DISSERTATION

# ECOVOLTAICS AND GRASSLAND RESPONSES TO SOLAR ENERGY CO-LOCATION

Submitted by

Matthew Anders Sturchio

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2024

Doctoral Committee:

Advisor: Alan K. Knapp

Troy Ocheltree
Meagan Schipanski
Nathan Mueller

# ABSTRACT

## ECOVOLTAICS AND GRASSLAND RESPONSES TO SOLAR ENERGY CO-LOCATION

The mitigation of climate change requires a transition to renewable sources of energy, and of all available options solar photovoltaic (PV) energy generation has the greatest potential to reduce $CO_2$ emissions by the year 2030. Even so, ground mounted PV is land use intensive, and ideal locations for solar development often overlap with sensitive natural ecosystems and highly productive agricultural land. A scalable approach with potential to alleviate the land use tension created by solar development is the co-location of PV arrays and grassland ecosystems. While this approach has many positive implications for land sparing, the ecological consequences of PV presence above grassland ecosystems are not well understood. In this dissertation I discuss how the unique microenvironments created by PV arrays alter patterns of productivity, physiological response, and forage quality in a semi-arid grassland in Colorado, USA. I also outline a new approach to PV development, Ecovoltaics, that is informed by several fundamental ecological concepts. An Ecovoltaic approach to solar development co-prioritizes energy generation and ecosystem services by intentional design and management through all aspects of array development. With this work, I hope to inform a more sustainable future for solar energy.

# ACKNOWLEDGMENTS

First and foremost, I want to thank my parents for always supporting whatever I chose to do with my life. It's been quite the ride, but you've had my back the entire way. To Jen, the cooler Sturchio kid, I couldn't ask for a better sister. Thank you to the awesome group of friends Nikki and I have made in Fort Collins. This town has become a very special place for us and that is due in great part, to you all. The Graduate Degree Program in Ecology at Colorado State University for providing a huge group of built in friends and future colleagues. I never take for granted how influential joining this community of collaborative, smart, and thoughtful individuals has been on my career. Thank you to the members of my graduate committee, Troy Ocheltree, Nathan Mueller, and Meagan Schipanski, for sharing insight and new perspectives.

I should thank Mendy for forcing Alan to take that first meeting with me when I was a prospective student. It ended up working out pretty well! Alan, thank you for allowing me to pursue interesting questions and for helping me craft ideas into experiments. Thank you for pursuing Ecovoltaics even when your careers work has already been highly influential to the field of grassland ecology. You've provided a blueprint for how to run a lab where people feel included, motivated, and supported, all at the same time. To members of the Knapp Lab, past, present, and future, it has been an honor to collaborate and learn from you all. Undergraduate researchers Kellie, Tillie, Ben, and Colby, this work could not have been done without you, thank you. One of the great privileges of being a grad student is working with motivated undergraduates and watching them grow in all facets of life.

This work was funded by the US Department of Agriculture's National Institute of Food and Agriculture (NIFA) through the Sustainable Agricultural Systems project entitled

“Sustainably Co-locating Agricultural and Photovoltaic Electricity Systems (SCAPES),” led by the University of Illinois Urbana-Champaign, Grant Number: 2021-68012-35898, 2021–2025. Thank you also to the InSPIRE project funded through the US DOE Office of Energy Efficiency and Renewable Energy (EERE) Solar Energy Technologies Office under award DE-EE00034165. I would also like to acknowledge funding received through the Stavros Family Fund for Biological Research at CSU, the department of biology travel grants, and the GDPE small research and travel grants.

Finally, to my wife, thank you to my wife. Your unconditional love and support made grad school a lot less stressful than it could have been. Hendrix, first of his name, I appreciate our morning walks, even when you pull.

# TABLE OF CONTENTS

# CHAPTER 1: INTRODUCTION

The elimination of fossil fuel related emissions is the most effective strategy for reducing the future impacts of climate warming (Lee et al. 2023). As such, the development of renewable energy projects (e.g., solar, wind, hydro, geothermal, nuclear), which have tremendous materials acquisition, emission, and waste benefits compared to their fossil fuel counterparts (Fthenakis and Kim 2009, Miller et al. 2019, Mirletz et al. 2023), will be needed to meet energy needs. Of all renewable forms of energy, photovoltaics (i.e., PV) are considered to have the greatest potential to reduce global emissions over the next decade (i.e., PV, Lee et al. 2023). This is due in great part to the combined effects of a precipitous drop in PV energy cost (Feldman et al. 2021) and policies aimed at transitioning energy grids to renewable sources (von Loesecke & Chermak 2023). Indeed, PV has emerged as the leading form of renewable energy globally, resulting in a dramatic increase in the number of ground-mounted solar arrays. For example, in the United States, the combination of PV and battery storage is set to account for approximately 80% of all new utility-scale electricity-generating capacity installed in 2024 (US EIA 2023).

Although ground mounted PV energy infrastructure is a tremendous step forward for sustainable energy production, the spatial footprint is substantially (~20x, van Zalk and Behrens 2018) larger than that of a fossil fuel power plant. In addition, utility scale PV projects are often sited in croplands, grasslands, and arid rangelands because of their limited topography and exposure to high light conditions (Adeh et al. 2019). This approach causes tension with farmers, landowners, and community members, especially when energy production is prioritized at the expense of the underlying ecosystem. An agrivoltaic (i.e., AV) approach, where PV energy and agriculture (e.g., crops, grazing, agriculturally important pollinator habitat) are co-located on the same piece of land, supports moderate ecosystem functionality through agricultural management. This approach has been shown to improve the acceptance of PV projects in rural communities (Pascaris et al. 2022), however very few experiments have evaluated how diverse forms of AV might be implemented at scale. To understand the potential tradeoffs and benefits for agricultural land uses like crop production, grazing, and pollinator habitat, more research must be done.

In the United States, over 99% of the land occupied by agrivoltaic facilities are co-located on land managed for grazing or pollinator habitat (Inspire AV Map). These sites are ideal for AV co-location because, unlike croplands, they do not require irrigation or the use of large machinery. Because these lands rely on rainfall to support plant growth, the way that solar panels re-distribute precipitation to distinct microsites beneath them plays an important role in controlling patterns of soil moisture. At present, all grassland AV arrays use sun-tracking programs that maximize energy production by following the sun east to west across the sky. As this happens, PV panels concentrate rainfall at panel edges and restrict rainfall from microsites directly beneath panels. In grassland ecosystems known for their short-statured vegetation and relatively homogenous environmental conditions (e.g., rainfall and sunlight), PV panels introduce spatial and temporal heterogeneity through the redistribution of precipitation events and patterns of dynamic shade from panels.

