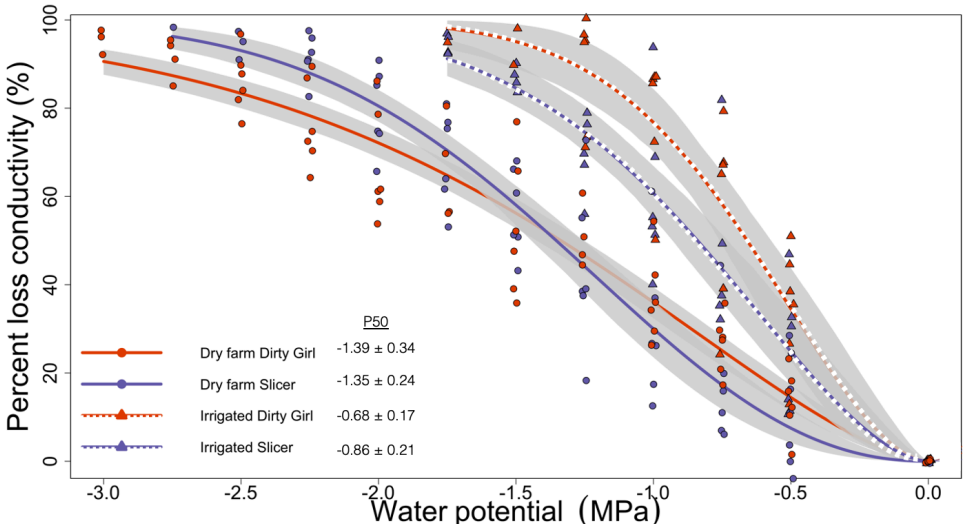

Figure 2.10. Vulnerability to embolism in stems of dry-farmed (solid) an irrigated (dashed) varieties of Dirty Girl (orange) and Slicer (purple) measured in n=6 individuals. Mean vulnerability curves of each variety and treatment group are fitted following the pfit r package with the standard error of the estimated parameters is represented by light gray areas.

I observed that dry-farm crops were more resistant to embolism than irrigated crops (Figure 2.10). Dry-farm dirty girls had an average p50 of -1.39 MPa whereas when irrigated, the p50 was -0.68 MPa. This indicates that dry-farmed Dirty girls lose 50% of their hydraulic conductivity at lower water potentials than its irrigated counterpart and is therefore more drought tolerant. Similarly, dry-farm Slicers had an average p50 of -1.35 MPa whereas when irrigated, the p50 was -0.86 MPa. These findings align well with other drought-tolerant traits. For example, when comparing P88 to our pressure volume curve analyses, I observed that stems that could withstand lower

xylem pressure aligned with lower turgor loss point in the leaves (Figure 2.11 A-C).

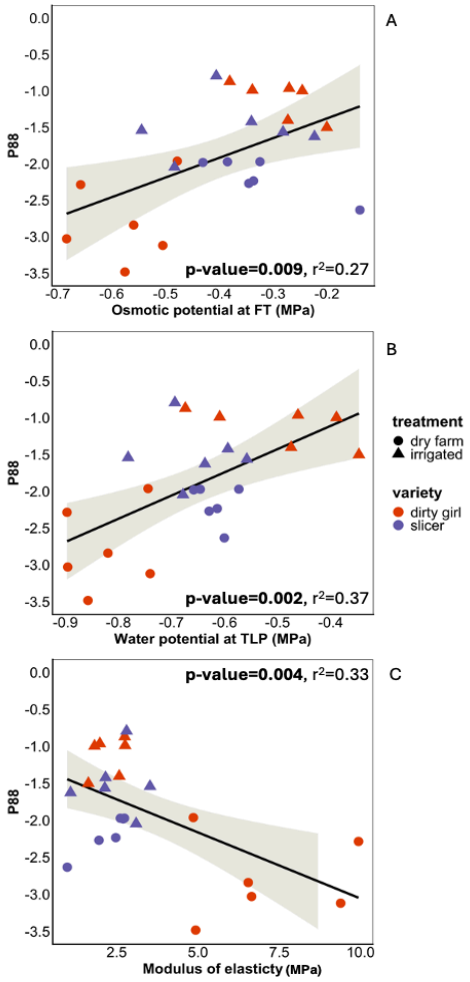

Figure 2.11. Regressions for leaf pressure volume curve analyses (the predictor variable) with P88 (the response variable) (n=24). (A) osmotic potential at full turgor (B) water potential at turgor loss point, (C) modulus of elasticity, where variety is represented by orange (Dirty Girl) and purple (Slicer). Treatment is represented by circles (dry-farm) and triangles (irrigated).

2.4.7 Soil attributes

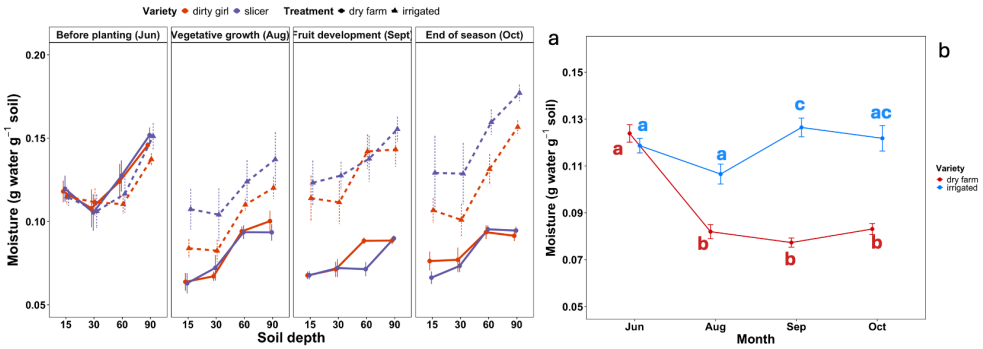

Figure 2.12. (a) Seasonal data for soil moisture measured at four timepoints in the experiment: at the beginning of the season (before planting), in August (during vegetative growth), in September (during fruit development), and in October (at the end of the growing season), at four different depths in the soil column (15, 30, 60, 90 cm). Data was collected for n=4 plots of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (circles with solid lines) and irrigated (triangles with dashed line) conditions. Points represent mean values and vertical lines overlayed on points represent ± SD. (b) Seasonal data for soil moisture measured at four timepoints in the experiment for two treatments represented by blue (irrigated) and red (dry-farmed) points and lines (n=8). Points represent mean values and vertical lines overlayed on points represent ± SD. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests.

Soil moisture differed between treatments, with dry-farmed soils containing 48.5% less moisture than irrigated soils by the end of the season. Across depth, however, moisture at 90 cm exceeded those at 15 cm by 27.9%. Moisture varied significantly with both depth (X^2=17.64, p<0.001, table S1) and month (X^2=42.64, p<0.0001). A significant month x treatment interaction (X^2=14.68, p=0.002, Figure 2.12b) indicated that the effect of irrigation treatment on soil moisture changed over the course of the season. No significant effects of variety or higher-order interaction were detected. Tukey comparisons were therefore averaged across variety (Figure 2.12b).

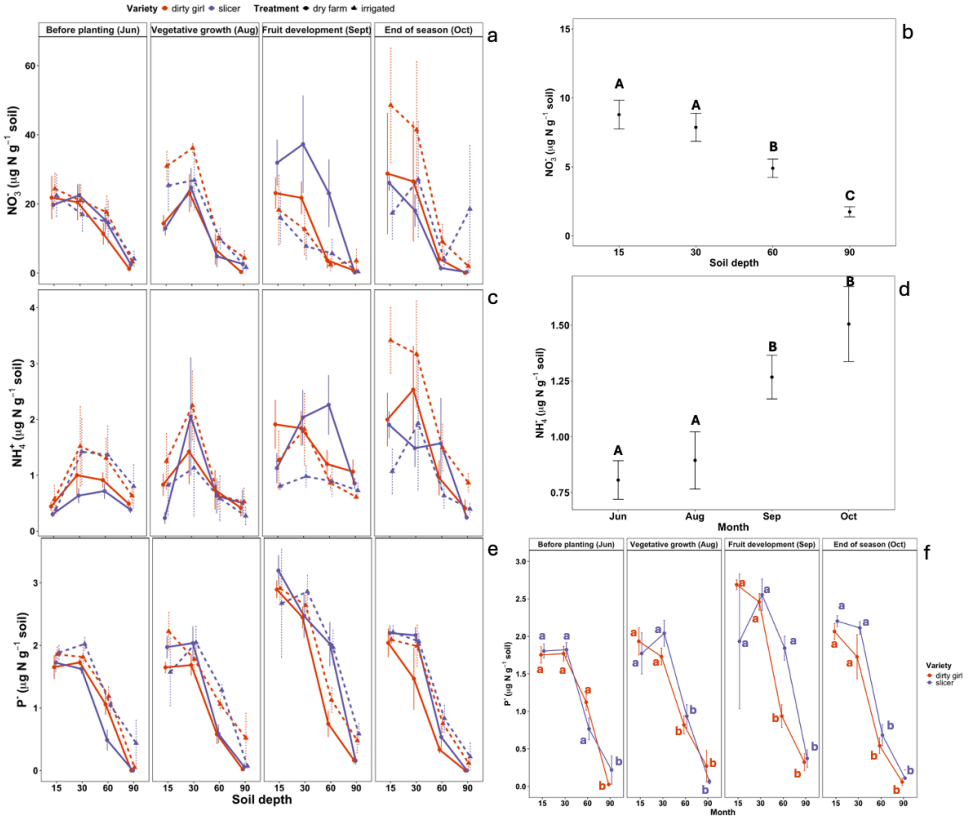

Figure 2.13. Seasonal data for soil moisture measured at four timepoints in the experiment - at the beginning of the season (before planting), in August (during vegetative growth), in September (during fruit development), and in October (at the end of the growing season) and at four different depths in the soil column (15, 30, 60, 90 cm) for (a) nitrate, (c) ammonium, (e) phosphorus. Data was collected for n=4 plots of both Dirty Girl (orange) and Slicer (purple) varieties, grown under dry-farmed (circles with solid lines) and irrigated (triangles with dashed line) conditions. Points represent mean values and vertical lines overlayed on points represent ±SD. (b) Nitrate measured at the four different depths. Points represent mean values and vertical lines overlayed on points represent ±SD. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. (d) Seasonal data for ammonium measured at four timepoints. Points represent mean values and vertical lines overlayed on points represent ±SD. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests. (e) Seasonal data for phosphorus measured at four timepoints in the experiment and at four different depths in the soil column. Data was collected for n=8 plots from the combined treatments of both Dirty Girl (orange) and Slicer (purple) varieties.

Soil nitrate (NO_3^-) decreased significantly with depth (X^2=23.53, $p<0.001$), with concentrations at 15cm exceeding those at 90 cm by 157.17%. No significant effects of treatment, month, or their interactions were observed. Accordingly, Tukey comparisons were averaged across month, treatment, and variety (Figure 2.13b).

Soil ammonium (NH_4^+) increased over the growing season, with concentrations 60.51% higher at the end of the season compared to the beginning. This pattern was supported by a significant effect of month (X^2=23.53, $p<0.001$), while no significant effects of higher-order interactions were detected. Tukey comparisons were averaged over across depth, treatment, and variety (Figure 2.13d).

Soil phosphorus (P) declined significantly with depth (X^2=66.75, $p<0.001$), with overall concentrations at 15 cm 169.33% higher than at 90 cm. Soil phosphorus also varied significantly with month (X^2=10.28, $p=0.016$). A significant depth x month x variety interaction (X^2=14.68, $p=0.002$) indicated that varieties varied across both depth and season. Tukey comparisons were therefore averaged across treatments (Figure 2.13f).

2.5 Discussion

Dry-farming conditions reduced individual plant yield by 35.32% in Dirty Girls and 59.91% in Slicers, indicating a stronger decline in Slicers, although this difference is not statically supported by significant interaction.

Dirty Girl success appears to be driven, in part, by a physiological strategy during fruit development in which plants allow water potentials to drop while maintaining relatively high stomatal conductance (Figure 2.3A panel a and b). In addition, dry-farmed Dirty Girls invested in other traits that enhanced carbon acquisition, including greater above-ground growth (plant height; Figure 2.4A), potentially higher leaf conductance (higher leaf vein density; Table 2.1); both attributes may have been supported by potentially higher root conductance, given the wider vessel diameters in this variety (Figure 2.7C panel b). Concurrently, these plants expressed traits associated with drought-tolerance in stems, such as a safer xylem network (smaller stem vessel diameters; Figure 2.7C panel a), and greater resistance to stem xylem embolism (Figure 2.10). Other drought tolerant traits were observed in leaves through increased leaf thickness (higher LMA; Figure 2.4B), increased resistance to leaf wilting (lower values of Ψ_{TLP}), increased solute concentrations in cells (lower π_{FT}), and higher cell wall flexibility (higher ε; Figure 9 A-C). This combination of traits suggests a strategy that combines carbon gain with hydraulic safety. As a result, Dirty Girls maintained higher photosynthetic capacity (Figure 2.5A panel a) which is aligned with higher leaf C:N ratios (Figure 2.6A panel a), ultimately sustaining yields under minimal irrigation, with smaller fruits that had elevated soluble solids (°Brix) (Figure 2.2A panel a-c).

Dirty Girls maintained higher stomatal conductance as compared to Slicers and did so by dropping water potentials. While this strategy has been described as risky behavior that can lead to plant mortality under severe drought stress (Zhao et al., 2023), in this case, it is seen as an adaptive strategy to support yield by sustaining carbon assimilation under moderate stress, as I observed water potentials did not drop lower than -1.5 MPa (Sade et al., 2012; Serrano et al., 2024).

High levels of photosynthesis are an outcome of a robust hydraulic system that facilitated more growth. Previous studies have found allocation strategies that prioritize leaf growth also promotes high reproductive capacity, as high assimilation rates means more carbon will be available to produce seeds (Holland et al., 2019). Similarly, it has been found that high vein density conveys high leaf hydraulic efficiency (Brodribb et al., 2007). High investment in above-ground biomass, however, may lead to tradeoffs in below-ground biomass as a result of resource allocation (Ding et al., 2025). It is possible that dry-farmed Dirty Girls resulted in reduced root biomass as above ground plant growth was not penalized under water deficit.

While I did not directly measure root biomass, I measured root vessel diameters and found the dry-farmed Dirty Girls have larger root vessels (Figure 7C panel b). This aligns with literature where researcher found that the increase in root traits maintained productivity during drought, such as the

investment in deeper roots or roots with wider vessels (Pockman and Sperry, 2000; Wasson et al., 2012).

As previously mentioned, while dry-farmed Dirty Girls had traits that increase carbon assimilation, they also exhibited drought tolerant traits. Throughout the growing season I observed higher LMA in dry-farmed Dirty Girls, which has been reported to be a function of water conservation because of its role in reducing water loss. For example, higher LMA is associated with thicker and denser leaves due to larger cell size, as well as a longer lifespan, both of which increase water holding capacity (Aneja et al., 2025; John et al., 2017). Concurrently, I observed that Dirty Girls had higher $\delta^{13}C$, which has been linked to higher WUE, as higher $\delta^{13}C$ reflects the balance of stomatal conductance and photosynthesis (Ma et al., 2023; Renninger et al., 2024). While higher LMA and $\delta^{13}C$ relationship may be beneficial to crops growing under dry-farmed condition, I did observe a tradeoff in yield, as higher WUE was correlated to lower yields (Figure 5B, panel c).

Interestingly, I also observed that dry-farmed Dirty Girls had significantly lower nitrogen content (N%) in leaves than all other groups. Higher N% is typically associated with high rubisco availability, which results in the fixation of CO_2 and leads to higher rates of photosynthesis (Evans, 1989; Luo et al., 2021). However, low N% does not seem to inhibit

the photosynthetic capability of dry-farmed Dirty Girls. Likewise, dry-farmed Dirty Girls were found to have higher LMA, a trait typically associated with lower photosynthetic rates (Wright et al., 2004). Our finding of high photosynthesis in the dry-farmed Dirty may be accomplished as a result of higher stomatal conductance.

The decrease in N% content influenced the ratio of carbon to nitrogen found in leaf tissue (C:N). I found the dry-farm Dirty Girls had higher C:N ratios, which are associated with robust leaves that grow slow and have more conservative strategies (Colesie et al., 2020). Additionally, the pressure volume curves analyses indicate that leaves in dry-farmed Dirty Girls have other drought-adaptive leaf traits such as lower water potentials at turgor loss point (Ψ_{TLP}), increased osmotic accumulation (π_{FT}) and increased flexibility of cells in leaves (ε).

In stems, I observed that dry-farmed crops are more embolism resistant than irrigated crops. This aligns with our vessel diameter data, as dry-farmed crops have 18.48% smaller vessel diameters than irrigated crops. This multi-organ response to drought indicates a functional coordination of traits throughout the plant, as stem P88 is correlated to leaf traits that have been associated with drought-tolerance, such as $\Psi_{TLP,}$ $\pi_{FT,}$ and ε (Figure 2.11 A-C).