In the water limited semi-arid grasslands of Colorado, the consequences of such environmental heterogeneity are unknown. Many foundational studies have determined that precipitation and soil moisture are great predictors of grassland productivity across space and over time (Sala et al. 1988, Lauenroth and Sala 1992, Heisler-White et al. 2008). Meanwhile, newer research has indicated that atmospheric demand for water will be an increasingly important factor regulating arid and semi-arid ecosystem health as global temperatures continue to rise (Novick et al. 2016, Konings et al. 2017, Novick et al. 2024). The microenvironmental conditions within a PV array are unique in that they host a number of distinct environmental conditions in a small spatial area, usually less than 1m$^2$. Apart from the redistribution of water, these grassland ecosystems are also characterized by high light conditions. Little research has been done to quantify how these plants, which are adapted to high light conditions, will respond to significant reductions in light availability. Another topic of particular interest is how the timing of such light availability (i.e., morning vs. afternoon) will alter plant physiological response, and ultimately aboveground productivity.

It has long been known that environmental heterogeneity, including spatial and temporal variability in resource availability, is an important determinant of ecosystem structure and function, and that this heterogeneity translates to biotic diversity and variability in ecological processes (e.g., Ricklefs 1977, Scheiner and Willig 2008). The application of this principle has been successful in the field of restoration ecology, where recent studies have demonstrated that increasing soil heterogeneity in restored fields can increase plant diversity compared to communities restored on homogeneous soils (Scott & Baer et al. 2019, Baer et al. 2020). Environmental heterogeneity has also been proposed as a means for overcoming biotic homogenization, and thus improving resilience to climate extremes such as droughts and heat waves (Holl et al. 2022).

Although PV panels create environmental heterogeneity and environmental heterogeneity is regarded as an important promoter of biodiversity, PV energy facilities are rarely designed, constructed, and managed to leverage these abiotic patterns to restore degraded lands. Many PV sites located in sensitive or degraded ecosystems could benefit from a throatful and ecologically informed perspective that evaluates the ecological consequences of altering environmental conditions. A new approach to PV development is needed to ensure a sustainable energy future.

In the following chapters I will discuss how the unique microenvironments created by PV arrays alter the productivity, physiological response, and forage quality of a semi-arid grassland in Colorado. I will also outline a new approach to PV development, Ecovoltaics, that is informed by several fundamental ecological concepts. Through this work, I hope to inform a more sustainable future for solar energy.

# LITERATURE CITED

Baer, S.G., Adams, T., Scott, D.A., Blair, J.M. and Collins, S.L. (2020). Soil heterogeneity increases plant diversity after 20 years of manipulation during grassland restoration. Ecological Applications, 30(1), p.e02014.

Feldman, D., Ramasamy, V., Fu, R., Ramdas, A., Desai, J., & Margolis, R. (2021). US solar photovoltaic system and energy storage cost benchmark (Q1 2020) (No. NREL/TP-6A20-77324). National Renewable Energy Lab. (NREL), Golden, CO (United States).

Fthenakis, V., & Kim, H. C. (2009). Land use and electricity generation: A life-cycle analysis. Renewable and Sustainable Energy Reviews, 13(6-7), 1465-1474.

Heisler-White, J. L., Knapp, A. K., & Kelly, E. F. (2008). Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia, 158, 129-140.

Holl, K. D., Luong, J. C., & Brancalion, P. H. (2022). Overcoming biotic homogenization in ecological restoration. Trends in Ecology & Evolution, 37(9), 777-788.

Konings, A. G., Williams, A. P., & Gentine, P. (2017). Sensitivity of grassland productivity to aridity controlled by stomatal and xylem regulation. Nature Geoscience, 10(4), 284-288.

Lauenroth, W. K., & Sala, O. E. (1992). Long-term forage production of North American shortgrass steppe. Ecological applications, 2(4), 397-403.

Lee, H., Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P., ... & Park, Y. (2023). IPCC, 2023: Climate Change 2023: Synthesis Report, Summary for Policymakers. 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.

Mirletz, H., Hieslmair, H., Ovaitt, S., Curtis, T. L., & Barnes, T. M. (2023). Unfounded concerns about photovoltaic module toxicity and waste are slowing decarbonization. Nature Physics, 19(10), 1376-1378.

Miller, I., Gençer, E., Vogelbaum, H. S., Brown, P. R., Torkamani, S., & O'Sullivan, F. M. (2019). Parametric modeling of life cycle greenhouse gas emissions from photovoltaic power. Applied energy, 238, 760-774.

Novick, K. A., Ficklin, D. L., Stoy, P. C., Williams, C. A., Bohrer, G., Oishi, A. C., ... & Phillips, R. P. (2016). The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. Nature climate change, 6(11), 1023-1027.

Novick, K. A., Ficklin, D. L., Grossiord, C., Konings, A. G., Martínez-Vilalta, J., Sadok, W., … & McDowell, N. G. (2024). The impacts of rising vapor pressure deficit in natural and managed ecosystems. Plant, Cell & Environment.

Pascaris, A. S., Schelly, C., Rouleau, M., & Pearce, J. M. (2022). Do agrivoltaics improve public support for solar? A survey on perceptions, preferences, and priorities. Green Technology, Resilience, and Sustainability, 2(1), 8.

Ricklefs, R.E., (1977). Environmental heterogeneity and plant species diversity: a hypothesis. *The American Naturalist*, 111(978), pp.376-381.

Sala, O. E., Parton, W. J., Joyce, L. A., & Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. Ecology, 69(1), 40-45.

Scheiner, S.M. and Willig, M.R., (2008). A general theory of ecology. *Theoretical ecology*, *1*(1), pp.21-28.

Scott, D.A. and Baer, S.G., (2019). Diversity patterns from sequentially restored grasslands support the 'environmental heterogeneity hypotheses. Oikos, 128(8), pp.1116-1122.

U.S. Energy Information Administration, Preliminary Monthly Electric Generator Inventory, Visited December 2023. https://www.eia.gov/todayinenergy/detail.php?id=61424

Van Zalk, J., & Behrens, P. (2018). The spatial extent of renewable and non-renewable power generation: A review and meta-analysis of power densities and their application in the US. Energy Policy, 123, 83-91.

von Loesecke, E., & Chermak, C. (2023). The Inflation Reduction Act: Impacts on Utilities and Power Producers. Climate and Energy, 39(7), 1-10.

# CHAPTER 2: GRASSLAND PRODUCTIVITY RESPONDS UNEXPECTEDLY TO DYNAMIC LIGHT AND SOIL WATER ENVIRONMENTS INDUCED BY PHOTOVOLTAIC ARRAYS[1]

## 2.1 Summary

Agrivoltaic systems (AVs) are designed to co-produce renewable photovoltaic (PV) energy on lands simultaneously supporting agriculture (food/forage production). PV infrastructure in agroecosystems alters resources critical for plant growth, and water-limited agroecosystems such as grasslands are likely to be particularly sensitive to the unique spatial and temporal patterns of incident sunlight and soil water inherent within AV systems. However, the impact of resource alteration on forage production, the primary ecosystem service from managed grasslands, is poorly resolved. Here, we evaluated seasonal patterns of soil moisture (SM) and diurnal variation in incident sunlight (PPFD, photosynthetic photon flux density) in a single-axis tracking AV system established in a formerly managed semi-arid $C_3$ grassland in Colorado. Our goals were to (1) quantify dynamic patterns of PPFD and SM within a 1.2 MW PV array in a perennial grassland, and (2) determine how aboveground net primary production (ANPP) and photosynthetic parameters responded to the resource patterns created by the PV array. We hypothesized that spatial variability in ANPP would be strongly related to SM patterns, typical of most grasslands. We measured significant reductions in ANPP directly beneath PV panels, where SM and PPFD were both low. However, in locations with significantly increased SM from the shedding and redistribution of precipitation by PV panels, ANPP was not increased. Instead, ANPP was greatest in locations where plants were shaded in the afternoon but received high

---

[1] Sturchio, M. A., Macknick, J. E., Barron-Gafford, G. A., Chen, A., Alderfer, C., Condon, K., ... & Knapp, A. K. (2022). Grassland productivity responds unexpectedly to dynamic light and soil water environments induced by photovoltaic arrays. *Ecosphere*, 13(12), e4334.

levels of PPFD in the morning hours, when air temperatures and vapor pressure deficits were relatively low. Thus, contrary to expectations, we found relatively weak relationships between SM and ANPP despite significant spatial variability in both. Further, there was little evidence that light saturated photosynthesis ($A_{sat}$) and quantum yield of $CO_2$ assimilation ($\phi CO_2$) differed for plants growing directly beneath (lowest PPFD) vs. between (highest PPFD) PV panels. Overall, the AV system established in this semi-arid managed grassland did not alter patterns of ANPP in ways predictable from past studies of controls of ANPP in open grasslands. However, our results suggest that the diurnal timing of low vs. high periods of PPFD incident on plants is an important determinant of productivity patterns in grassland AV systems.

## 2.2 Introduction

The carbon emissions advantages of renewable solar-generated electricity for meeting global energy demands are well-known (Tsoutsos et al. 2005, Edenhofer et al. 2011, Bevan et al. 2012, Burkhardt et al. 2012, Raturi 2019). However, infrastructure for photovoltaic (PV) energy generation is land-use intensive (Hernandez et al. 2014, 2015, Trainor et al. 2016), and the climatic regions best suited for PV panel efficiency overlap strongly with land used for food and forage production (Adeh et al. 2019). Competing demands for land devoted to energy generation vs. food and forage production can be alleviated by co-locating solar infrastructure and agriculture (Goetzberger and Zastrow 1982, Dupraz et al. 2011, Macknick et al. 2013, Ravi et al. 2016) with potential benefits and trade-offs associated with such “agrivoltaic” systems now emerging (Barron-Gafford et al. 2019, Maia et al. 2020, Pascaris et al. 2020).

Semi-arid regions cover ~15 % of the Earth’s land surface (Huang et al. 2016), and the managed grasslands (planted and native) common in these sunny climates are particularly attractive for potential agrivoltaic use, in part, because these lands have lower agricultural value compared to more humid productive regions. Further, the current use of these expansive ecosystems for forage production may be more compatible with the co-location of PV arrays than intensively managed row-crop agricultural systems. Indeed, the presence of PV panels may even provide a valuable shade resource for livestock when radiant heat loads are high (Maia et al. 2020).

Grassland productivity, particularly in semi-arid ecosystems, is strongly limited by precipitation inputs (Sala and Lauenroth 1982, Sala et al. 1988, Gherardi and Sala 2019), and this is true of managed pastures as well (Karn et al. 1999, Smeal et al. 2005). In contrast, only the most productive grasslands (those with high leaf area or with significant standing dead biomass) are likely to be limited by light availability (Knapp and Seastedt 1986, Knapp et al. 1993, Borer et al. 2014). It has been well-documented that PV panels deployed in grasslands alter patterns and amounts of sunlight incident on plant canopies (Armstrong et al. 2016, Valle et al. 2017, Weselek et al. 2019). However, patterns of soil moisture beneath and between rows of PV panels are also altered because PV panels not only intercept and redistribute precipitation inputs, but also the shade cast by PV panels can significantly modify spatial patterns of evapotranspiration (ET; Armstrong et al. 2014, Valle et al. 2017, Weselek et al 2019) throughout a day. The net effects of altered precipitation and ET on soil moisture patterns within PV arrays can vary dramatically - with reports of reduced as well as increased soil moisture levels directly beneath vs. between PV panels (Adeh et al. 2018, Andrew et al. 2021, Graham et al. 2021, Weselek et al. 2021a, 2021b). Further, the potential exists for enhanced levels of soil water to occur along PV panel driplines due to interception and runoff of precipitation (Choi et al. 2020). Thus, the presence of PV arrays in semi-arid grasslands can be expected to shift these ecosystems from being characterized by relatively limited spatial variability in soil moisture and light availability to ecosystems with highly dynamic spatial and temporal patterns of these, and potentially other, resources.

To better understand how a key grassland ecosystem service, forage production (aboveground net primary production, ANPP), responds to the unique resource environment generated by PV arrays, we assessed seasonal patterns of soil moisture and diurnal variation in incident sunlight in a formerly managed semi-arid $C_3$ grassland in Colorado. Our goals were to (1) quantify dynamic patterns of light and soil water beneath a 1.2 MW PV array recently established in this perennial grassland, and (2) determine how ANPP responds to the spatial and temporal patterns of light and soil water induced by the PV array.

We expected that 1) spatial patterns of ANPP within the array would be more strongly related to soil moisture patterns than light, 2) ANPP would be lowest directly beneath PV panels (due to low light and potentially dry soils) and, 3) the photosynthetic physiology (light saturated photosynthesis and quantum yield of $CO_2$ assimilation) of grasses growing directly beneath PV panels would differ markedly from grasses growing in full sun between panels.