Finally, the soil patterns I observed suggest that plants in dry-farmed systems experience substantially greater water limitations over the season, as soil moisture was nearly 50% lower than in irrigated systems by the end of the season. At the same time the reduction in nitrate and phosphorus with depth demonstrates that nutrient availability was concentrated closer to the soil surface, creating shallow zones with higher nutrients and deeper, higher, water sources that dry-farmed plants potentially have access to. The drier soil conditions are consistent with shifts toward more drought-tolerant strategies, including increased LMA, lower Ψ_{TLP}, and higher WUE. These results highlight how declines in water availability over time and soil nutrient availability at different depths can influence plant physiological responses, particularly in plants adapted to reduced water-availability.

2.6 Conclusion

As climatic conditions grow warmer and drier, there is a dire need for agriculture to transition to sustainable practices. Dry-farming is an exemplary water-saving practice, however, there are many limitations that prevent this transition including: limited geographic range of use, limited resources for farmers who may want to transition, and limited information regarding the crops that are successful under these conditions (Socolar et al., 2024a). Our findings highlight the versatility of the dry-farm-adapted Dirty Girl tomato as a variety capable of performing across a range of water-

availability conditions. Under dry-farming, Dirty Girls balanced carbon gain with hydraulic safety, maintaining yields while producing fruit with elevated °Brix. Under irrigation, plants maximized carbon acquisition and produced 50% higher yields. Although irrigated fruit was less sweet than those dry-farmed, they still contained higher soluble sugar concentrations than the other heirloom variety.

This degree of plasticity may provide growers with flexibility as weather patterns become increasingly variable.Dry-farm-adapted varieties can produce marketable fruit under both irrigated and water-limited conditions, allowing growers to adjust management practices in response to annual climate fluctuations. These findings can be used to contextualize important drought-resistant traits for other herbaceous crops and can improve future breeding efforts. However, more studies are needed to measure the range of adaptive traits in other dry-farmed crop types, such as corn, winter squash, and beans.

Chapter 3: The physiological tradeoffs of dry-farm-adapted *Phaseolus vulgaris* (common bean) varieties

3.1 Abstract

Dry-farming is an agricultural practice that relies on little to no irrigation and is increasingly being explored as a strategy to reduce water use under climate change. However, unlike dry-farmed crops such as tomatoes, factors influencing bean crops are less wee understood. In this study, I investigated the impacts of dry-farming on varieties of common bean grown during the 2024 and 2025 growing seasons. I evaluated yield, morphological, anatomical, and physiological traits associated with drought including vein density, stomatal density, vessel diameter, plant height and leaf mass per area. Across both years, dry-farming significantly reduced yield in all varieties despite shifts in anatomical traits associated with drought tolerance. In 2024, a warmer growing season produced stronger treatment responses, including increased vein density and stomatal density and reduced vessel diameters under dry-farming conditions, which may reflect increased leaf water loss to support evaporative cooling. These changes suggest that plants attempted to maintain hydraulic function and carbon assimilation under limited irrigation, but these responses did not increase yields. I observed fewer trait responses during the cooler 2025 season, supporting the idea that crop responses to drought are strongly influenced by temperature. Varieties also differed in allocation strategies.

Hopi beans consistently allocated more resources toward reproductive output where Black beans invested more in vegetative growth and leaf thickness. While no variety consistently maintained productivity under dry-farm conditions, Hopi beans allocated more carbon toward reproductive output, resulting in the highest dry mass per pod across all varieties and years. These finding suggest that, despite overall reductions in performance among fast-growing annual bean crops, heirloom Hopi beans may serve as a relatively low-maintenance crop that can maintain reproductive investment under minimal-input conditions.

3.2 Introduction

Dry-farming is a sustainable farming practice where crops receive little to no irrigation (Socolar et al., 2024). Instead, these crops rely on the water that saturates the soil during the rainy season, therefore, dry-farming is typically practiced in areas that receive approximately 20 inches of annual rainfall. While this farming technique has been practiced in many countries throughout the world and for many years (Stewart and Thapa, 2016), there is little scientific work to understand what physiological traits may arise when crops are grown under dry-farming. Instead, studies have focused on characterizing the many species that can produce yield under no irrigation (Garrett, 2019). One crop that has been successfully cultivated under dry-farming is *Phaseolus vulgaris*, or the common bean.

P. vulgaris is an important crop worldwide due to its versatility, rapid growth, high nutritional value, and ability to provide ecosystem services in agricultural systems (Myers and Kmiecik, 2017; Petry et al., 2015). Bean varieties are widely consumed throughout the world, with over 30 million tons produced annually (Uebersax et al., 2023). Originating in Mesoamerica, *P. vulgaris* encompasses a diverse range of varieties (Frascarelli et al., 2025). Some varieties are classified as "dry beans", meaning they are harvested when the beans seeds have completely dried within their pod. Other bean types are harvested while pods are still fleshy and consumed fresh.

Another defining characteristic of common beans is their short life cycle. Beans are herbaceous, annual crops that grow quickly while prioritizing relatively high reproductive rates, with an average lifespan of 60-120 days. As such, they fall on the "fast" end of the fast-slow growth continuum, a framework that is described as the tradeoff between a species that is fast-growing, short-lived, and has high reproductive capacity in comparison to one that is slow-growing, long-lived, and has shorter reproductive periods (Stearns, 1983). Research has found that this aligns with the leaf-economic spectrum (LES), which in-part, predicts that fast-living species produce relatively inexpensive leaves that have high photosynthetic capacity (Salguero-Gómez, 2017; Wright et al., 2004).

From a physiological framework, these life-history strategies are useful to contextualize with functional traits. In the case of fast-living bean plants in well-watered environments, plants are expected to have lower investment in leaf mass per area (LMA), higher stomatal conductance (g_{sw}) and photosynthetic capabilities, as well as shorter leaf lifespans (LL), as predicted by the LES. Other traits that would be important to consider under this framework include anatomical traits such as leaf venation, stomatal density, and vessel dimensions, all of which would be higher for fast-growing plants growing in moist environments that prioritize the efficiency of hydraulic transport over the safety from hydraulic failure. This strategy enhances reproductive capacity by maximizing carbon assimilation and allocating higher carbon allocation to reproductive structures (Franklin et al., 2023). With reproduction as a high priority, plants may invest in greater seed production of higher quality. Beans are particularly valued for their high nutritional content and contribute substantially to human dietary protein, with approximately 65% of the protein consumed by humans in derived from legumes such as beans (Parker et al., 2022). Bean proteins contain high levels of nitrogen, making nitrogen acquisition critical for both plant growth and seed nutritional quality (Pedrinho et al., 2019).

As members of the legume family, beans have a symbiotic relationship with nitrogen-fixing rhizobia bacteria, which convert atmospheric nitrogen into plant-available forms in exchange for

carbohydrates supplied by the plant. Nitrogen availability is especially important because a large portion of plant nitrogen (approximately 40%) is allocated to the enzyme rubisco (Luo et al., 2021). In agricultural systems where nitrogen leaching occurs frequently, the symbiosis between legumes and rhizobia can also benefit surrounding crops by enhancing soil nitrogen availability.

Despite these advantages, common beans remain highly sensitive to water limitation, particularly during flowering and pod development, when adequate soil moisture is essential for reproductive success. In Rosales et al (2012), a study highlighting the susceptibility of pod production during drought, it was found the drought-susceptible beans maintained steady leaf production even when water was limited, ultimately resulting in penalized yields. In contrast, drought resistant beans reduced their biomass under limited irrigation, leading to increased mobilization of photosynthates to fruits rather than vegetative growth.

These observations are critical as changing climatic conditions have resulted in erratic weather conditions and reduced crop production. Without intervention through breeding or farming practices, it is predicted that by the year 2100 areas in the Southern Hemisphere will no longer be suitable for growing beans due to hot and dry conditions (Ramirez-Cabral et al., 2016). One potential strategy to address this challenge is dry-farming, a water-conserving agricultural practice that relies primarily on stored moisture

rather than irrigation. Finding the traits that make dry-farm adapted beans successful under limited irrigation may be useful for breeders cultivating beans adapted to drier conditions and may help sustain production in regions facing reduced water availability.

In this study, I investigated the traits associated with drought resistance in three common bean varieties grown under dry-farm conditions. Specifically, I address the following questions: (1) How do dry-farm beans use water throughout the season? (2) Do bean plants become more drought tolerant as the season progresses? (3) What are the physiological and structural costs of different water-use strategies and potential shifts in drought tolerance? (4) How will the physiological response factor into bean crop quality and crop quantity?, and lastly, (5) What drought-tolerant traits are shared among varieties, and how do they differ?

During the summers of 2024 and 2025, I evaluated dry-farm-adapted and non-adapted bean varieties of *Phaseolus vulgaris* (Hopi, Green, and Black) and measured a variety of physiological, anatomical, and morphological traits. Plants were grown under two water treatments, irrigated and dry-farmed, to quantify plant vulnerability to water-deficit. In addition, a complementary greenhouse experiment conducted in 2025 exposed plants to controlled drought treatments to assess the plant response to progressive dehydration. These experiments allowed me to evaluate

resistance to xylem embolism events, which can block water transport within plant vascular tissue.

I hypothesized that dry-farmed-adapted crops will be less vulnerable to drought and maintain higher physiological functionality under water-limited conditions compared with non-adapted varieties. Specifically, I expected dry-farm-adapted crops to prioritize hydraulic safety over efficiency. This would result in more stable water-use efficiency (WUE) and sustained pod production throughout the growing season. In contrast, I predicted that non-adapted varieties would initially prioritize hydraulic efficiency early in the season, but experience declines in physiological performance and productivity as the season became warmer and drier.

3.3 Methods and Materials

Figure 3.1. The panels on the top half of the figure show study plants growing in the field for each variety grown under dry-farmed conditions. The bottom panels show bean yields for each variety.

3.3.1 Study Site

This study was conducted at the University of California, Santa Cruz Center for Agroecology (CFA). The site experiences a subhumid, mesothermal climate characterized by moderately cool, foggy summers and cool, wet winters. Mean annual precipitation is approximately 18 inches, occurring primarily during the winter months. Summer temperatures typically range

from lows of 10 °C to highs of 33 °C. The soil at the site is well-drained and classified as fine ("Official Series Description - ELKHORN Series," n.d.).

Prior to the initiation of the experiment, plots were prepared using soil amendments recommended in the CFA grower guide for organic dry-farmed tomato production on California's Central Coast (Leap et al., 2017). Weed and pest management practices were implemented through the experiment in accordance with the guidelines outlined in the same grower guide.

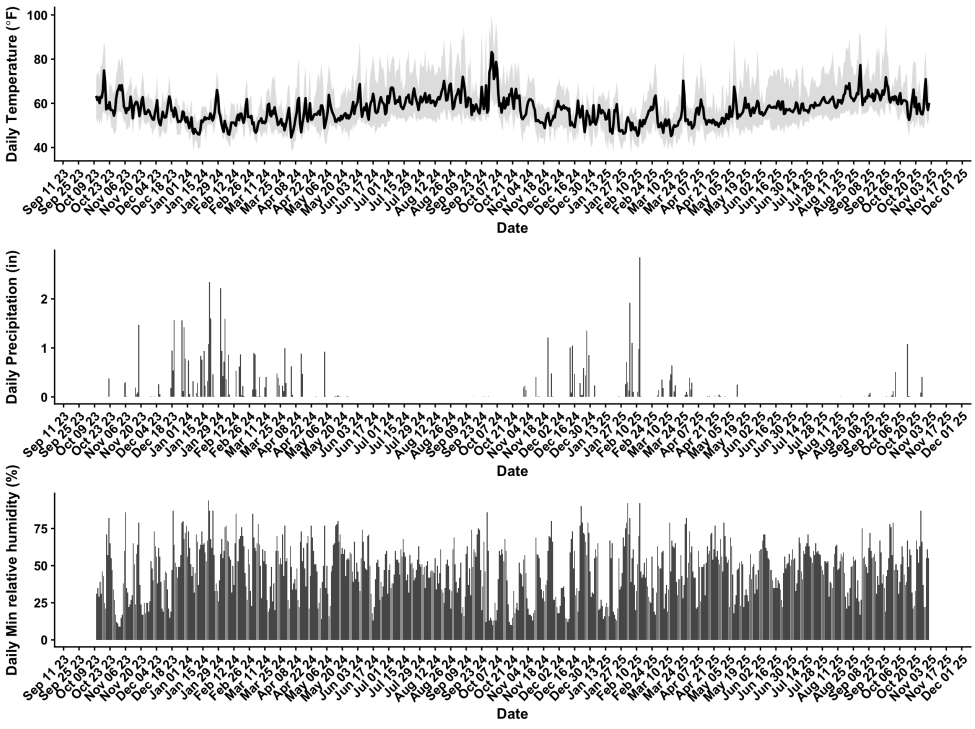

Figure 3.2. Climate data recorded in 2024 and 2025.

3.3.2 Experimental design for field work

Plants were grown in both irrigated and dry-farmed conditions. In the summer of 2024, I worked with Hopi dry beans and Black Turtle dry beans. These seeds were sourced from plants that had undergone multiple generations of dry-farm selection at the CFA.

On June 20, 2024, seeds were sown into two adjacent 37 x 37 m blocks: one managed under dry-farmed conditions and the other under irrigated conditions. The treatment blocks were separated by a 15-foot buffer zone to prevent any water movement from the irrigated plots into the dry-farm plots. Within each block, four subplots of each variety were established, with subplot positions randomized. Each subplot contained approximately 40 plants.

Immediately after planting, all plants received 1 inch of water delivered through a drip tape irrigation system. Because transplanting coincided with a heatwave, supplemental irrigation of 0.25 inches per week was applied to all plots for three weeks to promote root establishment. After this point, only the irrigated plots received weekly watering to replace evaporative and transpiration losses. Data were collected throughout the bean growing season, from June through September 2024.

In the next growing season of 2025, I added an additional variety to the experiment with the goal of incorporating a fleshy bean type of *P. vulgaris* that may respond differently to dry-farm conditions as fresh bean

pods may use more water. The variety I selected was the Jade Green bean, which I sourced from Botanical Interests seed company (Broomfield, Colorado, USA). In June 2026, I sowed the three varieties of beans into the ground in the same experimental setup as was used in 2024, only this time I had 2 subplots of each variety under each treatment with approximately 40 plants each.

3.3.3 Experimental design for greenhouse work

For the greenhouse dry down experiments, I selected to grow two varieties of *P. vulgaris* - the Hopi and French Green bean - under two treatments, irrigated and drought. Equipment constraints necessitated a reduced experimental approach. Because bean lifespan is approximately 3 months, I staggered the growth of multiple replicates (n=40) into different growth cycles from May 2025 – April 2026. In these cycles, I grew each variety and treatment and then randomly selected plants that were to be sampled. Again, this was due to equipment constraints, as will be described in the cavicam section.

At the beginning of each cycle, seeds were pre-germinated in a seedling tray for uniformity. Once the seedlings were germinating (germination starts approximately 5 days after planting), I moved move one seedling into a 1-gallon pots with potting mix (0-80% Canadian Sphagnum Peat Moss, coarse perlite, dolomite lime, gypsum, and wetting agent;

Sungrow, Agawam, MA) and 30 grams of 4-4-4 N-P-K organic fertilizer mix (Dr. Earth, Winters, CA).

Throughout the experiment, the greenhouse was programmed to stay above 13°C, and to start cooling if the temperature rises above 24°C.The photoperiod was set at 14 hours and the greenhouse lights were set to turn on to supplement lighting on days when daylength was shorter or if conditions were overcast.

3.3.4 Greenhouse Watering regime

Once seedlings were transplanted to the individual pots, they were irrigated manually to maximum water retention capacity of the soil substrate, 1-2 times a week. 15 days after sowing, irrigation was cut down to 25% watering in drought treatments so that plants meet minimum water potential values that were found in the field (approximately -1.2 MPa). Drought plants were rewatered when leaves began to visibly lose turgor.

3.3.5 Optical vulnerability curves

After growing plants under drought conditions, I standardized plant phenological stage before performing optical vulnerability curves by waiting for plants to enter the flowering stage. Then I randomly selected the plant that would be taken back to the lab, fully irrigated to saturation, double bagged for approximately 3 hours, after which, a psychrometer would be attached to one leaf on a leaflet. A Cavicam was attached to another leaf on the same leaflet. Leaves that were measured were young, but fully

developed. Once equipment was attached, I removed the plant from its pot and promptly, but carefully, removed the soil. Once soil was removed, I turned on both the camera and psychrometer to continuously log data every five minutes. The equipment was set to record data until no further embolism events were observed in the Cavicam footage, which usually took somewhere between 2-5 days per plant.

3.3.6 Field physiological measures

Leaf stomatal conductance (g_{sw}; μmol m^{-2} s^{-1}) was measured bi-weekly throughout the growing season using a Decagon porometer(model). For each sampling event. 16 irrigated and 16 dry-farmed plants from each variety were randomly selected and measured between 10:00 and 14:00, when solar radiation was near its daily maximum. Measurements were taken on fully expanded, sun-exposed leaves located at the apical portions of the plants and oriented toward the south.

The same leaves used for stomatal conductance measurements were subsequently used to determine leaf water potential (Ψ; MPa) using a Scholander-type pressure chamber (PMSInstruments.com). Leaves were excised at the petiole, immediately placed into the chamber head, and pressurized until xylem sap became visible at the cut surface.
Net carbon assimilation (Anet; μmol CO2 m^{-2} s^{-1}) was measured on September 29, 2024, using eight fully expanded leaves per treatment. Photosynthetic measurements were conducted with a LI-6400 portable

photosynthesis system (Li-Cor, Lincoln, Nebraska, USA). Chamber conditions were maintained at 400 ppm CO_2, a temperature of 22 °C, and a leaf to air vapor pressure deficit of 1-3 kPa. Stomatal conductance (g_{sw}) and instantaneous water use efficiency were recorded simultaneously using the same instrument.

3.3.7 Plant growth and leaf traits

Plant height was measured biweekly throughout the growing season. Height was recorded from the base of the stem at the soil surface to the uppermost apical leaf.

Leaf area was also assessed biweekly using a leaf area meter (LI-3100). After measurement, leaves were dried in a drying oven at 60°C for a minimum of 72 hours before weighing leaf dry mass. Leaf area and dry mass values were then used to calculate leaf mass per are (LMA).

3.3.8 Plant anatomical measures

Quantitative image analysis was used to characterize xylem anatomy in stems and roots, as well as stomatal and vein density in leaves (n=6 plants). Samples were imaged using brightfield and fluorescence microscopy (Leica DM6 B, leica.com). Stem sections were prepared with a microtome (Lab-Microtome, Swiss Federal Research Institute, Switzerland), stained with safranin-alcian blue solution (0.35 g safranin in 35 mL 50% EtOH; 0.65 g alcian blue in 65 mL distilled water), mounted in glycerin, and imaged at 100x magnification. Vessel lumen diameter and lumen area were measured

for all vessels in each cross section using ImageJ (Rueden et al., 2017). Root samples were prepared using the same protocol. Root cross sections were collected 20cm from the root-shoot junction at the end of the growing season.

Leaves were cleared in 1 M KOH, stained with the same safranin-alcian blue solution, and mounted on slides. Veins and stomata were imaged at 100-200x magnification. Vein density was calculated as vein length per lamina area (vein length divided by lamina area; mm mm−2) from three randomly selected fields per leaf. Stomatal density was determined as the number of stomata per unit area from three randomly selected fields per leaf.

3.3.9 Pressure-Volume analysis

Pressure-volume (PV) curves were used to quantify leaf responses to drought by progressively dehydrating leaves and measuring changes in leaf water potential and mass over time. These measurements were then used to calculate the water potential at turgor loss point (Ψ_{TLP}), osmotic potential at turgor loss point (π_{TLP}), and the bulk modulus of elasticity (ε).

Fully expanded leaves from the apical portions of plants were sampled during the peak of the growing season. Leaves were collected early in the morning, prior to direct sun exposure, placed in humidified bags, and transported to the lab. In the lab, petioles were recut under water and leaves were allowed to rehydrate for at least two hours until leaf water potential approached 0 MPa. PV curves were then generated following the protocol of

Sack et al 2003. Measurements were conducted on six plants per variety within each treatment.

3.3.10 Yields

Dry bean yields were harvested at the end of the growing season, once the pods were completely dried out. In 2025, the green beans were harvested fresh twice throughout their harvest season to account for its indeterminate growth pattern. The yields from both harvests were combined to get total marketable yields. Pods for both dry beans and fresh beans were dried at 60°C for 72 hours to weigh total marketable dry mass (n=12).

3.3.11 Statistics

Data obtained on the Black and Hopi beans in 2024 and 2025 were analyzed using a three-way ANOVA with variety, treatment, and year as fixed effects, including interaction terms. Prior to analysis, data was checked for normality and homogeneity of variance using Shapiro-Wilk tests and visual inspection of residual plots. If the data did not pass those inspections, then the data was transformed. Post hoc comparisons were conducted using estimated marginal means (emmeans) with pairwise contrasts to evaluate treatment effects within each variety and year.

When models were evaluated for normality and homogeneity of variance and the assumptions were not met, then I used a mixed-effects model (LMM), with the fixed effects for variety, treatment, and year, along with all interaction terms. Model significance was assessed using a type III

ANOVA with Satterthwaite's approximation for degrees of freedom. Model assumptions were evaluated by visual inspection of residual plots. Although minor deviations from normality were observed, mixed-effects models are robust to such violations.

Traits that were measured in 2025 for Black, Hopi, and Green were analyzed using a two-way ANOVA with variety and treatment as fixed factors was used to analyze all physiological, anatomical, and fruit-related traits. Assumptions of normality and homogeneity of variance were assessed prior to analysis and were met. Post hoc comparisons of treatment effects within each cultivar and treatment interaction were performed using estimated marginal means with Tukey-adjusted p-values.

The lm() function in R was used to create linear regression models. Results were significant if $p<0.05$. Correlation matrices were calculated using Pearson's correlation coefficients with pairwise complete observations. The correlation plots in the supplemental material were created using the "corrplot" package.

Principal component analysis (PCA) was conducted to examine multivariate relationships among physiological, anatomical, and yield-related traits. PCA was preformed using the prcomp() function in R with centering and scaling applied to standardize variables to unit variance. Loadings (eigenvectors) were used to assess the contribution of each trait in

principal components, while scores were used to visualize sample distribution in multivariate space. A scree plot was used to evaluate the proportion of variance explained by each principal component and to guide component selection. This analysis is also found in the supplemental material. All statistical analyses were performed in R (version 4.2).

3.4 Results

Table 3.1. Traits measured, units, and abbreviations for the three cultivars grown under dry-farmed (D) and regularly irrigated (I) conditions during flowering. Data are means with standard error in parentheses. Spaces with dashes are left empty because there was no measure recorded for that trait during that year. Traits that are italicized are those that have been previously reported in Hekannen, Castro, et al. (in review).

		2024						2025					
Trait	Units; Abbreviation	Hopi		Black		Green		Hopi		Black		Green	
		D	I	D	I	D	I	D	I	D	I	D	I
Total dry yield per plant	g	16.67 (17.68)	47.44 (38.39)	23.95 (18.34)	108.14 (35.09)	_	_	34.85 (10.67)	50.67 (16.50)	37.22 (18.01)	59.66 (25.01)	16.57 (6.82)	29.16 (15.42)
Total pods per plant	Count	18.00 (9.65)	42.00 (20.58)	34.00 (19.25)	112.38 (45.99)	_	_	18.67 (5.60)	21.42 (6.17)	35.50 (13.61)	46.08 (17.61)	27.83 (10.56)	45.92 (21.78)
Dry mass per pod	g	0.74 (0.53)	2.13 (0.36)	0.64 (0.15)	0.89 (0.30)	_	_	1.87 (0.22)	2.37 (0.30)	1.02 (0.14)	1.29 (0.15)	0.59 (0.07)	0.63 (0.12)
Leaf water potential	MPa; Ψl_{eaf}	-0.77 (0.23)	-0.59 (0.26)	-0.52 (0.21)	-0.41 (0.27)	_	_	-0.70 (0.20)	-0.46 (0.25)	-0.68 (0.20)	-0.73 (0.19)	-0.50 (0.12)	-0.45 (0.13)
Stomatal Conductance (Decagon)	µmol m^{-2} s^{-1}; g_{sw}	351.05 (81.56)	500.39 (157.84)	383.88 (158.40)	560.39 (83.73)	_	_	175.50 (82.86)	339.92 (229.33)	345.08 (249.38)	371.25 (242.25)	319.58 (226.06)	478.08 (196.02)
Height (cm)	cm	36.13 (9.34)	45.38 (11.84)	41.31 (9.49)	46.69 (8.16)	_	_	43.92 (7.65)	36.17 (3.49)	46.58 (4.74)	65.92 (3.42)	37.50 (6.29)	43.21 (4.75)
Leaf mass per area	LMA	55.71 (4.94)	52.65 (7.75)	68.27 (9.58)	52.91 (10.35)	_	_	51.57 (20.46)	49.02 (9.06)	62.49 (18.54)	60.69 (13.70)	81.17 (26.89)	59.95 (8.31)
Photosynthesis	µmol CO_2 m^{-2} s^{-1}; A_{net}	18.66 (6.01)	28.45 (5.23)	20.22 (5.51)	26.02 (2.99)	_	_	_	_	_	_	_	_

Stomatal Conductance (Li-Cor 6400)	μmol m^{-2} s^{-1}; g_{sw}	1.11 (0.57)	3.43 (2.78)	0.93 (0.67)	2.09 (1.03)	_	_	_	_	_	_	_	_
Water use efficiency	A_{net} g_{sw}^{-1}; WUE	22.39 (14.25)	12.13 (6.21)	27.87 (10.31)	14.27 (4.38)	_	_	_	_	_	_	_	_
Vein density	mm mm^{-2}	0.010 (0.001)	0.009 (0.000)	0.011 (0.002)	0.010 (0.001)	_	_	0.009 (0.001)	0.009 (0.001)	0.010 (0.001)	0.009 (0.001)	0.012 (0.002)	0.010 (0.002)
Stomatal density	no. mm^{-2}	579.95 (75.44)	321.41 (153.98)	689.79 (143.67)	614.63 (52.81)	_	_	418.55 (69.67)	445.74 (59.44)	581.40 (141.45)	543.68 (132.06)	510.84 (128.51)	330.89 (102.49)
Mean stem vessel diameter	μm	40.89 (8.08)	40.89 (4.80)	37.84 (4.44)	51.01 (4.60)	_	_	44.75 (5.68)	51.02 (7.50)	42.78 (10.64)	53.79 (14.09)	49.52 (2.65)	48.60 (2.74)
Osmotic potential at full turgor	MPa; π_{FT}	-0.42 (0.13)	-0.55 (0.09)	-0.53 (0.24)	-0.54 (0.11)	_	_	_	_	_	_	_	_
Water potential at turgor loss point	MPa; Ψ_{TLP}	-0.64 (0.13)	-0.79 (0.08)	-0.74 (0.24)	-0.77 (0.14)	_	_	_	_	_	_	_	_
Modulus of elasticity at total relative water content	Mpa; ε	3.96 (1.57)	5.16 (1.61)	5.51 (1.41)	4.30 (0.76	_	_	_	_	_	_	_	_
P12	_	_	_	_	_	_	_	-1.70 (0.55)	-1.39 (0.44)	_	_	-2.37 (1.02)	-1.56 (1.05)
P50	_	_	_	_	_	_	_	-1.92 (0.61)	-1.53 (0.48)	_	_	-2.79 (1.56)	-1.97 (1.42)
P88	_	_	_	_	_	_	_	-2.11 (0.74)	-1.66 (0.53)	_	_	-3.45 (2.66)	-2.31 (1.93)

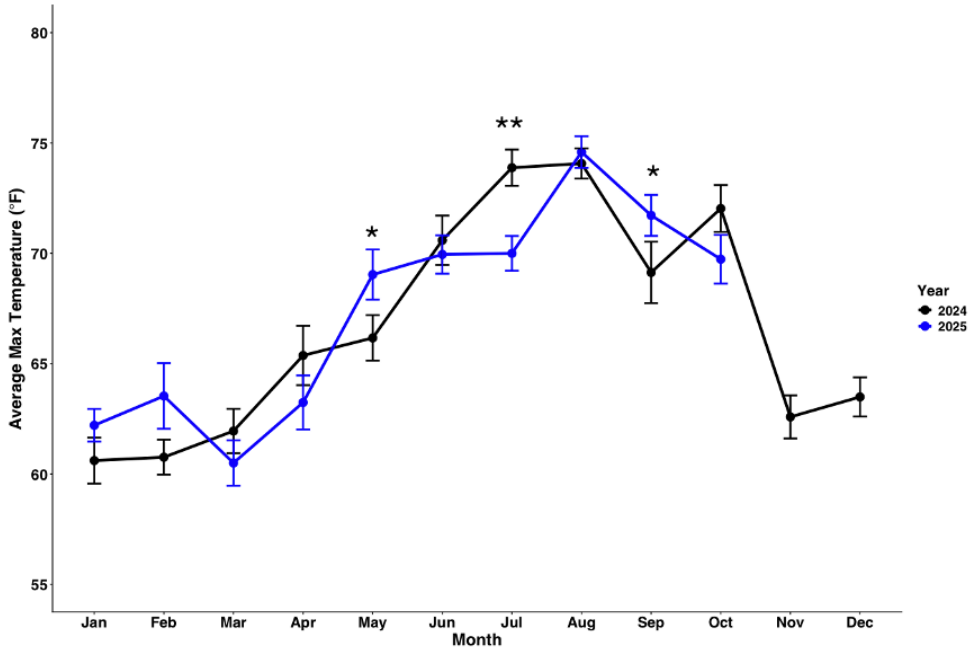

Figure 3.3. The average maximum temperature (F°) for each month recorded in years 2024 (black) and 2025 (blue). Points represent mean values and vertical lines overlayed on points represent ± SD. The significant difference between years for each month in denoted by *, where * if $p<0.05$, ** if $p<0.01$, and *** if $p<0.001$.

3.4.1 Climate

I found that temperature was significantly different between months when comparing 2024 to 2025 ($F_{9,647}=58.30$, $p<0.001$; Figure 3.3). Specifically, temperature was significantly higher in July 2024. During both years, the month of July was a time for plant growth and flower initiation,

therefore, temperature increase during this time could severely impact stress when plants are dry-farmed and may drive the differences between years.

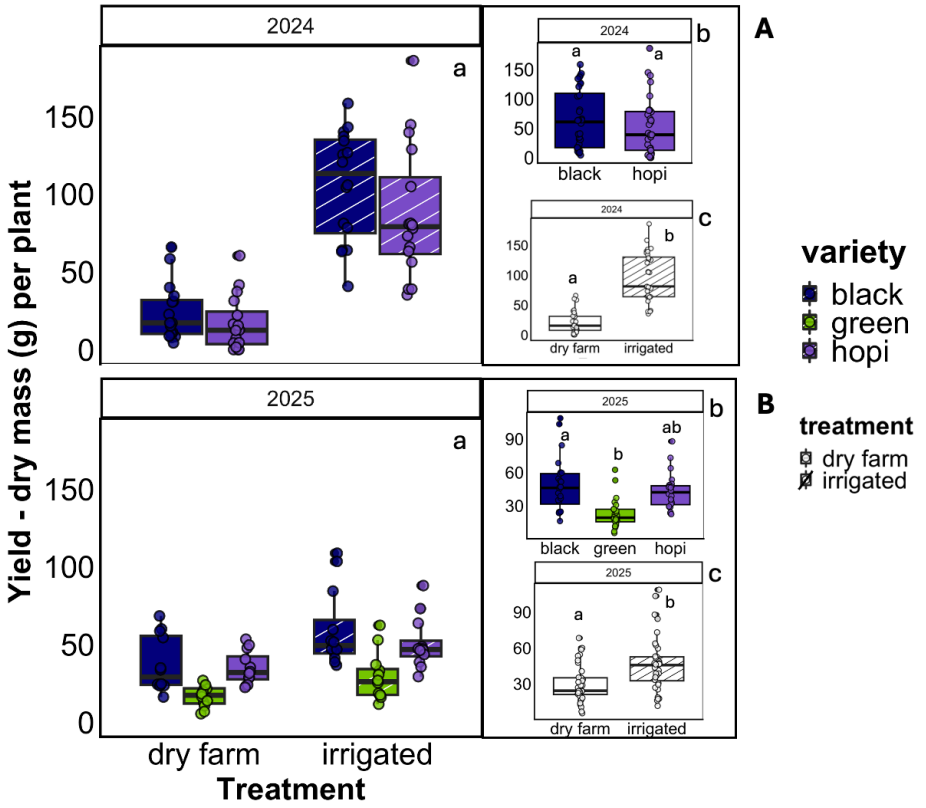

Figure 3.4. Yield dry mass (g) per plant in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=12 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests.

3.4.2 Yields

Overall, dry-farming significantly reduced yields (Figure 3.4). When I measured Black and Hopi beans in both 2024 and 2025, total dry biomass was significantly affected by both variety ($F = 5.40$, $p=0.022$) and treatment ($F = 129.42$, $p<0.001$), while year had no significant main effect ($F= 0.28$,

p=0.599), suggesting that there was no difference in yield between the two years. When treatments were averaged across varieties and years, I found that dry-farm differed from irrigated yields by 98.72%.

When the three varieties were compared in 2025, total dry biomass was significantly affected by both variety ($F = 25.86$, $p<0.001$) and treatment ($F = 23.47$, $p<0.001$), however there was no interaction between treatment and variety (Figure 3.5). When I averaged treatments across varieties, I found that dry-farm differed from irrigated dry yields by 44.58%. While I predicted that dry-farm adapted Hopi under no irrigation would have an advantage over the other varieties, I found no evidence of increased performance for any variety when dry-farmed.