## 2.3 Methods

### 2.3.1 Study Site

Research was conducted at Jack's Solar Garden (JSG), an agrivoltaic learning and research facility (https://www.jackssolargarden.com/) near Longmont, CO (elevation 1508m, 40°07'18.9"N 105°07'49.9"W, Fig. A1.1). The climate is semi-arid with a mean annual temperature of 9.7 °C and 365 mm of precipitation annually (Colorado Climate Center http://ccc.atmos.colostate.edu/). Historically, the 1.5 ha site was managed for hay production, but active management (mowing) ended in 2019 when the PV array was installed. The grassland at JSG is dominated (>80% cover) by a perennial nonnative $C_3$ grass (*Bromus inermus*) with scattered individuals of *Dactylis glomerata* ($C_3$ Orchard grass), *Medicago sativa* (Alfalfa) and *Tragopogon dubius* ($C_3$ forb) interspersed.

Individual PV panels at JSG are 2m (east-west) × 1m (north-south) and are mounted in series on a single axis tracking system (tracking east-west, Fig. 2.1). When PV panels are parallel with the ground (at solar noon and overnight) there is ~3.2 m of interspace between the western edge of one row of panels and the eastern edge of the next row (Fig. 2.1, locations 5-11). A 5 m wide walkway separates the eastern half of the solar garden from the western half. Panels on the eastern half are mounted 1.8 m (6 ft) above the ground while panels on the western half are mounted 2.4 m (8 ft) above the ground.

### 2.3.2 Experimental Design

We established four 15.5 m transects perpendicular to the rows of PV panels within a portion of JSG that remains as undisturbed perennial grassland (Fig. A1.1). Two replicate transects, each comprised of 32 sampling points 0.5 m apart, were delineated in areas with either 1.8 m or 2.4 m tall PV rows (Fig. A1.1) and 128 plots were established. These transects partially spanned three PV rows, with the eastern most plots located underneath (Location 2, Fig. 1.1) the second panel in from a walkway or edge (Fig. A1.1). We named replicates after the cardinal direction they were oriented (North/South) and based on panel heights (N6, S6, N8, S8, numbers refer to feet above the ground, Fig. A1.1).

### 2.3.3 Environmental Measurements

Diurnal patterns of air temperature ($T_{\mathrm{air}}$) and relative humidity (RH%), as well as precipitation inputs and other standard meteorological data were continuously recorded at a meteorological station adjacent to JSG throughout the 2021 growing season (May-August).

As noted above, Photosynthetic Photon Flux Density (PPFD) varies quite predictably beneath PV arrays and has been quantified and successfully modelled in the past (Marrou et al. 2013a, Amaducci et al. 2018). Nonetheless, to confirm patterns specific to JSG, PPFD was measured under full sun conditions on a mostly cloud-free day (August 5th) with an AccuPAR LP-80 Ceptometer (Decagon Devices, Pullman, WA). PPFD measurements were recorded above grass canopy height (~1 m from soil surface) for each plot, at three key times of day: three hours before solar noon (10am), at solar noon (1pm), and three hours after solar noon (4pm) to quantify how light availability changed throughout the day under this single-axis-tracking PV system. Soil moisture (SM) responses to PV arrays are much less predictable and thus we focused more on quantifying spatial and temporal (seasonal) patterns of SM at JSG. We measured SM (volumetric soil water content from 0-20 cm) at all plots at 4–8-day intervals between May 3rd and August 30th using a HydroSense II Handheld Soil Moisture Sensor (Campbell Scientific, Logan, UT). Measurements were made during morning hours, typically between 07:00 and 10:00 hours local time (US Mountain Time zone). This sampling scheme resulted in 1920 measurements of SM recorded at JSG in 2021.

### 2.3.4 Measuring and Modeling Light Response of Photosynthesis

Plants directly beneath PV panels (between location 2 and 3, Fig. 2.1) and plants in the middle of the interspace between panels (location 8) were used to assess differences in light saturated photosynthesis ($A_{\mathrm{sat}}$) and the quantum yield of $CO_2$ assimilation ($\phi CO_2$) in *B. inermis*. Measurements were replicated (n=4) beneath and between both 1.8 and 2.4 m tall PV panels. Light responses of leaf-level photosynthesis were measured before peak inflorescence on July 27th and 28th using a portable photosynthesis system (LI-6400, LiCor., Inc., Lincoln NE, USA). The LI-6400 was fitted with a 3×2 cm cuvette head and a red-blue LED light source. For all measurements, flow rate was held constant at 600 μmol s-1. The LI-6400 temperature exchanger was set to 30 °C (approximate midday temperature for both dates), which resulted in an average leaf temperature ($T_{\text{leaf}}$) of 30.8 ± 1.7 °C (standard deviation) across all measurements. Chamber reference $CO_2$ was set to 410 μmol mol-1 and photosynthetic photon flux density (PPFD) was set to 1600 μmol m-2 s-1 before leaves were placed into the chamber. Once placed in the chamber, leaves typically reached steady state within 5-10 min, at which time a light response curve was initiated.

All measurements occurred between 10:00 and 14:00 local time and were made on recently mature, fully expanded, upper canopy leaves. One-sided surface area of leaves within the chamber was estimated by measuring leaf length and width. Light response curves were constructed by measuring A at 10 reference [PPFD] values in a descending fashion (2000, 1600, 1200, 800, 600, 400, 250, 200, 100, 50 μmol m-2 s-1, Fig. A1.2). Each light response curve was parameterized using a non-rectangular parabola (Marshall and Biscoe 1980) through least squared parameter estimation in R version 4.1.2 (R Core Team 2017). The model was fit using the photosynthesis package (Stinziano et al. 2021) to estimate light saturated net $CO_2$ assimilation rate ($A_{\text{sat}}$) and quantum yield of $CO_2$ assimilation ($\phi CO_2$).

### 2.3.5 Estimating ANPP

At the end of the growing season (September 19th, 2021), all plots were sampled for ANPP. For each plot, we harvested all biomass to ground level within 0.1-$m^2$ quadrats centered on the sampling point for soil moisture measurements. Because the site had been mowed in 2020, aboveground biomass accumulating in 2021 represented ANPP. While harvesting, biomass was sorted by functional group (grass vs. forb). Harvested biomass was dried at 60 °C for 72 hours before being weighed to the nearest 0.01 g.