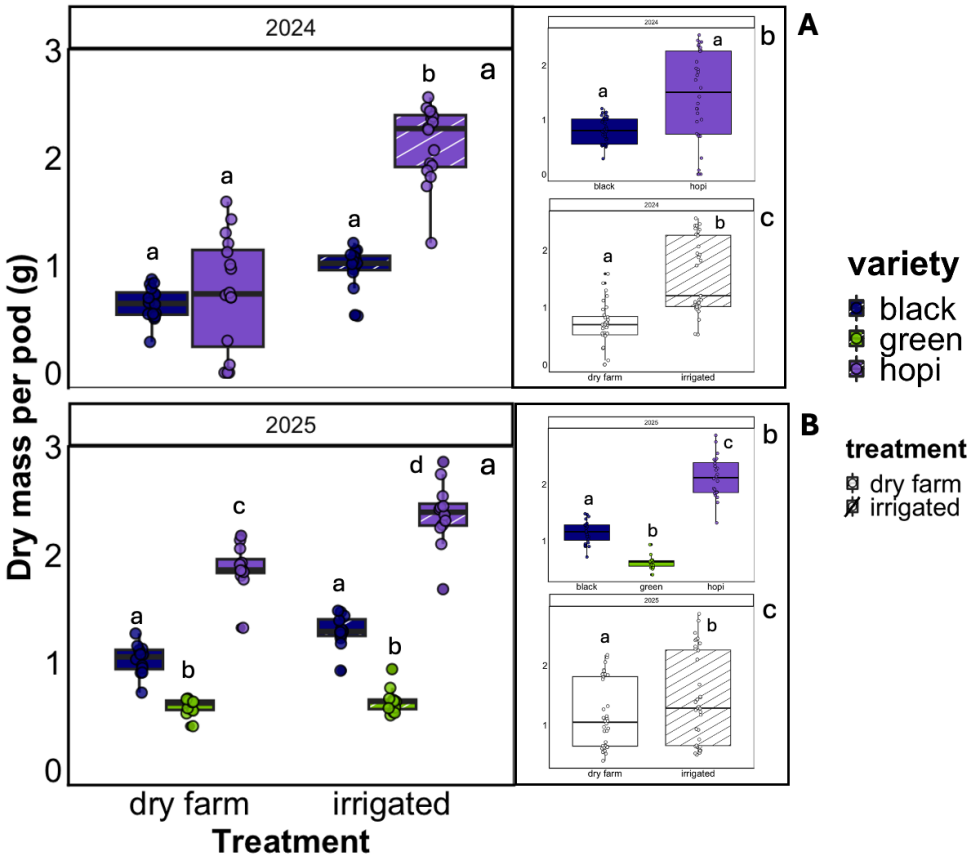

Figure 3.5. Dry mass per pod (g) per plant in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=12 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests.

Like yield dry mass per plant, dry-farming significantly impacted dry mass per pod in 2024 and 2025 (Figure 3.5). In addition, there was a significant difference between varieties, as well as an interaction between variety and treatment. I observed the same patterns in 2025, where the dry-farm treatment led to a decrease in dry mass per pod and I observed

significant differences in varieties and the interaction of variety and treatment. In both years, the Hopi variety produced the highest dry mass per pod out of the three varieties.

Bean plants had differences in carbon allocation. In 2024 I observed that lower vein density was related to higher dry mass per pod ($p<0.001$, Figure 3.6A). Then in 2025 I observed that lower LMA was related to higher dry mass per pod ($p<0.001$, Figure 3.6B).

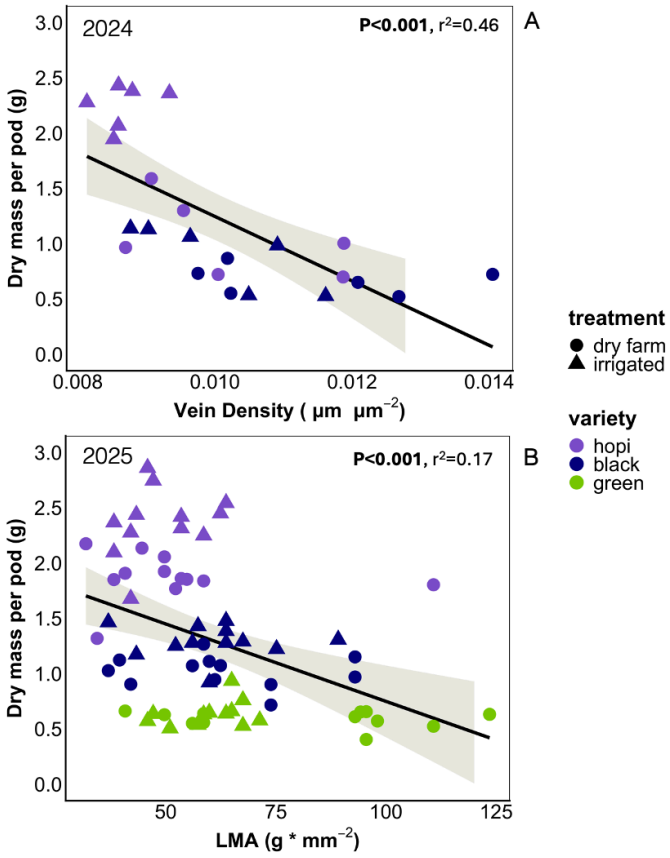

Figure 3.6. Regression for structural investment in (A) 2024 vein density and (B) 2025 LMA (the predictor variables) with dry mass per pod (g) (the response variables). The varieties are represented by the colors purple (Hopi), dark blue (Black), and green (Green) and treatment by circles (dry-farm) and triangles (irrigated). Panel A is n=24 and panel B is n=72.

3.4.3 Water potential

Dry-farming reduced water potentials across both varieties in 2024 and 2025 ($F=8.46$, $p<0.001$) while variety had no effect ($F=2.59$, $p=0.110$), suggesting that these two varieties behaved similarly. In contrast, when the three varieties were compared in 2025, water potentials were significantly impacted by variety ($F=9.28$, $p<0.001$) and I found an interaction between variety and treatment ($F=3.71$, $p=0.020$). Specifically, while there was no difference between treatments within the Green or Black varieties, there was a significant difference ($p=0.003$) between the treatments in the Hopi variety, where water potential was 41.38% lower under dry-farmed conditions.

3.4.4 Stomatal conductance

Dry-farming significantly reduced rates of stomatal conductance across Hopi and black varieties in 2024 and 2025 ($F=6.06$, $p=0.032$). Additionally, stomatal conductance was also impacted by variety ($F=4.37$, $p=0.043$) and year ($F=23.17$, $p<0.001$). There was no interaction between any fixed variables. In contrast, when the three varieties were compared in 2025, I found no significant difference in any of the treatment groups.

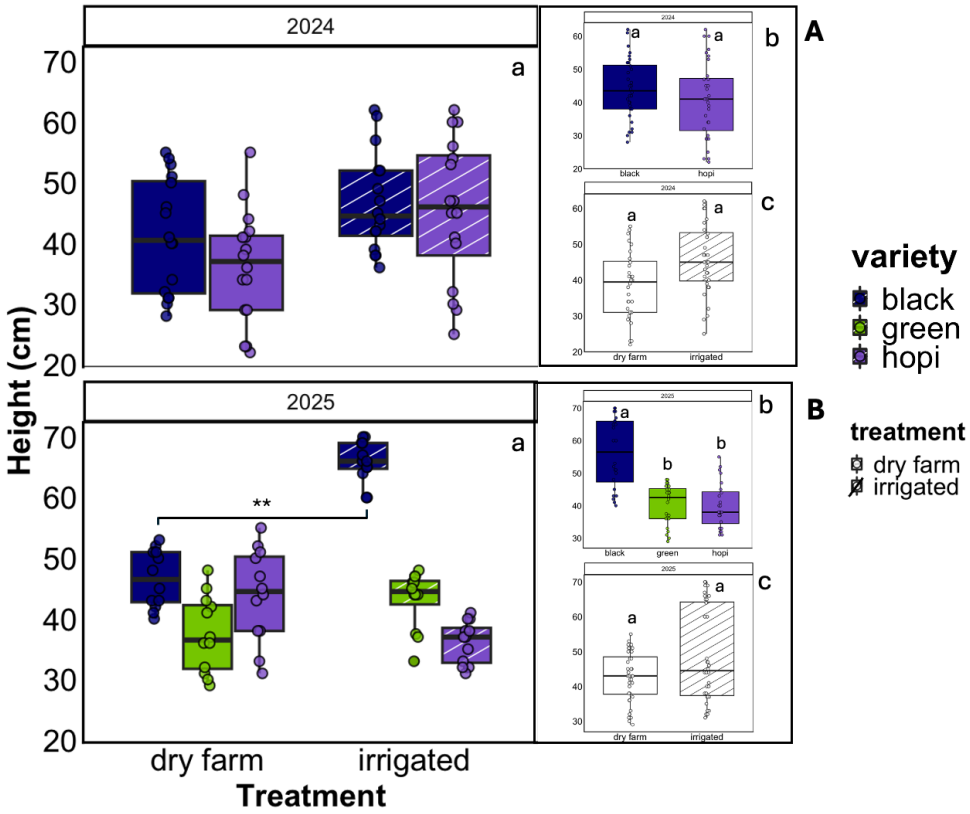

Figure 3. 7. Height (cm) for plants in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=12 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests.

3.4.5 Height

Variety impacted heights in Hopi and Black beans in 2024 and 2025 ($F=21.20$, $p<0.001$) while treatment had no effect ($F=4.89$, $p=0.056$; Figure 3.7). I observed the same patterns in 2025 where variety impacted heights ($F=14.18$, $p=0.005$) as well as an interaction between variety and treatment ($F=7.57$, $p=0.023$), where Black beans were significantly shorter under dry-farming ($P<0.05$) by 34.38%. I observed that height was significantly

correlated to yield under dry-farmed conditions (P=0.025; Figure 3.8). However, I did not see this relationship for irrigated Black or for the other varieties under either treatment.

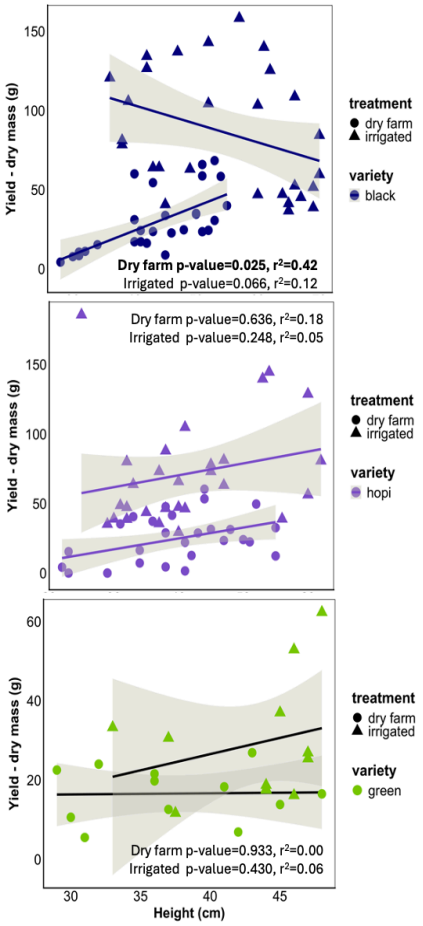

Figure 3.8. Regression for height (cm) (the predictor variable) with yield (g) (the response variables) (a) black (b) Hopi and (c) Green, where treatment by circles (dry-farm) and triangles (irrigated). n=28 for Black and Hopi, n=12 for Green.

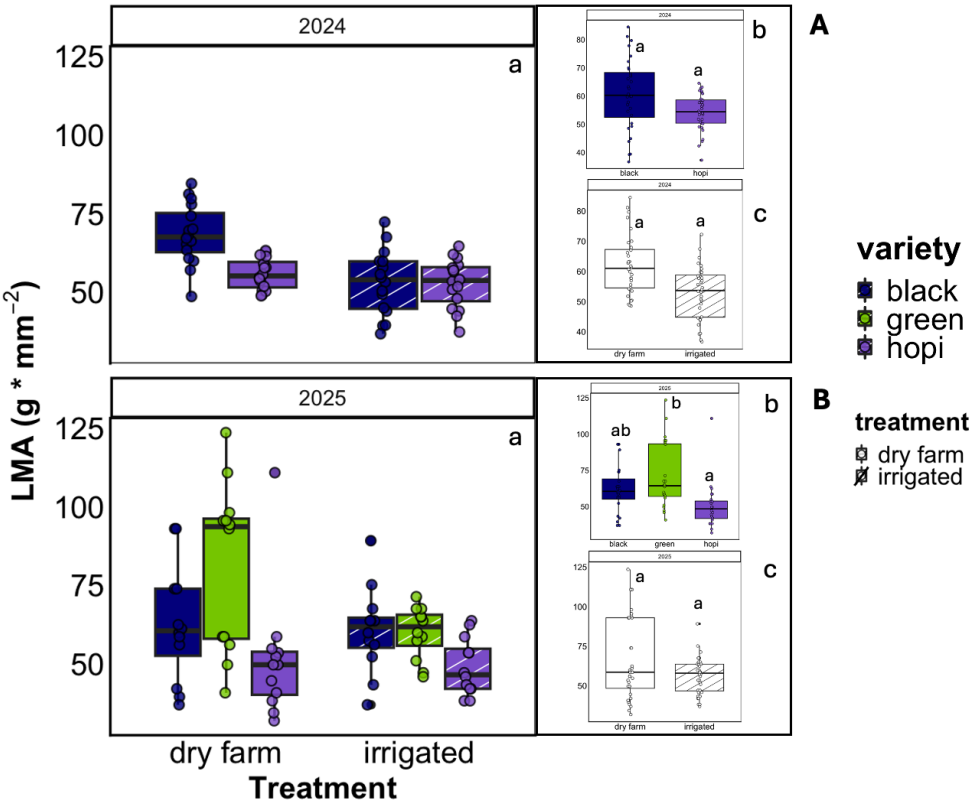

Figure 3.9. LMA for plants in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=12 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests.

3.4.6 Leaf mass per area

Following the trend of height, I observed that variety impacted LMA in Hopi and Black beans in 2024 and 2025 ($F=12.79$, $p<0.001$) while treatment had no effect ($F=4.52$, $p=0.059$), as well as no interaction between treatment and variety (Figure 3.9). In 2025, I observed the LMA was only impacted by variety ($F=9.15$, $p<0.001$), but had no effect between treatment

or interaction. These results indicate that the three varieties had different expression of the LMA trait, regardless of treatment. Green had the highest LMA compared to other varieties, where Green was 13.38 % different from black and 33.54% different from Hopi.

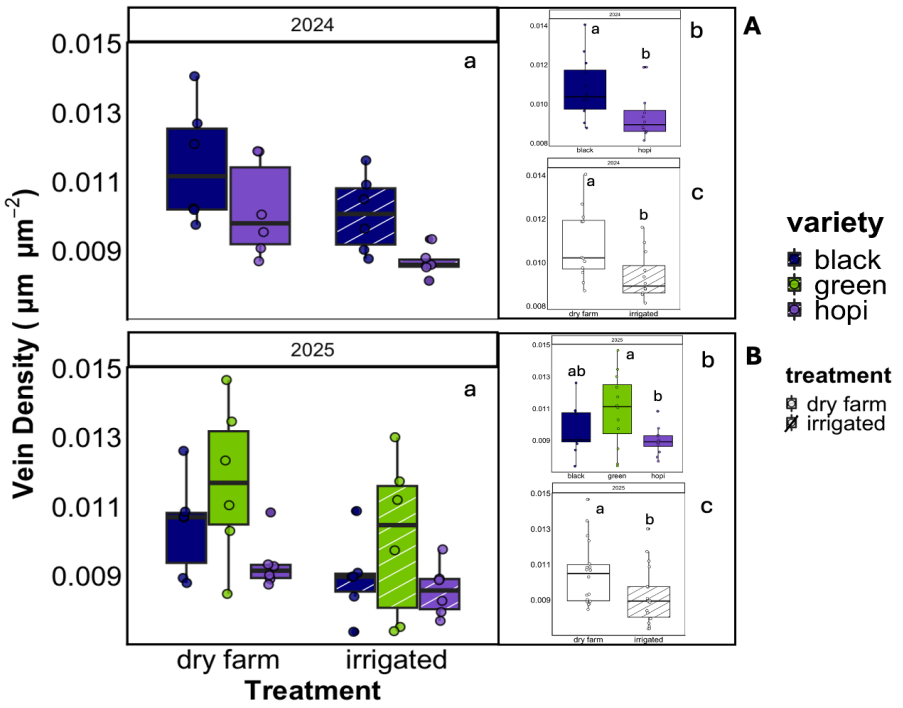

Figure 3.10. Vein density for plants in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=6 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests.