### 2.3.6 Data Analysis

Our primary goal was to assess spatial patterns of soil moisture and PPFD and their relationship to ANPP. End of season biomass accumulation, a standard method for estimating ANPP in ungrazed grasslands (Fahey and Knapp 2007), is a single measure of seasonally cumulative processes. In contrast, we measured soil moisture as it varied seasonally and PPFD as it varied diurnally. Thus, we initially averaged soil moisture and PPFD measurements to single values to be consistent with ANPP estimates. A three-way analysis of variance (ANOVA) was then used to test the effects of plot location (L) (1,2,3…11), PV height (H) (1.8 m, 2.4 m), replicate (R), and their respective interactions (L × H, L × R, H× R, L × H × R) on mean growing season SM measurements ($n = 2762$) mean daily PPFD ($n = 128$) and end of season ANPP ($n = 128$).

A three-way ANOVA was used to test the effects of PV location (underneath PV vs. interspace between PV), PV height, replicate, and their respective interactions (Location x Height, Location x Replicate, Height x Replicate, Location x Height x Replicate) on photosynthetic parameters obtained from light response measurements ($A_{sat}$, $\phi CO_2$).

Finally, to assess overall relationships between abiotic factors and productivity, one-way ANOVA was used to relate SM and PPFD to ANPP across plot locations. Multiple linear regression was used to evaluate the interactive effect of SM and PPFD on patterns of productivity. In addition to mean growing season values, relationships between monthly SM values and ANPP were assessed to determine how SM in different seasons was related to patterns of productivity. All analyses were performed using R version 4.1.2 (R Core Team 2017).

## 2.4 Results

### 2.4.1 Environmental Context

In 2021 annual precipitation at the site was 10% higher than the long-term average (401 mm vs. 365 mm, respectively). Seasonally, the early growing season (April, May and June) was ~30% wetter than normal (192 mm in 2021 vs. 146 mm average), while the late growing season (July and August) received less rainfall than the long-term average (40 mm vs 66 mm, Colorado Climate Center http://ccc.atmos.colostate.edu/ ). Mean annual air temperatures were only slightly above the long-term average (10.6 °C vs. 9.7 °C).

### 2.4.2 Light

As expected, mean daily PPFD was significantly lower under PV panels compared to between panels with spatial patterns varying predictably among morning, solar noon and afternoon sampling periods (Fig. 2.2). Averaged across time of day and locations, PPFD levels were slightly lower within 1.8 vs 2.4 m PV arrays (1126 vs 1190 µmol m-2 s-1, respectively, Table 2.1), but the ecophysiological significance of this for C3 grasses is likely small.

### 2.4.3 PPFD Effects on Photosynthesis

The results of a three-way ANOVA indicated no significant differences between $A_{sat}$ or $\phi CO_2$ in *B. inermus* grown directly beneath or between PVs, across panel heights (1.8 and 2.4 m), across replicates, or their interactions (Fig. 2.3). Differences beneath and between panels were more pronounced for $A_{sat}$ in 1.8 m plots while differences in $\phi CO_2$ were similar across panel height.

### 2.4.4 Soil moisture

Spatial patterns of growing season SM were consistent across all replicate transects throughout the growing season. Along one transect (N8), we recorded consistently higher SM values (by ~4%) relative to the other transects, and this resulted in a significant panel Height and a Height × Replicate interaction effect (Table 2.1). The edaphic or other cause for this deviation in SM levels is unknown but importantly, it did not impact patterns or amounts of ANPP (Table 2.1). Averaged over the growing season, and particularly in the latter half of the growing season, SM was highest near the western edge of the PV panels (Fig. 2.4, locations 10-11; July Aug SM = 29.8%) relative to between PV panels (Fig. 2.4, locations 7-8; July-Aug SM = 26.5%). In contrast, SM directly beneath the PV panels (locations 2-3) was consistently low with growing season mean SM ~8% lower than along the western edge of PV panels (Fig. 2.4).

### 2.4.5 Productivity

There were no statistical differences between panel heights (Table 2.1) or in patterns of forb and grass production across locations (Fig. A1.3), therefore spatial patterns of productivity were analyzed as total ANPP (grass + forb) along all transects. Overall, there was significant spatial variation in aboveground productivity (Table 2.1) with ANPP at the eastern edge of PV panels (Fig. 2.5, Location 5) significantly higher (by ~33%) than at the western edge (Fig. 2.5, Location 11, 716.2 g m-$^{2}$ and 539.8 g m-$^{2}$, respectively). In contrast, ANPP directly beneath PV panels (Fig. 2.5, location 2 and 3 mean = 488.2 g m-$^{2}$) was reduced ($p<0.05$) by ~20% relative to those locations least impacted by PV panels, locations 8-9). Overall, the presence of the PV array and resultant variability in SM and PPFD resulted in ANPP varying by 254 g m-$^{2}$ (the difference between locations 5 and 2, Fig. 2.5) in this grassland. This magnitude of spatial variability is ~40% of the mean ANPP in locations least impacted by PV panels (locations 8-9).

### 2.4.6 Light and soil moisture relationships with ANPP

Results of separate one-way ANOVAs indicated that SM and PPFD were both significantly related to patterns of ANPP, but surprisingly neither explained >10% of the spatial variation in productivity (Fig. 2.6, panel a and b). Multiple regression analyses that included both SM and PPFD as predictors were not significant. We were also interested if spring (May and

June) soil moisture measurements were more strongly related to productivity than timepoints later in the growing season (July and August). We found weak relationships between ANPP and early growing season SM (Fig. 2.6, panel c and d), and no relationship between ANPP and late growing season SM (Fig. 2.6, panel e and f).

## 2.5 Discussion

The primary goal of our study was to assess how spatial variability in soil moisture (SM) and sunlight (PPFD), induced by the presence of a PV array in a managed grassland, affected aboveground plant productivity (ANPP) - a key ecosystem service (forage production) of semi-arid grasslands in the western US. In these water-limited grasslands, as well as in non-irrigated managed pastures, soil moisture (SM) responds directly to precipitation amounts and patterns (e.g., Hoover et al. 2021, Griffin-Nolan et al. 2021) and both precipitation inputs and SM are strongly related to ANPP (Sala et al. 1988, Knapp et al. 2002, La Pierre et al. 2016, Post and Knapp 2021). However, despite substantial variation in SM and PPFD (Fig. 2.2 and 2.4) within the PV arrays at JSG, spatial variation in ANPP, which was also substantial (~ 275 g m-$^2$ along the transects, Fig 2.5) was not strongly related to patterns of light and/or water availability (Fig. 2.6). Early season soil moisture was a better predictor of ANPP compared to growing season or late season SM, consistent with other grasslands in the region (Derner et al 2008, Parton et al. 2012, Chen et al. 2017), but overall, most variation in ANPP could not be attributed to water availability.

We did find that ANPP was significantly reduced directly under PV panels, where both light and SM were lowest (Fig. 2.6). But despite these much-reduced PPFD levels, $A_{\mathrm{sat}}$ and $\phi CO_2$ of *B. inermus* growing directly under PV panels did not differ significantly from plants receiving full sun between rows of PV panels (Fig. 2.3). Thus, of our initial predictions - that ANPP would be strongly related to soil moisture, that ANPP would be lowest directly beneath PV panels, and that the photosynthetic physiology of grasses growing beneath PV panels would differ markedly from grasses in full sun - only the substantial reduction in ANPP beneath panels was realized. Other studies have also reported reduced productivity in the low light environments directly beneath PV panels (Andrew et al. 2021), although this is not always the case. Indeed, some plant species are more productive in the partial shade provided by PV panels (Marrou et al. 2013b, Barron-Gafford et al. 2019, Graham et al. 2021). The beneficial effects of shading may be particularly important when soil moisture is higher beneath vs. between panels (Adeh et al. 2018). This was clearly not the case in the managed grassland we studied, however.

At JSG, soil moisture was significantly lower directly beneath PV panels, and we hypothesize that low water availability may be as important as low PPFD for reducing ANPP. Supporting this interpretation was the lack of large photosynthetic differences between grasses growing between vs. beneath PV panels (Fig. 2.3). Although there was a trend for grasses growing in the shade of PV panels to have reduced photosynthetic capacity relative to those between PV panels (Fig. 2.3), we expected to see clear evidence of physiological acclimation to this low light environment, consistent with past studies of sun vs. shade plants in forest understories (Boardman 1977, Anderson and Osmond 1987, Givnish 1988, Murchie and Horton 1997), as well as in productive grasslands (Knapp 1985, Knapp and Gilliam 1985). Specifically, we predicted that Asat would be reduced in grasses beneath PV panels whereas $\phi CO_2$ would be increased in shaded leaves (suggesting an increase in $\phi CO_2$, Walters 2005, Yamori et al. 2016). This lack of acclimation suggests that the PPFD levels beneath PV panels (~250 µmol m-2 s-1) remained above those needed to induce alterations in photosynthesis, at least in *B. inermis*.

Indeed, the low light levels in a forest understory (~2-10% of mean daily PPFD, Messier et al. 1998) tend to be much lower than PPFD available under PV panels (~25-30%).

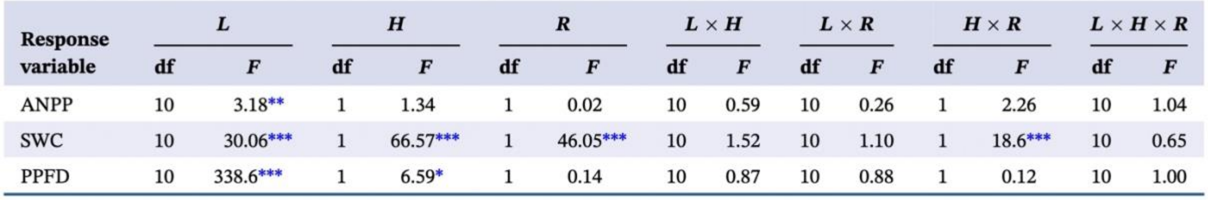
Understanding the drivers of maximum ANPP in this semiarid grassland PV array is more of a challenge. Consistent with previous studies (Choi et al. 2020), soil moisture was highest at the western drip edge of PV panels (Fig. 2.4 and 2.5) which can be attributed to the high proportion of summer precipitation occurring in the afternoon in Colorado (Taylor et al. 2012, Cioni and Hohenegger 2017, Welty et al. 2020) when PV panels face west. However, ANPP did not appear to respond to this increase in water availability. Instead, peak ANPP was consistently measured at the eastern edge of PV panels (Fig. 2.5). We consider two, non-exclusive explanations for this peak in ANPP. First, nighttime dew formation on PV panels oriented parallel to the ground can lead to inputs of moisture in the morning as panels reorient to face east (Schindler et al. 2016). These relatively small inputs of unknown frequency were not reflected in our SM measurements, perhaps because the temporal frequency of these measurements was too low. Nonetheless, shallow SM resources are known to be important in grasslands (Nippert and Knapp 2007) and dew inputs can positively affect carbon uptake and the water balance of plants in semi-arid ecosystems (Aguirre-Gutierrez et al. 2019, Liu et al. 2020). Thus, these small but consistent moisture inputs may be an important driver of patterns of productivity in AV systems. A second driver of increased ANPP near the eastern edges of PV panels is the unique diurnal timing of periods of high PPFD vs. PV shading. At this location with PV arrays, direct sunlight is received in the morning hours when $T_{\mathrm{air}}$ and VPD are both relatively low throughout the growing season (Fig. A1.4, A1.5), likely enhancing $A_{\mathrm{sat}}$ and water-use-efficiency in the dominant $C_3$ grass. In the afternoon, when $T_{\mathrm{air}}$ and VPD are much higher, these plants are shaded. The opposite diurnal pattern occurs at the western edge and may explain the lack of response of ANPP to increased SM here. There is evidence that grassland productivity can be controlled by VPD in addition to SM (Novick et al. 2016, Konings et al. 2017, Ding et al. 2018). Within PV arrays, unique interactions between the timing of light availability and environmental conditions may increase the importance of VPD as a determinant of productivity in dryland agrivoltaic systems. As such, future measurements throughout a diel period could assess how these concomitant spatiotemporal drivers of photosynthesis determine diel pattern of $A_{\mathrm{sat}}$ and daily cumulative $CO_2$ assimilation.

## 2.6 Conclusion

While Agrivoltaics have the potential to satisfy competing demands for land required for photovoltaic energy generation vs. land currently used to produce forage in semi-arid regions, understanding the ecological consequences of combining these land uses via Agrivoltaics should be a research priority (Barron-Gafford et al. 2019). Compared to more topographically complex ecosystems, spatial heterogeneity in the availability of key resources is generally considered to be relatively low in grasslands with similarly low heterogeneity in ecosystem processes. Here, in a managed grassland in Colorado, we quantified substantial spatial and temporal variation in light and water availability resulting from an Agrivoltaic land use. Over relatively short spatial scales (~10 m) light availability varied by up to 8-fold, and soil moisture by 30%, and aboveground plant productivity by ~40%. As a result, the expected primary determinant of forage production in this grassland, soil moisture, was replaced by more complex interactions among soil moisture, the time of day when light was available, and diurnal variation in air temperature and evaporative demand. Understanding how co-locating PV panels in grasslands can alter key resources, ecological interactions, and resulting ecosystem services should facilitate the design of new Agrovoltaic systems that can better balance renewable energy generation and agricultural productivity.