3.4.7 Anatomy

During both 2024 and 2025, I observed differences across varieties and treatments for vein density, stomatal density and stem mean vessel diameter, however, no interaction between factors occurred in any trait

(Figure 3.10). Specifically, in Hopi and Black beans in 2024 and 2025, I observed that variety ($F=9.77$, $p<0.001$), treatment ($F=15.17$, $p<0.001$), and year ($F=5.48$, $p=0.024$) impacted vein density. In 2024, I found that Black bean was 10% different from Hopi bean and that dry-farming and irrigated treatments differed by 10%. When I compared anatomical traits across Green, Black, and Hopi varieties in 2025, I observed that variety ($F=4.69$, $p=0.017$) and treatment ($F=6.10$, $p=0.020$) significantly impacted vein density. Specifically, treatments differed by 10.17% and varieties Green and Hopi differed by 20.0%. Black was not different from either variety in 2025.

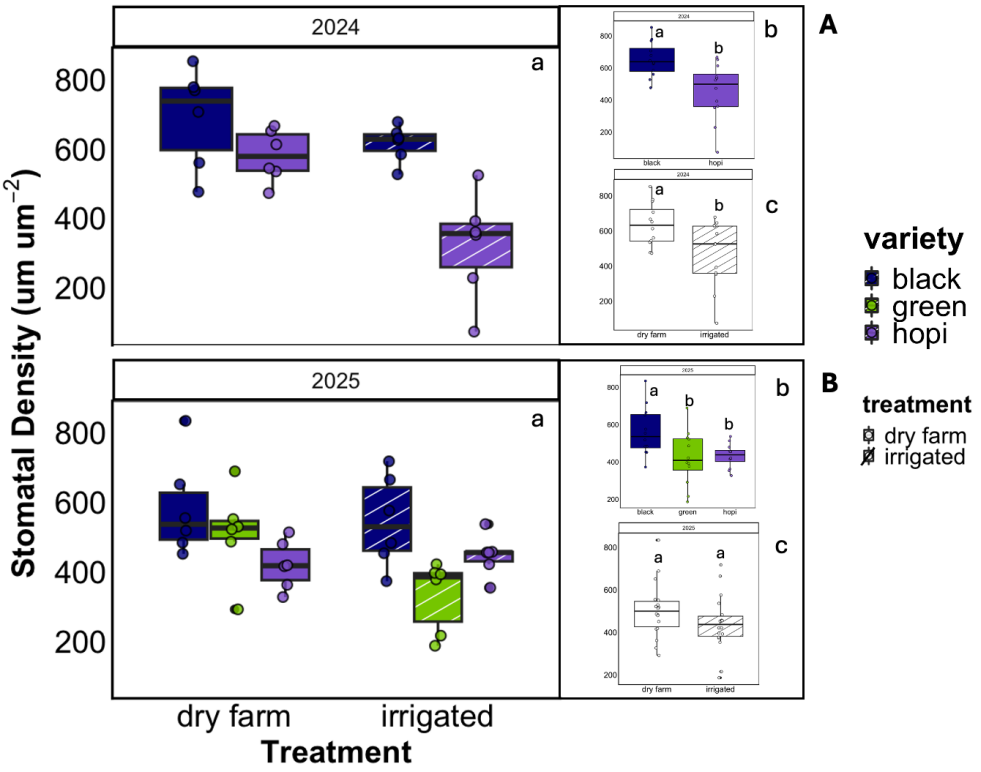

Figure 3.11. Stomatal density for plants in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=6 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests.

Similarly in Hopi and Black beans in 2024 and 2025, I observed that variety ($F=26.8$, $p<0.001$) and treatment ($F=7.21$, $p=0.010$) impacted stomatal density (Figure 3.11). However, year did not have an effect ($F=2.95$, $p=0.090$). Specifically, Hopi and black differed by 36.55% and irrigated and dry-farm differed by 30.26%. In 2025, I observed that only variety ($F=6.13$, $p=0.006$) significantly impacted stem density. While Black

was significantly different from Hopi (by 26.22%) and Green (by 28.81%) varieties, while Hopi and Green did not differ.

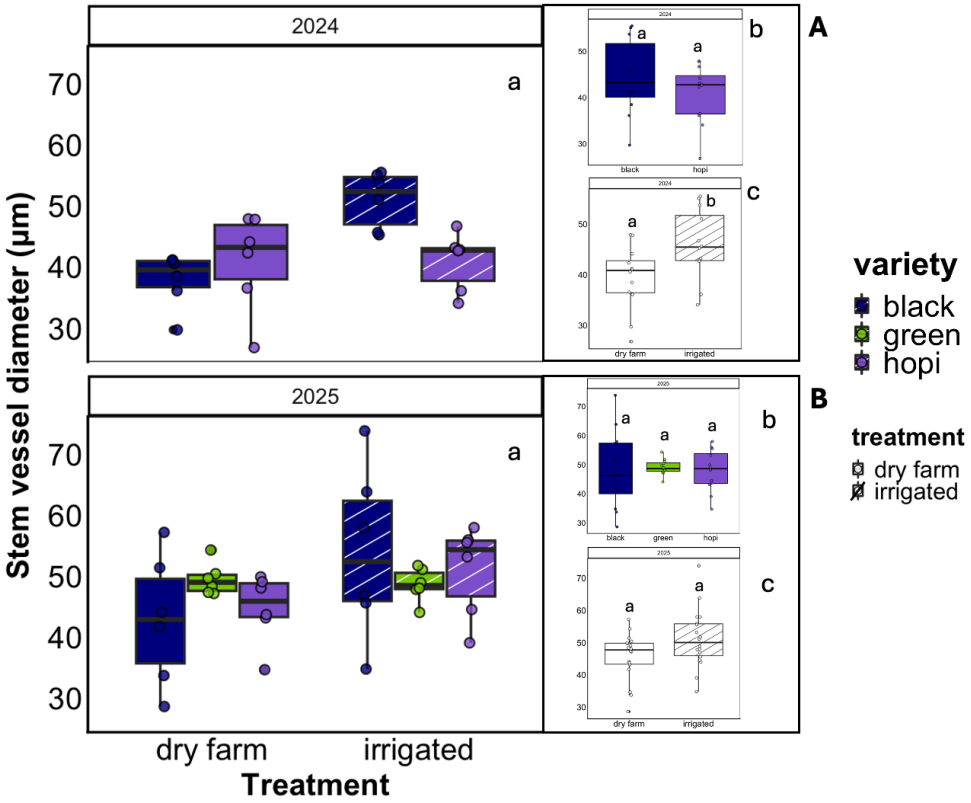

Figure 3.12. Stem vessel diameter for plants in (A) 2024 and (B) 2025, presented as boxplots, where midlines show medians, box edges, first and third quartiles, whiskers, minima and maxima, and points, outliers. Data was collected for n=6 plants of Black (dark blue), Hopi (purple), and Green (green) varieties, grown under dry-farmed (solid) and irrigated (dashed line) conditions. Each year has data summarized (a) across both varieties and treatments, (b) across varieties, and (c) across treatments. Letters indicate significant difference ($P < 0.05$) among groups based on Tukey's HSD tests.

In Hopi and Black beans in 2024 and 2025, I observed that treatment ($F=10.51$, $p=0.002$) and year ($F=5.34$, $p=0.026$) had an effect on mean vessel diameter (Figure 3.12). However, variety did not have an effect ($F=0.70$,

p=0.408). Specifically, I found that dry-farmed and irrigated treatments differed by 15.44%. Finally, I observed no significant differences between all three varieties, treatments, or interaction of the two for mean vessel diameter in 2025.

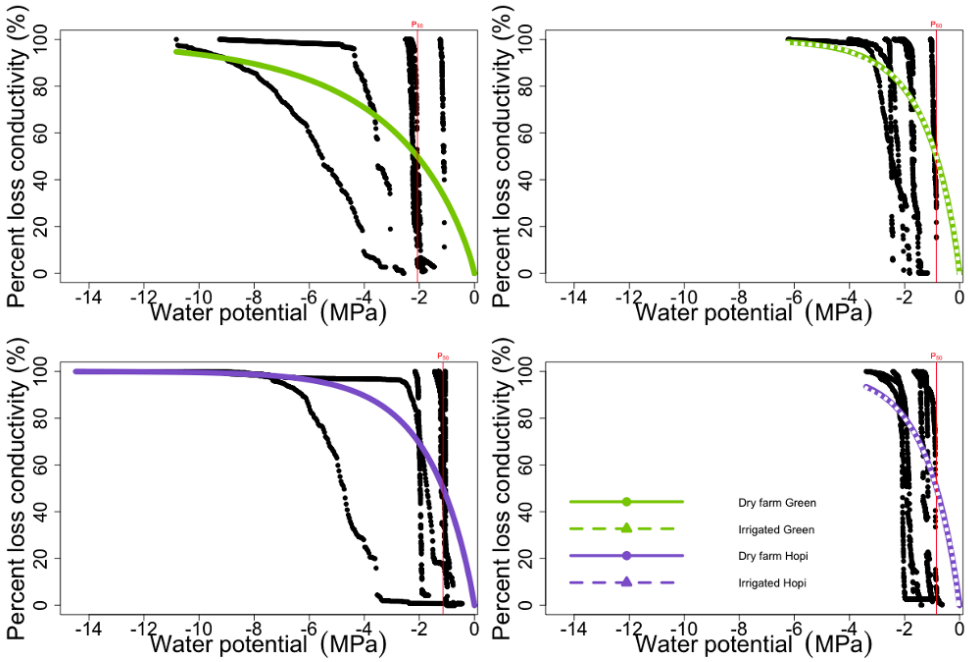

Figure 3.13. Vulnerability to embolism in leaves of dry-farmed (solid) an irrigated (dashed) varieties of Green (green) and Hopi (purple) *P. vulgaris*. This is the direct visualization of embolism spread in leaves of six individuals (black points). Mean vulnerability curves of each variety and treatment group are fitted following the pfit r package with the standard error of the estimated parameters is represented by light gray areas. Solid red lines correspond to P50.

3.4.8 Cavicam vulnerability curves

In 2025, a greenhouse experiment was conducted to incorporate vulnerability curves into our analysis (Figure 3.13). I compared Green and Hopi varieties and found no differences in treatment, variety, or interaction

between p12, p50, and p88. However, I observed more variability in individual plant response when plants were grown under a water deficit.

3.4.9 Photosynthetic measures

In 2024, I measured photosynthetic rates in the field for Black and Hopi varieties. I found that treatment had a significant effect across both varieties ($F_{1,60}$= 37.85, p<0.001). Specifically, I observed that carbon assimilation for dry-farmed crops significantly differed from irrigated crops by 30.49%. However, there was no effect on variety and there was no interaction between variety and treatment. I observed this same trend for stomatal conductance that was simultaneously measured, where treatment significantly differed in g_{sw} by 92.06% ($F_{1,60}$= 32.42, p<0.001). When the two parameters were used to calculate WUE (Anet/ g_{sw}), I observed that treatment significantly differed in WUE in dry-farmed crops by 62.25% ($F_{1,60}$= 27.95, p<0.001).

3.4.10 Leaf traits

In 2024, I performed pressure volume curves for Hopi and Black bean leaves. I found there was no difference between varieties, treatments, or interactions between the two variables for both π_{TLP} and Ψ_{TLP}. There was a significant interaction between variety and treatment for ε (F=4.55, p=0.046), where Hopi plants had higher modulus of elasticity under irrigation.

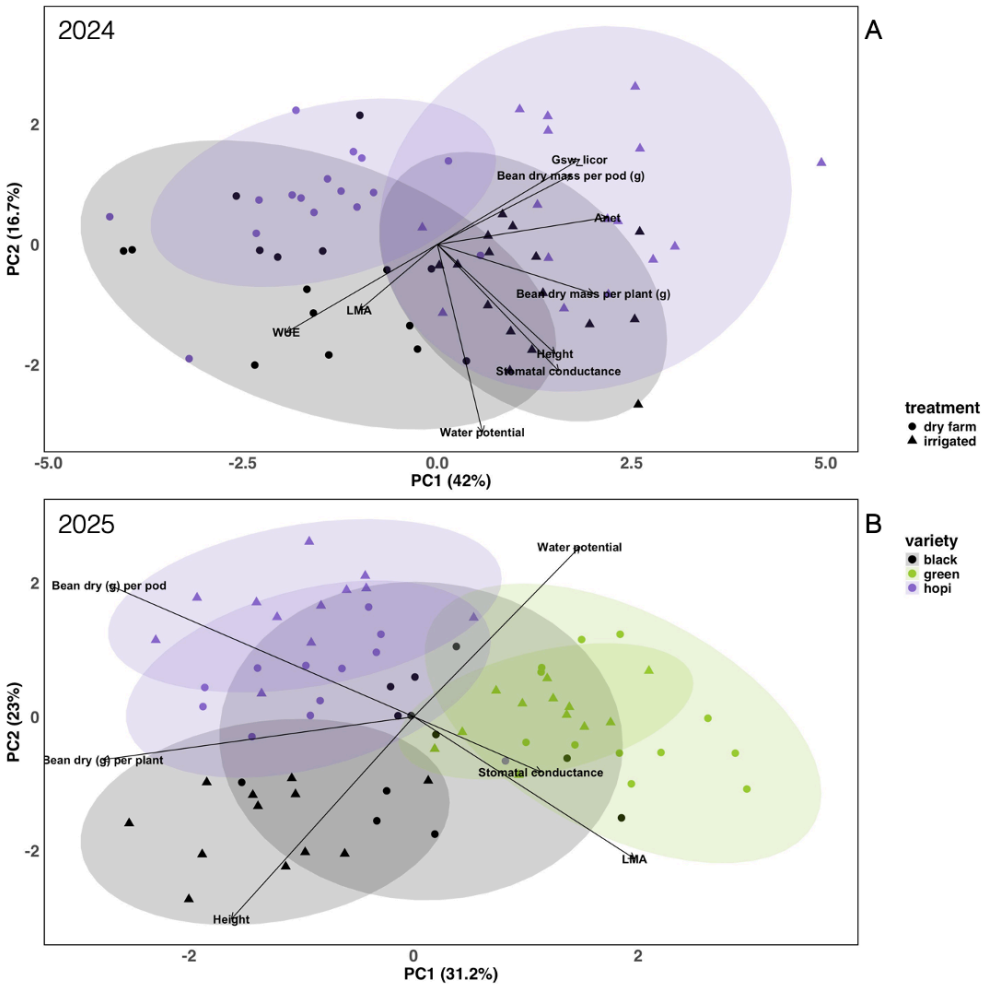

Figure 3.14. Principal component analysis (PCA) of (a) physiological traits (n=12) for Black (black) and Hopi (purple), and Green (green) varieties grown under dry-farmed (circle) and irrigated (triangle) conditions Variables are centered and scaled prior to analysis. Points represent individual samples plotted along the first two principal components (PC1 and PC2). Plot (A) explains 42.00% and 16.70% of the total variance that occurred in 2024 and plot (B) explains 31.20% and 23.00% of the total variance in 2025. Arrows indicate trait loadings, with direction and magnitude reflecting their contribution to each principal component.

3.4.11 Principle component analysis

When I compare Hopi, Green, and Black varieties, I observed that physiological traits seem to have distinctive groupings, emphasizing a clear

separation between all three varieties (Figure 3.14). In the 2024, the Black and Hopi beans (Figure 3.14A), the right side of the PCA demonstrates that photosynthesis, bean dry mass per pod, total dry yield per plant, and stomatal conductance are all most strongly related to Hopi irrigated plants. The left side demonstrates that drought tolerant traits (WUE and LMA) are associated with the dry-farmed Black beans variety.

When I perform the same analysis in 2025, the right side of the PCA demonstrates that LMA, stomatal conductance, and water potential are increasing trait values for the Green variety, where stomatal conductance and LMA seem to overlap for both treatments (Figure 3.14B). On the left side, bean dry mass per pods and total dry yield per plant grouped within the Hopi variety, where bean dry mass per pod overlaps for both treatments.

Finally, in the bottom of the analysis, height is associated with the Black variety under both treatments, and that there is some overlap with LMA. This analysis demonstrates a tradeoff between physiological traits and yield traits, and it also establishes how each variety behaves differently from one another, regardless of treatment. Additionally, it is important to note that I observed consistent traits across 2024 and 2025 for Black and Hopi varieties, such that Hopi prioritizes reproductive strategies while Black prioritizes carbon investment in vegetative growth (LMA and height).

3.5 Discussion

This study investigated the effects of dry-farming on three varieties of commercial beans grown across two seasons. Overall, dry-farming reduced

crop performance, most consistently through reductions in yield (Figure 3.4), while effects on morphology and anatomy varied between years. Treatment differences were more pronounced in 2024, when dry-farming increased vein (Figure 3.10) and stomatal density (Figure 3.11) and reduced mean vessel diameter (Figure 3.12), whereas fewer differences occurred in 2025. July temperatures were significantly higher in 2024 than in 2025 (Figure 3.3), suggesting that greater evaporative demand may have intensified water limitation and contributed to greater differences between treatments that were observed that year. This is consistent with measurements showing lower leaf water potential and stomatal conductance in dry-farmed plants during 2024 (Hekkanen, Castro, et.). Despite anatomical responses, dry-farmed plants did not exhibit greater resistance to cavitation (Figure 3.13) nor leaf osmotic adjustments (Table 3.1), suggesting that shifts in leaf and xylem traits did not translate into substantial improvements in drought resistance or living tissue adjustments in leaves.