## 2.7 Tables

**Table 2.1** Results of three-way ANOVAs to assess how transect location, height of the PV panels and each replicate varied for ANPP (n=128), SWC (n=2762), and PPFD (n=384). F-values with “*,” “**” and “***” are significant at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively.



| Response variable | $L$ | | $H$ | | $R$ | | $L \times H$ | | $L \times R$ | | $H \times R$ | | $L \times H \times R$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **df** | ***F*** | **df** | ***F*** | **df** | ***F*** | **df** | ***F*** | **df** | ***F*** | **df** | ***F*** | **df** | ***F*** |
| ANPP | 10 | 3.18** | 1 | 1.34 | 1 | 0.02 | 10 | 0.59 | 10 | 0.26 | 1 | 2.26 | 10 | 1.04 |
| SWC | 10 | 30.06*** | 1 | 66.57*** | 1 | 46.05*** | 10 | 1.52 | 10 | 1.10 | 1 | 18.6*** | 10 | 0.65 |
| PPFD | 10 | 338.6*** | 1 | 6.59* | 1 | 0.14 | 10 | 0.87 | 10 | 0.88 | 1 | 0.12 | 10 | 1.00 |

## 2.8 Figures

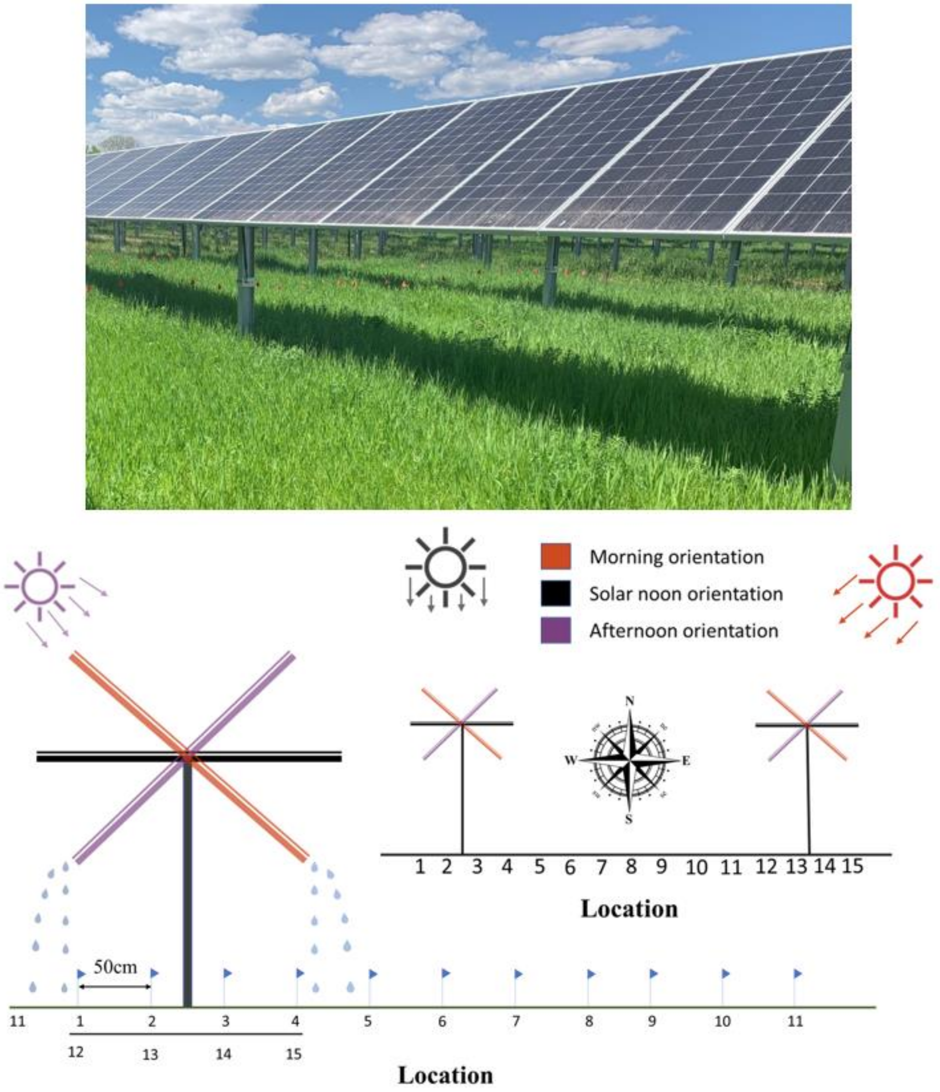


**Figure 2.1.** Top: Late spring view of a row of PV panels in the perennial $C_3$ grassland at Jack's Solar Garden. Bottom: Transects and sampling locations (numbers) in relationship to the locations of PV panels. Also shown are morning, noon, and afternoon location of the sun and the corresponding angle of solar panels (east facing, parallel with the ground, west facing – note color coding). Water drops show the approximate location of the eastern drip edge (between location 4 and 5) and the western drip edge (between locations 11 and 1) where rain would be shed in the morning and afternoon, respectively. Note that for data analyses, only true replicates of plot locations 1-11 were used, but to more clearly illustrate spatial patterns within the AV system, figures show two PV panels where data for locations 12-15 are identical to locations 1-4.