Additionally, there was little evidence that any of the three varieties possessed a coordinated suite of traits that allowed for greater drought resistance. A drought-adapted variety might be expected to have coordinated responses in traits such as stomatal regulation, xylem anatomy, and resistance to embolism that maintain hydraulic functioning during drought (Lens et al., 2022). Instead, trait response varied among varieties and between years, while yield declined under dry-farming across varieties. This suggests that the differences among varieties were relatively small compared

with the overall effect of water limitation. Green beans appeared least suited to dry-farming, whereas neither Black nor Hopi demonstrated a clear physiological advantage that prevented yield loss.

The most consistent difference among varieties instead involved how carbon was allocated between vegetative and reproductive tissue. Hopi beans had lower LMA, consistent with a more acquisitive leaf strategy characterized by lower structural investment per unit leaf area (Reich, 2014). At the same time, Hopi beans consistently produced greater dry mass per pod across growing seasons (Figure 3.5). The relationship between LMA and reproductive investment (Figure 3.6 A-B) therefore suggest that Hopi plants allocated relatively fewer resources toward leaf structure and more toward reproduction. In contrast, Black beans exhibited greater vegetative investment, including greater plant height and LMA. These differences did not result in a clear advantage in overall drought resistance, but they demonstrate different carbon-allocation strategies among varieties.

The limited physiological differences among varieties and treatments may also reflect the fast-growing life history of *Phaseolus vulgaris*. Fast-growing species generally favor rapid resource acquisition, photosynthesis, and growth over investment in long-lived, drought-resistant traits. For an annual crop with a relatively short growing season, maintaining reproductive output may therefore be a higher priority than investing in structural traits that increase the likelihood of survival. Under dry-farming, however, reduced water availability limits the resources available for growth and

reproduction and contributes to yield loss. These limitations are further supported by concurrent work that found reduced nitrogen fixation under dry-farming, which potentially limited carbon gain (Hekkanen, Castro, et al.).

3.6 Conclusion

Overall, dry-farming reduced bean yield, while physiological and anatomical responses varied between years. Despite some differences in individual traits, there was little evidence for major or consistent differences in drought resistance among the three varieties. Green beans appeared least suited to dry-farming, while Hopi beans had higher acquisitive and reproductive strategy. Lower LMA combined with greater dry mass per pod suggest that Hopi beans allocated relatively more carbon toward reproduction rather than vegetative tissues. Thus, Hopi beans may be of interest for low-input production because they prioritize reproductive output. More broadly, this study highlights the importance of integrating both physiological performance and yield related traits into crop development and developing varieties for water-limited systems.

Synthesis

The management of carbon and water resources during variable climatic conditions represents a durable challenge for crop plants around the globe. Plants have evolved numerous traits to survive in water-limited environments. While numerous studies have investigated drought-tolerant traits, few have taken a multi-faceted approach and studied crops under a wide lens, incorporating a multi-trait analysis to identify what suite of plant characteristics leads to drought resistance while maintaining fruit production. It is important to identify crops that employ a variety of traits to maintain hydraulic safety, efficiency, and photosynthetic features as climatic conditions continue to change (Torres-Ruiz *et al*., 2024). My work aims to identify this suite of traits to provide a physiological framework for sustainably grown crops.

In Chapter 1, I investigated the effect of reduced irrigation in ten strawberry (*Fragaria ananassa* Duch.) cultivars. Water stress consistently increased leaf mass per area and fruit soluble solids (°Brix) while reducing stomatal conductance, phloem fraction, and fruit size, revealing clear trade-offs between water conservation and yield. Strawberry is an economically important but drought-sensitive crop due to its shallow root system and high transpiration demand. Therefore, our findings highlight a set of traits that contribute to improved water-use efficiency while elucidating the yield penalties associated with drought resilience, offering valuable insights for

cultivar selection and breeding under water-limited conditions in sensitive crop-types.

The results from Chapter 1 provided a strong foundation for understanding the effects of water deficit on physiology, anatomy, and yield of herbaceous crops. In Chapter 2, I expanded the number of traits that I wanted to explore to fully capture the numerous traits plants adjust when they are water stressed. To fully capture these traits, I limited my sampling to two cultivars of tomatoes (*Solanum lycopersicum* L.) grown under irrigated and water-stressed conditions. Additionally, I pivoted to studying dry-farming, another form of sustainable agriculture that has becoming increasing popular in the western United States. Dry-farming is a method for growing crops under minimal water. I know dry-farming has many benefits, but more information is needed to understand how these plants maintain high productivity during the summer with limited water. In Chapter 2, I found that the dry-farm adapted variety Dirty Girl uses multiple traits to successfully produce yields without manual irrigation. Specifically, I observed that dry-farming conditions reduced individual plant yield by only 35.32% in Dirty Girl. Dry-farmed adapted Dirty Girls were associated with a physiological strategy of reduced water potentials alongside relatively high stomatal conductance during fruit development. Dry-farmed Dirty Girls also exhibited enhanced carbon acquisition traits, including greater plant height, increased vein density, and larger root vessel diameters. Concurrently, these plants expressed drought-tolerance traits such as smaller vessel diameters,

lower water potential at turgor loss point, and greater resistance to embolism. These traits resulted in sustained CO_2 assimilation and higher C:N ratios, resulting in sustained yields under no irrigation, with smaller fruits that had elevated °Brix.

Studies looking into the diversity of dry-farmed crops have shown that various crop-specific techniques are needed to grow successful dry-farm-adapted plants, such as soil and bed preparation, plant timing, and crop varietal selections (Garrett, 2019). However, much is still unknown about the physiological costs associated with crops grown in limited water. An improved understanding of the variation of dry-farmed crop physiology will allow scientists and growers to better strategize breeding and growing efforts. To further expand on the novel research of dry-farming, Chapter 3 further investigates these traits in a two-year experiment with three varieties of the common bean (*Phaseolus vulgaris*). I found that across both years, dry-farming significantly reduced yield in all varieties despite shifts in anatomical traits associated with drought tolerance. In 2024, a warmer growing season produced stronger treatment responses, including increased vein density and stomatal density and reduced vessel diameters under dry-farming conditions. These changes suggest that plants attempted to maintain hydraulic function and carbon assimilation under limited irrigation, but these responses did not increase yields. I observed fewer trait responses during the cooler 2025 season, supporting the idea that crop responses to drought are strongly influenced by temperature. While no variety consistently

maintained productivity under dry-farm conditions, Hopi beans allocated more carbon toward reproductive output, resulting in the highest dry mass per pod across all varieties and years. These finding suggest that, despite overall reductions in performance among fast-growing annual bean crops, heirloom Hopi beans may serve as a relatively low-maintenance crop that can maintain reproductive investment under minimal-input conditions.

Overall, my dissertation research has shed light on the physiological adjustment that occurs as the result of water-deficit on agricultural crops, while simultaneously describing the impacts on yields. While each species of crop, and each variety within a species, had contrasting responses to drier conditions, I found one common theme in all plants: limited irrigation leads to lower yields. The degree of yield loss then varies depending on the crop and response strategy. In strawberries, I observed a dramatic response to water-deficit, where some cultivars lost over 70% of their yields when grown under limited irrigation. Dry-farmed tomatoes, however, only loss 35% of yields. In common beans, I observed that the amount of yield loss greatly depended on the interaction with temperature. While yield loss may dissuade some growers from moving towards more sustainable farming practices, it is crucial to note that yield quality was improved or maintained under limited irrigation. Both strawberries and tomatoes had increases in Brix° sugar concentrations, which contributes towards taste and can provide growers with a competitive advantage within their respective markets.

Additionally, Hopi beans were able to maintain dry mass per pod even when dry-farmed.

Ultimately the goal with this dissertation is to provide valuable information to the people who may most benefit from it. This has been made possible through meeting and collaborating with growers and scientists in the field of agriculture. With Chapter 1, I worked with Driscoll's Berries, an international company that produces over one billion pounds of berries annually. While working there, I collaborated with industry level researchers who must prioritize efficient outcomes. With Chapters 2 and 3, I partnered with the UCSC Center of Agroecology (CFA). My work with the CFA helped me establish relationships with organic farmers in Santa Cruz County, work collaboratively with scientist in different fields within UCSC, and establish a multi-state collaborative project with Oregon State University. Just last year, the CFA and I hosted a farmer field day for dry-farming, where I communicated our scientific results with local organic growers who also shared their valuable experiences. Additionally, I have had the opportunity to work with UCSC undergraduates, many of which continue to contribute to plant research. This work included hands-on training and mentoring to develop scientific skills in organic food systems by involving students in work at both the CFA and in the Pittermann plant physiology lab.

In conclusion, my dissertation research has progressed our knowledge of the effects of water deficit on crop physiology and yield

performance, while establishing valuable relationships with growers, scientists, and students. This work provides an opportunity for additional research to assess crop response to multiple stressors that can arise due climate change.

References

Akhtar, H., Hameed, A., Binyamin, R., Riaz, K., Muhammad, H., Ali, F., Ali, S., Akash, Z., Zaheer, M., Ikram, K., Niaz, Y., Ali, H., 2025. Impact of Soil Microbes and Abiotic Stress on Strawberry Root Physiology and Growth: A Review. Phyton – International Journal of Experimental Botany 94, 561–581. https://doi.org/10.32604/phyton.2025.061262

Alonso-Forn, D., Sancho-Knapik, D., Ferrio, J.P., Peguero-Pina, J.J., Bueno, A., Onoda, Y., Cavender-Bares, J., Niinemets, Ü., Jansen, S., Riederer, M., Cornelissen, J.H.C., Chai, Y., Gil-Pelegrín, E., 2020. Revisiting the Functional Basis of Sclerophylly Within the Leaf Economics Spectrum of Oaks: Different Roads to Rome. Current Forestry Reports 6, 260–281. https://doi.org/10.1007/s40725-020-00122-7

Anderson, R., Bayer, P.E., Edwards, D., 2020. Climate change and the need for agricultural adaptation. Curr. Opin. Plant Biol., Biotic interactions AGRI 2019 56, 197–202. https://doi.org/10.1016/j.pbi.2019.12.006

Aneja, P., Sanyal, R., Ranjan, A., 2025. Leaf growth in third dimension: a perspective of leaf thickness from genetic regulation to ecophysiology. New Phytologist 245, 989–999. https://doi.org/10.1111/nph.20246

Asseng, S., Ewert, F., Martre, P., Rötter, R.P., Lobell, D.B., Cammarano, D., Kimball, B.A., et al., 2015. Rising temperatures reduce global wheat production. Nature Climate Change 5, 143–147. https://doi.org/10.1038/nclimate2470

Awad, H., Barigah, T., Badel, E., Cochard, H., Herbette, S., 2010. Poplar vulnerability to xylem cavitation acclimates to drier soil conditions. Physiologia Plantarum 139, 280–288. https://doi.org/10.1111/j.1399-3054.2010.01367.x

Bitocchi, E., Rau, D., Bellucci, E., Rodriguez, M., Murgia, M.L., Gioia, T., Santo, D., Nanni, L., Attene, G., Papa, R., 2017. Beans (Phaseolus ssp.) as a Model for Understanding Crop Evolution. Front. Plant Sci. 8. https://doi.org/10.3389/fpls.2017.00722

Brodribb, T.J. and Feild, T.S. (2000), Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. Plant, Cell & Environment, 23: 1381-1388. https://doi.org/10.1046/j.1365-3040.2000.00647.x

Brodribb, T.J., Feild, T.S., Jordan, G.J., 2007. Leaf Maximum Photosynthetic Rate and Venation Are Linked by Hydraulics. Plant Physiol 144, 1890–1898. https://doi.org/10.1104/pp.107.101352

Brodribb, T.J., 2009. Xylem hydraulic physiology: The functional backbone of terrestrial plant productivity. Plant Science 177, 245–251. https://doi.org/10.1016/j.plantsci.2009.06.001

Brodribb, T.J., Jordan, G.J., 2011. Water supply and demand remain balanced during leaf acclimation of Nothofagus cunninghamii trees. New Phytologist 192, 437–448. https://doi.org/10.1111/j.1469-8137.2011.03795.x

Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P.W., Trisos, C., Romero, J., et al., 2023. IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland. Intergovernmental Panel on Climate Change (IPCC). https://doi.org/10.59327/IPCC/AR6-9789291691647

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

Cao, Q., Huang, L., Li, J., Qu, P., Tao, P., Crabbe, M.J.C., Zhang, T., Qiao, Q., 2022. Integrated transcriptome and methylome analyses reveal the molecular regulation of drought stress in wild strawberry

(Fragaria nilgerrensis). BMC Plant Biology 22, 613. https://doi.org/10.1186/s12870-022-04006-9

Cardoso, A.A., Andrade, M.T., Bucior, E.R., Martins, S.C.V., 2025. Plant hydraulic traits influencing crop production in water-limited environments. Plant Physiol 199, kiaf521. https://doi.org/10.1093/plphys/kiaf521

Castronuovo, D., Cardone, L., Cruoglio, M., Lela, L., Benedetto, N., Carlucci, V., Candido, V., 2023. Productivity and quality of different tomato cultivars under intercropping system with maize and dry farming conditions in Southern Italy. Italus Hortus 30, 3. https://doi.org/10.26353/j.itahort/2023.1.0316

Colesie, C., Stangl, Z.R., Hurry, V., 2020. Differences in growth-economics of fast vs. slow growing grass species in response to temperature and nitrogen limitation individually, and in combination. BMC Ecol 20, 63. https://doi.org/10.1186/s12898-020-00333-3

Corso, D., Delzon, S., Lamarque, L.J., Cochard, H., Torres-Ruiz, J.M., King, A., Brodribb, T., 2020. Neither xylem collapse, cavitation, or changing leaf conductance drive stomatal closure in wheat. Plant Cell Environ. 43, 854–865. https://doi.org/10.1111/pce.13722

Dang, P., Ciais, P., Peñuelas, J., Lu, C., Gao, J., Zhu, Y., Batchelor, W.D., Xue, J., Qin, X., Ros, G.H., 2025. Mitigating the detrimental effects of climate warming on major staple crop production through adaptive

nitrogen management: A meta-analysis. Agricultural and Forest Meteorology 367, 110524. https://doi.org/10.1016/j.agrformet.2025.110524

Davis, M., Stone, A., Gallagher, A., Garrett, A., 2023. Site Factors Related to Dry Farm Vegetable Productivity and Quality in the Willamette Valley of Oregon. HortTechnology 33, 587–600. https://doi.org/10.21273/HORTTECH05287-23

Delgado-Baquerizo, M., Guerra, C.A., Cano-Díaz, C., Egidi, E., Wang, J.-T., Eisenhauer, N., Singh, B.K., Maestre, F.T., 2020. The proportion of soil-borne pathogens increases with warming at the global scale. Nat. Clim. Change 10, 550–554. https://doi.org/10.1038/s41558-020-0759-3

Ding, R., Nóbrega, R.L.B., Prentice, I.C., 2025. Global Assessment of Environmental and Plant-Trait Influences on Root: Shoot Biomass Ratios. Global Change Biology 31, e70543. https://doi.org/10.1111/gcb.70543

Dirty Girl [WWW Document], 2022. . The Dry Farming Institute. URL https://dryfarming.org/dry-farming-seed-directory/dirty-girl/ (accessed 12.19.25).

Duman, F., 2012. Uptake of Mineral Elements During Abiotic Stress, in: Ahmad, P., Prasad, M.N.V. (Eds.), Abiotic Stress Responses in Plants: Metabolism, Productivity and Sustainability. Springer, New

York, NY, pp. 267–281. https://doi.org/10.1007/978-1-4614-0634-1_15

Du, Y., Zhao, Q., Chen, L., Yao, X., Zhang, W., Zhang, B., Xie, F., 2020. Effect of drought stress on sugar metabolism in leaves and roots of soybean seedlings. Plant Physiology and Biochemistry 146, 1–12. https://doi.org/10.1016/j.plaphy.2019.11.003

Eckardt, N.A., Ainsworth, E.A., Bahuguna, R.N., Broadley, M.R., Busch, W., Carpita, N.C., Castrillo, G., et al., 2023. Climate change challenges, plant science solutions. Plant Cell 35, 24–66. https://doi.org/10.1093/plcell/koac303

Ernazarova, D.K., Safiullina, A.K., Kholova, M.D., Azimova, L.A., Hasanova, S.A., Nematullaeva, E.F., Rafieva, et al., 2025. Morphological and Molecular Insights into Genetic Variability and Heritability in Four Strawberry (Fragaria × ananassa) Cultivars. Horticulturae 11. https://doi.org/10.3390/horticulturae11101195

Evans, J.R., 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants. Oecologia 78, 9–19. https://doi.org/10.1007/BF00377192

Fahad, S., Bajwa, A.A., Nazir, U., Anjum, S.A., Farooq, A., Zohaib, A., Sadia, S., Nasim, W., Adkins, S., Saud, S., Ihsan, M.Z., Alharby, H., Wu, C., Wang, D., Huang, J., 2017. Crop Production under Drought and Heat Stress: Plant Responses and Management Options. Front Plant Sci 8, 1147. https://doi.org/10.3389/fpls.2017.01147

Fang, Y., Wang, J., Zhang, R., Li, F., Liang, L., Liu, S., Xu, B., Chen, Y., 2024. Assessing the impact of early and terminal droughts on root growth, grain yield and yield stability in old and modern wheat cultivars on the Loess Plateau. Agricultural Water Management 301, 108940. https://doi.org/10.1016/j.agwat.2024.108940

Farage, P.K., Ardö, J., Olsson, L., Rienzi, E.A., Ball, A.S., Pretty, J.N., 2007. The potential for soil carbon sequestration in three tropical dryland farming systems of Africa and Latin America: A modelling approach. Soil and Tillage Research 94, 457–472. https://doi.org/10.1016/j.still.2006.09.006

Franklin, O., Fransson, P., Hofhansl, F., Jansen, S., Joshi, J., 2023. Optimal balancing of xylem efficiency and safety explains plant vulnerability to drought. Ecology Letters 26, 1485–1496. https://doi.org/10.1111/ele.14270

Frascarelli, G., Galise, T.R., D'Agostino, N., Cafasso, D., Cozzolino, S., Cortinovis, G., Sparvoli, F., Bellucci, E., Di Vittori, V., Nanni, L., Pieri, A., Rossato, M., Vincenzi, L., Benazzo, A., Delledonne, M., Bitocchi, E., Papa, R., 2025. The evolutionary history of the common bean (Phaseolus vulgaris) revealed by chloroplast and nuclear genomes analysis. Theor Appl Genet 138, 47. https://doi.org/10.1007/s00122-025-04832-z

Garrett, A., 2019. Dry Farming in the Maritime Pacific Northwest: Intro to Dry Farming Organic Vegetables.

Gill, A.R., Rainey, C., Socolar, Y., Gil-Santos, Y., Bowles, T.M., 2024. Comparing dry farming of tomatoes across varieties and soil management history. Front. Sustain. Food Syst. 7. https://doi.org/10.3389/fsufs.2023.1301434

Gleason, S.M., Westoby, M., Jansen, S., Choat, B., Hacke, U.G., Pratt, R.B., Bhaskar, R., Brodribb, T.J., Bucci, S.J., Cao, K.-F., Cochard, H., Delzon, S., Domec, J.-C., Fan, Z.-X., Feild, T.S., Jacobsen, A.L., Johnson, D.M., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., McCulloh, K.A., Mencuccini, M., Mitchell, P.J., Morris, H., Nardini, A., Pittermann, J., Plavcová, L., Schreiber, S.G., Sperry, J.S., Wright, I.J., Zanne, A.E., 2016. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. New Phytologist 209, 123–136. https://doi.org/10.1111/nph.13646

Goeschl, J.D., Han, L., 2020. A Proposed Drought Response Equation Added to the Münch-Horwitz Theory of Phloem Transport. Frontiers in Plant Science. 11. https://doi.org/10.3389/fpls.2020.505153

González, A.M., Pesqueira, A.M., García, L., Santalla, M., 2023. Effects of Photoperiod and Drought on Flowering and Growth Development of

Protein-Rich Legumes under Atlantic Environments. Agronomy 13. https://doi.org/10.3390/agronomy13041025

Gouveia, C.S.S., Ganança, J.F.T., Slaski, J., Lebot, V., Pinheiro de Carvalho, M.Â.A., 2019. Variation of carbon and isotope natural abundances (δ15N and δ13C) of whole-plant sweet potato (*Ipomoea batatas* L.) subjected to prolonged water stress. Journal of Plant Physiology 243, 153052. https://doi.org/10.1016/j.jplph.2019.153052

Grant, O.M., Davies, M.J., Johnson, A.W., Simpson, D.W., 2012. Physiological and growth responses to water deficits in cultivated strawberry (Fragaria×ananassa) and in one of its progenitors, Fragaria chiloensis. Environ. Exp. Bot. 83, 23–32. https://doi.org/10.1016/j.envexpbot.2012.04.004

Guha, A., Chhajed, S.S., Choudhary, S., Sunny, R., Jansen, S., Barua, D., 2018. Hydraulic anatomy affects genotypic variation in plant water use and shows differential organ specific plasticity to drought in *Sorghum bicolor*. Environmental and Experimental Botany 156, 25–37. https://doi.org/10.1016/j.envexpbot.2018.08.025

Hacke UG, Sperry JS, Pittermann J. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. Basic and Applied Ecology 1: 31–41.

Hacke, U. G., J. S. Sperry. 2001. Functional and ecological xylem anatomy, Perspectives in Plant Ecology, Evolution and Systematics 4, 97-115.

Hancock, J.F., Sjulin, T.M., Lobos, G.A., 2020. Strawberries, in: Hancock, James F. (Ed.), Temperate Fruit Crop Breeding: Germplasm to Genomics. Springer Netherlands, Dordrecht, pp. 393–437. https://doi.org/10.1007/978-1-4020-6907-9_13

Hacke, U.G., Jacobsen, A.L., Pratt, R.B., 2022. Vessel diameter and vulnerability to drought-induced embolism: within-tissue and across-species patterns and the issue of survivorship bias. IAWA Journal 44, 304–319. https://doi.org/10.1163/22941932-bja10107

Harrison Day, B.L., Carins-Murphy, M.R., Brodribb, T.J., 2022. Reproductive water supply is prioritized during drought in tomato. Plant, Cell & Environment 45, 69–79. https://doi.org/10.1111/pce.14206

Hekkanen, H., V. Castro, H. Waterhouse, D. Wong, J. Pittermann. In review. Dry farming for resilience: productivity and physiological drivers of organic common bean production. Organic Agriculture.

Heino, M., Kinnunen, P., Anderson, W., Ray, D.K., Puma, M.J., Varis, O., Siebert, S., Kummu, M., 2023. Increased probability of hot and dry weather extremes during the growing season threatens global crop yields. Scientific Reports 13, 3583. https://doi.org/10.1038/s41598-023-29378-2

Holland, B.L., Monk, N.A.M., Clayton, R.H., Osborne, C.P., 2019. A theoretical analysis of how plant growth is limited by carbon allocation strategies and respiration. in silico Plants 1, diz004. https://doi.org/10.1093/insilicoplants/diz004

Holmes, G.J., 2024. The California Strawberry Industry: Current Trends and Future Prospects. International Journal of Fruit Science 24, 115–129. https://doi.org/10.1080/15538362.2024.2342900

Hu, T., Zhang, X., Khanal, S., Wilson, R., Leng, G., Toman, E.M., Wang, X., Li, Y., Zhao, K., 2024. Climate change impacts on crop yields: A review of empirical findings, statistical crop models, and machine learning methods. Environmental Modelling & Software 179, 106119. https://doi.org/10.1016/j.envsoft.2024.106119

Hummer, K.E., Bassil, N.V., Zurn, J.D., Amyotte, B., 2023. Phenotypic characterization of a strawberry (Fragaria ×ananassa Duchesne ex Rosier) diversity collection. PLANTS, PEOPLE, PLANET 5, 209–224. https://doi.org/10.1002/ppp3.10316

Husaini, A.M., Xu, Y.W., 2016. Challenges of climate change to strawberry cultivation: uncertainty and beyond. Strawberry: growth, development and diseases, CABI Books 262–287. https://doi.org/10.1079/9781780646633.0262

Isasa, E., Link, R.M., Jansen, S., Tezeh, F.R., Kaack, L., Sarmento Cabral, J., Schuldt, B., 2023. Addressing controversies in the xylem

embolism resistance–vessel diameter relationship. New Phytologist 238, 283–296. https://doi.org/10.1111/nph.18731

John, G.P., Scoffoni, C., Buckley, T.N., Villar, R., Poorter, H., Sack, L., 2017. The anatomical and compositional basis of leaf mass per area. Ecology Letters 20, 412–425. https://doi.org/10.1111/ele.12739

Kane, C., McAdam, S., 2023. Abscisic acid driven stomatal closure during drought in anisohydric Fagus sylvatica. Journal of Plant Hydraulics 9, 002–002. https://doi.org/10.20870/jph.2023.002

Keutgen, A., Pawelzik, E., 2007. Modifications of taste-relevant compounds in strawberry fruit under NaCl salinity. Food Chemistry 105, 1487–1494. https://doi.org/10.1016/j.foodchem.2007.05.033

Khan, F., Siddique, A.B., Shabala, S., Zhou, M., Zhao, C., 2023. Phosphorus Plays Key Roles in Regulating Plants' Physiological Responses to Abiotic Stresses. Plants (Basel) 12, 2861. https://doi.org/10.3390/plants12152861

Kroggel, M., 2014. Considerations For Greenhouse Strawberry Production. Report from Controlled Environment Agriculture Center.

Leakey, A.D.B., Ferguson, J.N., Pignon, C.P., Wu, A., Jin, Z., Hammer, G.L., Lobell, D.B., 2019. Water Use Efficiency as a Constraint and Target for Improving the Resilience and Productivity of C3 and C4 Crops. Annual Review of Plant Biology 70, 781–808. https://doi.org/10.1146/annurev-arplant-042817-040305

Leap, J., Wong, D., Yogg-Comerchero, K., Baier, A., O'Brien, D., 2017. Organic Dry-Farmed Tomato Production on California's Central Coast: A Guide for Beginning Specialty Crop Growers.

Ledesma, N., Sugiyama, N., 2005. Pollen Quality and Performance in Strawberry Plants Exposed to High-temperature Stress. Journal of the American Society for Horticultural Science 130. https://doi.org/10.21273/JASHS.130.3.341

Lens, F., Gleason, S.M., Bortolami, G., Brodersen, C., Delzon, S., Jansen, S., 2022. Functional xylem characteristics associated with drought-induced embolism in angiosperms. New Phytologist 236, 2019–2036. https://doi.org/10.1111/nph.18447

Leporino, M., Cardarelli, M., Bonini, P., Proietti, S., Moscatello, S., Colla, G., 2025. Impact of Drought and Biostimulant in Greenhouse Tomato: Agronomic and Metabolomic Insights. Plants (Basel) 14, 2000. https://doi.org/10.3390/plants14132000

Lin H, Y. Chen, H. Zhang, P. Fu, Z. Fan. 2017. Stronger cooling effects of transpiration and leaf physical traits of plants from a hot dry habitat than from a hot wet habitat. Functional Ecology, 31: 2202–2211.

Liu, X., Gao, T., Liu, C., Mao, K., Gong, X., Li, C., Ma, F., 2023. Fruit crops combating drought: Physiological responses and regulatory pathways. Plant Physiology 192, 1768–1784. https://doi.org/10.1093/plphys/kiad202

Luo, X., Keenan, T.F., Chen, J.M., Croft, H., Colin Prentice, I., Smith, N.G., Walker, A.P., Wang, H., Wang, R., Xu, C., Zhang, Y., 2021. Global variation in the fraction of leaf nitrogen allocated to photosynthesis. Nat Commun 12, 4866. https://doi.org/10.1038/s41467-021-25163-9

Lycopersicon; Cherokee Purple Tomato [WWW Document], n.d. . Lycopersicon; Cherokee Purple Tomato. URL https://www.uaex.uada.edu/yard-garden/resource-library/plant-week/Lycopersicon-Cherokee-Purple-Tomato-07-17-2020.aspx (accessed 1.24.26).

Ma, W.T., Yu, Y.Z., Wang, X., Gong, X.Y., 2023. Estimation of intrinsic water-use efficiency from δ13C signature of C3 leaves: Assumptions and uncertainty. Front. Plant Sci. 13. https://doi.org/10.3389/fpls.2022.1037972

Mano, N.A., Madore, B., Mickelbart, M.V., 2023. Different Leaf Anatomical Responses to Water Deficit in Maize and Soybean. Life (Basel) 13, 290. https://doi.org/10.3390/life13020290

May, G.M., Pritts, M.P., Kelly, M.J., 1994. Seasonal patterns of growth and tissue nutrient content in strawberries. Journal of Plant Nutrition. https://doi.org/10.1080/01904169409364795

McAvoy, J.D., Angelos Deltsidis, Ramsey Corn, Erick Smith, Camille, 2025. Productivity and Postharvest Quality of Strawberry Cultivars Grown in Southeast Georgia. CAES Field Report. URL

https://fieldreport.caes.uga.edu/publications/C1327/productivity-and-postharvest-quality-of-strawberry-cultivars-grown-in-southeast-georgia/ (accessed 3.31.26).

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G. and Yepez, E.A. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought?. New Phytologist 178, 719-739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Medyouni, I., Zouaoui, R., Rubio, E., Serino, S., Ahmed, H.B., Bertin, N., 2021. Effects of water deficit on leaves and fruit quality during the development period in tomato plant. Food Science & Nutrition 9, 1949–1960. https://doi.org/10.1002/fsn3.2160

Menzel, C.M., Smith, L., 2014. The growth and productivity of 'Festival' strawberry plants growing in a subtropical environment. New Zealand Journal of Crop and Horticultural Science 42, 60–75. https://doi.org/10.1080/01140671.2013.850439

Mirzabaev, A., Olsson, L., Kerr, R.B., Pradhan, P., Ferre, M.G.R., Lotze-Campen, H., 2023. Climate Change and Food Systems, in: von Braun, J., Afsana, K., Fresco, L.O., Hassan, M.H.A. (Eds.), Science and Innovations for Food Systems Transformation. Springer, Cham (CH).

Myers, J.R., Kmiecik, K., 2017. Common Bean: Economic Importance and Relevance to Biological Science Research, in: Pérez de la Vega, M., Santalla, M., Marsolais, F. (Eds.), The Common Bean Genome. Springer International Publishing, Cham, pp. 1–20. https://doi.org/10.1007/978-3-319-63526-2_1

Niklas, K.J., 1991. Effects of Tissue Volume and Location on the Mechanical Consequences of Dehydration of Petioles. American Journal of Botany 78, 361–369. https://doi.org/10.2307/2444958

Official Series Description - ELKHORN Series [WWW Document], n.d. URL https://soilseries.sc.egov.usda.gov/OSD_Docs/E/ELKHORN.html (accessed 1.18.26).

Onoda, Y., Wright, I.J., Evans, J.R., Hikosaka, K., Kitajima, K., Niinemets, Ü., Poorter, H., Tosens, T., Westoby, M., 2017. Physiological and structural tradeoffs underlying the leaf economics spectrum. New Phytologist 214, 1447–1463. https://doi.org/10.1111/nph.14496

Papp, J., Gracza, P., Simon, G., 2004. Anatomical relations of root formation in strawberry. International Journal of Horticultural Science 10. https://doi.org/10.31421/IJHS/10/3/493

Parajuli, R., Matlock, M.D., Thoma, G., 2022. Environmental life cycle impact assessment of fresh California strawberries: A full supply

chain perspective. Cleaner and Responsible Consumption 6, 100073. https://doi.org/10.1016/j.clrc.2022.100073

Parker, T.A., Gallegos, J.A., Beaver, J., Brick, M., Brown, J.K., Cichy, K., Debouck, D.G., Delgado-Salinas, A., Dohle, S., Ernest, E., de Jensen, C.E., Gomez, F., Hellier, B., Karasev, A.V., Kelly, J.D., McClean, P., Miklas, P., Myers, J.R., Osorno, J.M., Pasche, J.S., Pastor-Corrales, M.A., Porch, T., Steadman, J.R., Urrea, C., Wallace, L., Diepenbrock, C.H., Gepts, P., 2022. Genetic Resources and Breeding Priorities in Phaseolus Beans, in: Plant Breeding Reviews. John Wiley & Sons, Ltd, pp. 289–420. https://doi.org/10.1002/9781119874157.ch6

Pathak, T.B., Maskey, M.L., Dahlberg, J.A., Kearns, F., Bali, K.M., Zaccaria, D., 2018. Climate Change Trends and Impacts on California Agriculture: A Detailed Review. Agronomy 8, 25. https://doi.org/10.3390/agronomy8030025

Pedrinho, A. [UNESP, Mariano, E. [UNESP, Merloti, L.F. [UNESP, de Sá, M.E. [UNESP, 2019. Common bean seed quality as affected by cover crop mixtures and nitrogen fertilization.

Petry, N., Boy, E., Wirth, J.P., Hurrell, R.F., 2015. Review: The Potential of the Common Bean (Phaseolus vulgaris) as a Vehicle for Iron Biofortification. Nutrients 7, 1144–1173. https://doi.org/10.3390/nu7021144

Pittermann, J., 2010. The evolution of water transport in plants: an integrated approach. Geobiology 8, 112– 139. https://doi.org/10.1111/j.1472-4669.2010.00232.x

Pittermann, J., 2025. The Evolutionary Inevitability of Plant Water Transport: A Commentary on John Sperry's "Evolution of Water Transport and Xylem Structure." International Journal of Plant Sciences 186, 3–7. https://doi.org/10.1086/733726

Pockman, W.T., Sperry, J.S., 2000. Vulnerability to Xylem Cavitation and the Distribution of Sonoran Desert Vegetation. American Journal of Botany 87, 1287–1299. https://doi.org/10.2307/2656722

Pratt, R.B., Jacobsen, A.L., 2017. Conflicting demands on angiosperm xylem: Tradeoffs among storage, transport and biomechanics. Plant, Cell & Environment 40, 897–913. https://doi.org/10.1111/pce.12862

Prince, S.J., Murphy, M., Mutava, R.N., Durnell, L.A., Valliyodan, B., Shannon, J.G., Nguyen, H.T., 2017. Root xylem plasticity to improve water use and yield in water-stressed soybean. J Exp Bot 68, 2027–2036. https://doi.org/10.1093/jxb/erw472

Qin, Y., Horvath, A., 2020. Use of alternative water sources in irrigation: potential scales, costs, and environmental impacts in California. Environ. Res. Commun. 2, 055003. https://doi.org/10.1088/2515-7620/ab915e

Quandt, A., A.E. Larsen, G. Bartel, K. Okamura, D. Sousa. 2023. Sustainable groundwater management and its implications for agricultural land repurposing. Reg Environ Change 23, 1-12. https://doi.org/10.1007/s10113-023-02114-2

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raza A, A. Razzaq,S. S. Mehmood, X. Zou, X. Zhang, Y. Lv, J. Xu. Impact of Climate Change on Crops Adaptation and Strategies to Tackle Its Outcome: A Review. 2019. Plants (Basel) 34. doi: 10.3390/plants8020034. PMID: 30704089; PMCID: PMC6409995.

Ramirez-Cabral, N.Y.Z., Kumar, L., Taylor, S., 2016. Crop niche modeling projects major shifts in common bean growing areas. Agricultural and Forest Meteorology 218–219, 102–113. https://doi.org/10.1016/j.agrformet.2015.12.002

Reich, P.B., 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. Journal of Ecology 102, 275–301. https://doi.org/10.1111/1365-2745.12211

Renninger, H.J., Pitts, J.J., Wang, J., 2024. Leaf-level physiological strategies related to productivity and plasticity of Populus in the

Southeastern United States. Front. For. Glob. Change 7. https://doi.org/10.3389/ffgc.2024.1467381

Rico, C., Pittermann, J., Polley, H.W., Aspinwall, M.J., Fay, P.A., 2013. The effect of subambient to elevated atmospheric CO2 concentration on vascular function in Helianthus annuus: implications for plant response to climate change. New Phytologist 199, 956–965. https://doi.org/10.1111/nph.12339

Ripoll, J., Urban, L., Staudt, M., Lopez-Lauri, F., Bidel, L.P.R., Bertin, N., 2014. Water shortage and quality of fleshy fruits—making the most of the unavoidable. Journal of Experimental Botany 65, 4097–4117. https://doi.org/10.1093/jxb/eru197

Ristaino, J.B., Anderson, P.K., Bebber, D.P., Brauman, K.A., Cunniffe, N.J., Fedoroff, N.V., Finegold, C., Garrett, K.A., Gilligan, C.A., Jones, C.M., Martin, M.D., MacDonald, G.K., Neenan, P., Records, A., Schmale, D.G., Tateosian, L., Wei, Q., 2021. The persistent threat of emerging plant disease pandemics to global food security. Proceedings of the National Academy of Sciences 118, e2022239118. https://doi.org/10.1073/pnas.2022239118

Robinson, D., Handley, L.L., Scrimgeour, C.M., Gordon, D.C., Forster, B.P., Ellis, R.P., 2000. Using stable isotope natural abundances (δ15N and δ13C) to integrate the stress responses of wild barley

(Hordeum spontaneum C. Koch.) genotypes. J Exp Bot 51, 41–50. https://doi.org/10.1093/jexbot/51.342.41

Rosales, M.A., Ocampo, E., Rodríguez-Valentín, R., Olvera-Carrillo, Y., Acosta-Gallegos, J., Covarrubias, A.A., 2012. Physiological analysis of common bean (*Phaseolus vulgaris* L.) cultivars uncovers characteristics related to terminal drought resistance. Plant Physiology and Biochemistry 56, 24–34. https://doi.org/10.1016/j.plaphy.2012.04.007

Rueden, C.T., Schindelin, J., Hiner, M.C., DeZonia, B.E., Walter, A.E., Arena, E.T., Eliceiri, K.W., 2017. ImageJ2: ImageJ for the next generation of scientific image data. BMC Bioinformatics 18, 529. https://doi.org/10.1186/s12859-017-1934-z

Sack, L., Cowan, P.D., Jaikumar, N., Holbrook, N.M., 2003. The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. Plant, Cell & Environment 26, 1343–1356. https://doi.org/10.1046/j.0016-8025.2003.01058.x

Sade, N., Gebremedhin, A., Moshelion, M., 2012. Risk-taking plants. Plant Signal Behav 7, 767–770. https://doi.org/10.4161/psb.20505

Sade, N., Moshelion, M., 2014. The dynamic isohydric–anisohydric behavior of plants upon fruit development: taking a risk for the next generation. Tree Physiol 34, 1199–1202. https://doi.org/10.1093/treephys/tpu070

Salguero-Gómez, R., 2017. Applications of the fast–slow continuum and reproductive strategy framework of plant life histories. New Phytologist 213, 1618–1624. https://doi.org/10.1111/nph.14289

Samtani, J.B., Rom, C.R., Friedrich, H., Fennimore, S.A., Finn, C.E., Petran, A., Wallace, R.W., Pritts, M.P., Fernandez, G., Chase, C.A., Kubota, C., Bergefurd, B., 2019. The Status and Future of the Strawberry Industry in the United States. HortTechnology 29, 11–24. https://doi.org/10.21273/HORTTECH04135-18

Sánchez-Gómez, C., Posé, D., Martín-Pizarro, C., 2022. Insights into transcription factors controlling strawberry fruit development and ripening. Frontiers in Plant Science 13, 1022369. https://doi.org/10.3389/fpls.2022.1022369

Sartori, K., Vasseur, F., Violle, C., Baron, E., Gerard, M., Rowe, N., Ayala-Garay, O., Christophe, A., Jalón, L.G. de, Masclef, D., Harscouet, E., Granado, M. del R., Chassagneux, A., Kazakou, E., Vile, D., 2019. Leaf economics and slow-fast adaptation across the geographic range of Arabidopsis thaliana. Sci Rep 9, 10758. https://doi.org/10.1038/s41598-019-46878-2

Serrano, A.S., Martínez-Gascueña, J., Chacón-Vozmediano, J.L., 2024. Variability in water use behavior during drought of different grapevine varieties: Assessment of their regulation of water status

and stomatal control. Agricultural Water Management 291, 108642. https://doi.org/10.1016/j.agwat.2023.108642

Scoffoni, C., Rawls, M., McKown, A., Cochard, H., Sack, L., 2011. Decline of Leaf Hydraulic Conductance with Dehydration: Relationship to Leaf Size and Venation Architecture1[W][OA]. Plant Physiology 156, 832–843. https://doi.org/10.1104/pp.111.173856

Shewfelt, R.L., 1999. What is quality? Postharvest Biology and Technology 15, 197–200. https://doi.org/10.1016/S0925-5214(98)00084-2

Socolar, Y., Carlisle, L., Bowles, T.M., 2024a. Tomato dry farming as an agroecological model for California's drought resilient future: Farmers' perspectives and experiences. Elem Sci Anth 12, 00139. https://doi.org/10.1525/elementa.2023.00139

Socolar, Y., Matta, T.J., Fuentes, M.R., Andoko, B., Cook, J., Hernández, C.C., Mazariegos-Anastassiou, C., Mazariegos-Anastassiou, V., Schirmer, J., Socolar, J.B., Woodard, C., Wong, D.G., Bowles, T.M., 2024b. Deep nutrients and soil fungal communities support tomato fruit yield and quality in dry farm management systems. Environ. Res.: Food Syst. 1, 015005. https://doi.org/10.1088/2976-601X/ad382e

Sperry J.S., Donnelly J.R. & Tyree M.T. (1988) A method for measuring hydraulic conductivity and embolism in xylem. Plant, Cell and Environment, 11, 35-40.

Sperry, J. S. 2003. Evolution of water transport and xylem structure. International Journal of Plant Sciences 164: S115-S127.

Sperry, J.S., Hacke, U.G., Pittermann, J., 2006. Size and function in conifer tracheids and angiosperm vessels. American Journal of Botany 93, 1490–1500. https://doi.org/10.3732/ajb.93.10.1490

Stewart, B.A., Thapa, S., 2016. Dryland Farming: Concept, Origin and Brief History, in: Farooq, M., Siddique, K.H.M. (Eds.), Innovations in Dryland Agriculture. Springer International Publishing, Cham, pp. 3–29. https://doi.org/10.1007/978-3-319-47928-6_1

Sun, Y., Miao, F., Wang, Y., Liu, H., Wang, X., Wang, H., Guo, J., Shao, R., Yang, Q., 2023. L-Arginine Alleviates the Reduction in Photosynthesis and Antioxidant Activity Induced by Drought Stress in Maize Seedlings. Antioxidants 12. https://doi.org/10.3390/antiox12020482

Tao, H., Sun, H., Wang, Y., Wang, X., Guo, Y., 2023. Effects of water stress on quality and sugar metabolism in “Gala” apple fruit. Horticultural Plant Journal 9, 60–72. https://doi.org/10.1016/j.hpj.2022.03.008

Torres-Ruiz, J.M., Cochard, H., Delzon, S., Boivin, T., Burlett, R., Cailleret, M., Corso, D., Delmas, C.E.L., De Caceres, M., Diaz-Espejo, A., Fernández-Conradi, P., Guillemot, J., Lamarque, L.J., Limousin, J.-M., Mantova, M., Mencuccini, M., Morin, X., Pimont, F., De Dios, V.R., Ruffault, J., Trueba, S., Martin-StPaul, N.K., 2024. Plant

hydraulics at the heart of plant, crops and ecosystem functions in the face of climate change. New Phytologist 241, 984–999. https://doi.org/10.1111/nph.19463

Trueba, S., Pan, R., Scoffoni, C., John, G.P., Davis, S.D., Sack, L., 2019. Thresholds for leaf damage due to dehydration: declines of hydraulic function, stomatal conductance and cellular integrity precede those for photochemistry. New Phytol. 223, 134–149. https://doi.org/10.1111/nph.15779

Tyree, M.T., Zimmermann, M.H., 2002. Hydraulic Architecture of Whole Plants and Plant Performance, in: Tyree, M.T., Zimmermann, M.H. (Eds.), Xylem Structure and the Ascent of Sap, Springer Series in Wood Science. Springer, Berlin, Heidelberg, pp. 175–214.

Uebersax, M.A., Cichy, K.A., Gomez, F.E., Porch, T.G., Heitholt, J., Osorno, J.M., Kamfwa, K., Snapp, S.S., Bales, S., 2023. Dry beans (Phaseolus vulgaris L.) as a vital component of sustainable agriculture and food security—A review. Legume Science 5, e155. https://doi.org/10.1002/leg3.155

Ullah, I., Toor, M.D., Yerlikaya, B.A., Mohamed, Heba.I., Yerlikaya, S., Basit, A., Rehman, A. ur, 2024. High-temperature stress in strawberry: understanding physiological, biochemical and molecular

responses. Planta 260, 118. https://doi.org/10.1007/s00425-024-04544-6

Unnikrishnan, P., Ponnambalam, K., Karray, F., 2024. Influence of Regional Temperature Anomalies on Strawberry Yield: A Study Using Multivariate Copula Analysis. Sustainability 16. https://doi.org/10.3390/su16093523

Van Laere, J., Merckx, R., Hood-Nowotny, R., Dercon, G., 2023. Water deficit and potassium affect carbon isotope composition in cassava bulk leaf material and extracted carbohydrates. Frontiers in Plant Science. 14. https://doi.org/10.3389/fpls.2023.1222558

Ventrella, D., Charfeddine, M., Moriondo, M., Rinaldi, M., Bindi, M., 2012. Agronomic adaptation strategies under climate change for winter durum wheat and tomato in southern Italy: irrigation and nitrogen fertilization. Reg Environ Change 12, 407–419. https://doi.org/10.1007/s10113-011-0256-3

Vermeulen, S., Cools, J., Van Passel, S., 2025. Economic effects of drought on agriculture: Conceptual methods and stakeholders' perceptions. International Journal of Disaster Risk Reduction 116, 105073. https://doi.org/10.1016/j.ijdrr.2024.105073

Vicente, A.R., Ortugno, C., Rosli, H., Powell, A.L.T., Greve, L.C., Labavitch, J.M., 2007. Temporal Sequence of Cell Wall Disassembly Events in Developing Fruits. 2. Analysis of Blueberry (Vaccinium

Species). Journal of Agricultural and Food Chemistry 55, 4125–4130. https://doi.org/10.1021/jf063548j

Wang, X., Chen, S., Yang, X., Zhu, R., Liu, M., Wang, R., He, N., 2024. Adaptation mechanisms of leaf vein traits to drought in grassland plants. Science of The Total Environment 917, 170224. https://doi.org/10.1016/j.scitotenv.2024.170224

Wheeler J. K., J. S. Speery, U. G. Hacke, N. Hoang. 2005 Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: A basis for a safety versus efficiency trade-off in xylem transport. Plant Cell Environ 28: 800–812

Wright, I., Reich, P., Westoby, M., Ackerly, D., Baruch, Z., Bongers, F., Cavender-Bares, J., Cornelissen, J., Diemer, M., Flexas, J., Garnier, E., Groom, P., Gulias, J., Hikosaka, K., Lamont, B., Lee, T., Lee, W., Lusk, C., Villar, R., 2004. The world-wide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403

Wubetie, Y., Wubetu, A., 2025. Effects of staking techniques on growth and yield of tomato varieties in northwestern Ethiopia. Sci Rep 15, 20011. https://doi.org/10.1038/s41598-025-95659-7

Xie, Z., Forney, C.F., Xu, W., Wang, S., 2009. Effects of Root Restriction on Ultrastructure of Phloem Tissues in Grape Berry. HortScience 44, 1334–1339. https://doi.org/10.21273/HORTSCI.44.5.1334

Yao, G., Nie, Z., Turner, N.C., Li, F., Gao, T., Fang, X., Scoffoni, C., 2021. Combined high leaf hydraulic safety and efficiency provides drought tolerance in Caragana species adapted to low mean annual precipitation. New Phytol 229, 230–244. https://doi.org/10.1111/nph.16845

Ye, M., Wu, M., Zhang, H., Zhang, Zuolin, Zhang, Zujian, 2021. High Leaf Vein Density Promotes Leaf Gas Exchange by Enhancing Leaf Hydraulic Conductance in Oryza sativa L. Plants. Front Plant Sci 12, 693815. https://doi.org/10.3389/fpls.2021.693815

Yeh, D.A., Kramer, J., Calvin, L., Weber, C., 2023. The Changing Landscape of U.S. Strawberry and Blueberry Markets: Production, Trade, and Challenges from 2000 to 2020. USDA Economic Research Service.

Zacharaki, A.K., Monaghan, J.M., Bromley, J.R., Vickers, L.H., 2024. Opportunities and challenges for strawberry cultivation in urban food production systems. Plants, People, Planet 6, 611–621. https://doi.org/10.1002/ppp3.10475

Zhang, B., Archbold, D.D., 1993. Water Relations of a Fragaria chiloensis and a F. virginiana Selection during and After Water Deficit Stress. Journal of the American Society for Horticultural Science 118, 274–279. https://doi.org/10.21273/JASHS.118.2.274

Zhang, J., Jiang, H., Song, X., Jin, J., Zhang, X., 2018. The Responses of Plant Leaf CO2/H2O Exchange and Water Use Efficiency to Drought: A Meta-Analysis. Sustainability 10, 551. https://doi.org/10.3390/su10020551

Zhang, M., Gao, H., Chen, S., Wang, Xiaochun, Mo, W., Yang, X., Wang, Xue, Wang, Z., Wang, R., 2022. Linkages between stomatal density and minor leaf vein density across different altitudes and growth forms. Front. Plant Sci. 13. https://doi.org/10.3389/fpls.2022.1064344

Zhao, W., Liu, L., Shen, Q., Yang, J., Han, X., Tian, F., Wu, J., 2020. Effects of Water Stress on Photosynthesis, Yield, and Water Use Efficiency in Winter Wheat. Water 12, 2127. https://doi.org/10.3390/w12082127

Zhao, L., Gao, X., An, Q., Ren, X., Zhang, Y., Luo, L., Ma, N., Song, X., Cai, Y., Zhao, X., 2023. A shift from isohydric to anisohydric water-use strategy as a result of increasing drought stress for young apple trees in a semiarid agroforestry system. Agricultural and Forest Meteorology 336, 109484. https://doi.org/10.1016/j.agrformet.2023.109484