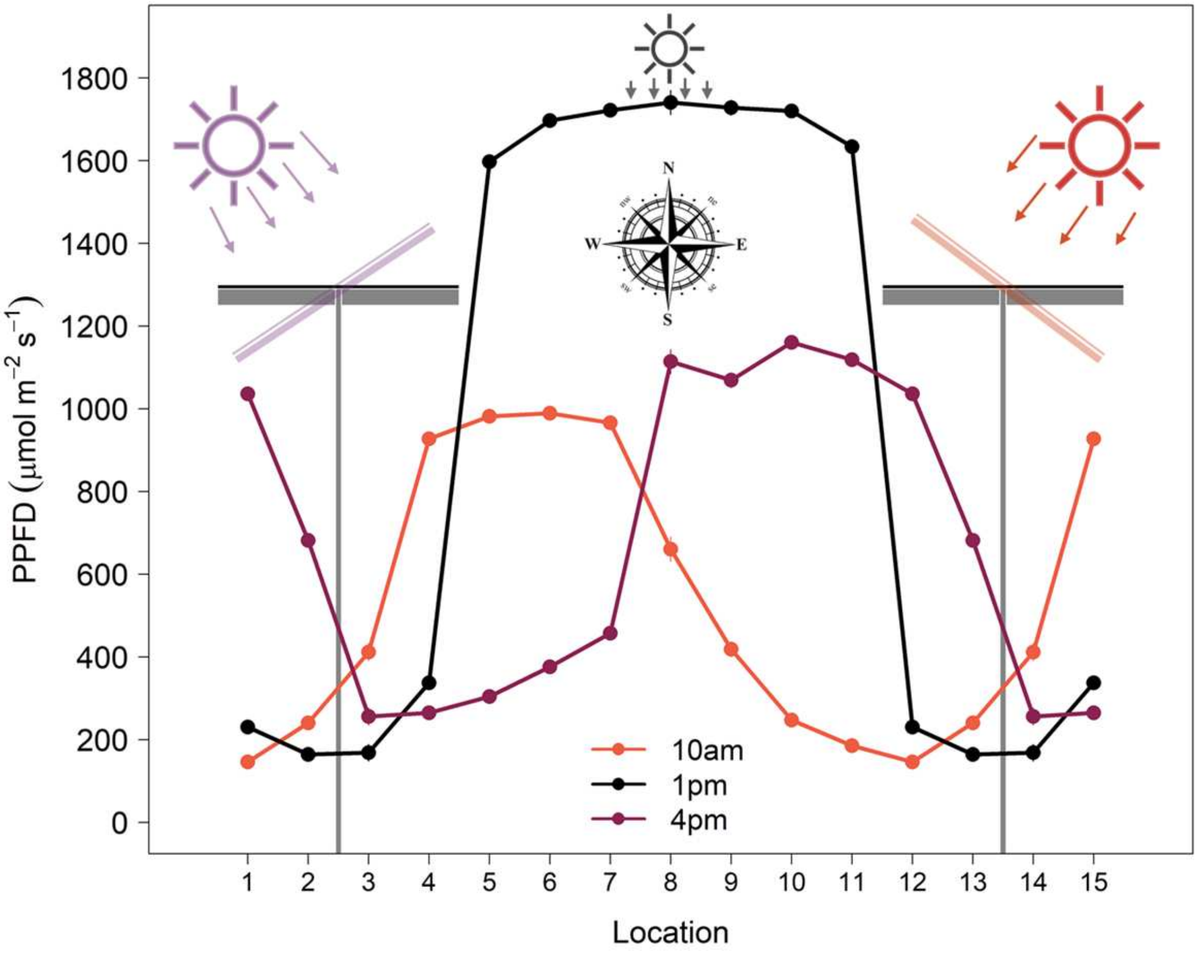


**Figure 2.2.** Mean photosynthetic photon flux density (PPFD) at 10am (orange line), solar noon or 1pm (black line), and 4pm (purple line) along a transect perpendicular to rows of PV panels. Because PV panels track diurnal movements of the sun, the three different panel orientations at the times of measurements are color coded to match PPFD data.

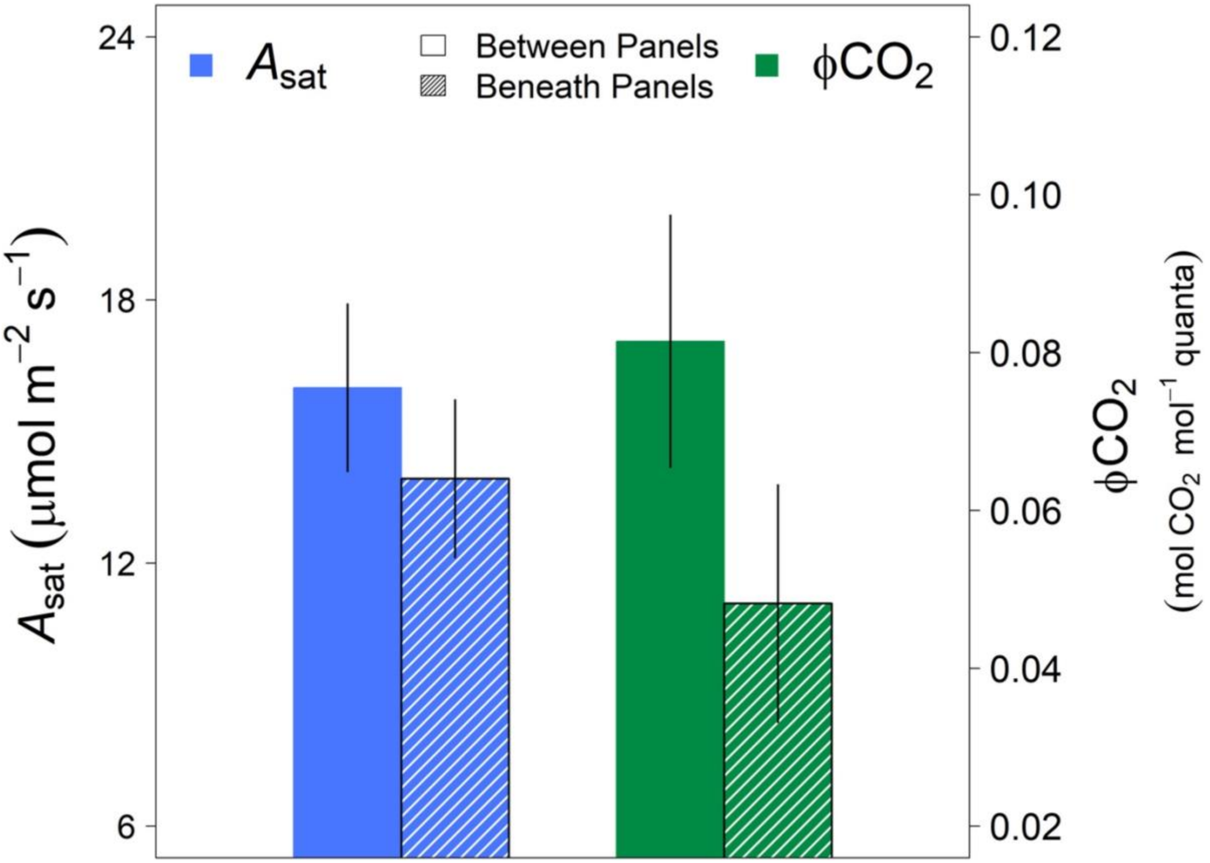


**Figure 2.3.** Results of a three-way ANOVA on photosynthetic light response measurements. Light saturated photosynthesis ($A_{sat}$), and quantum yield of $CO_2$ assimilation ($\phi CO_2$) beneath (hashed bars) and between (solid bars) PVs. Measurements were averaged (± standard error) across panel heights because differences were non-significant.

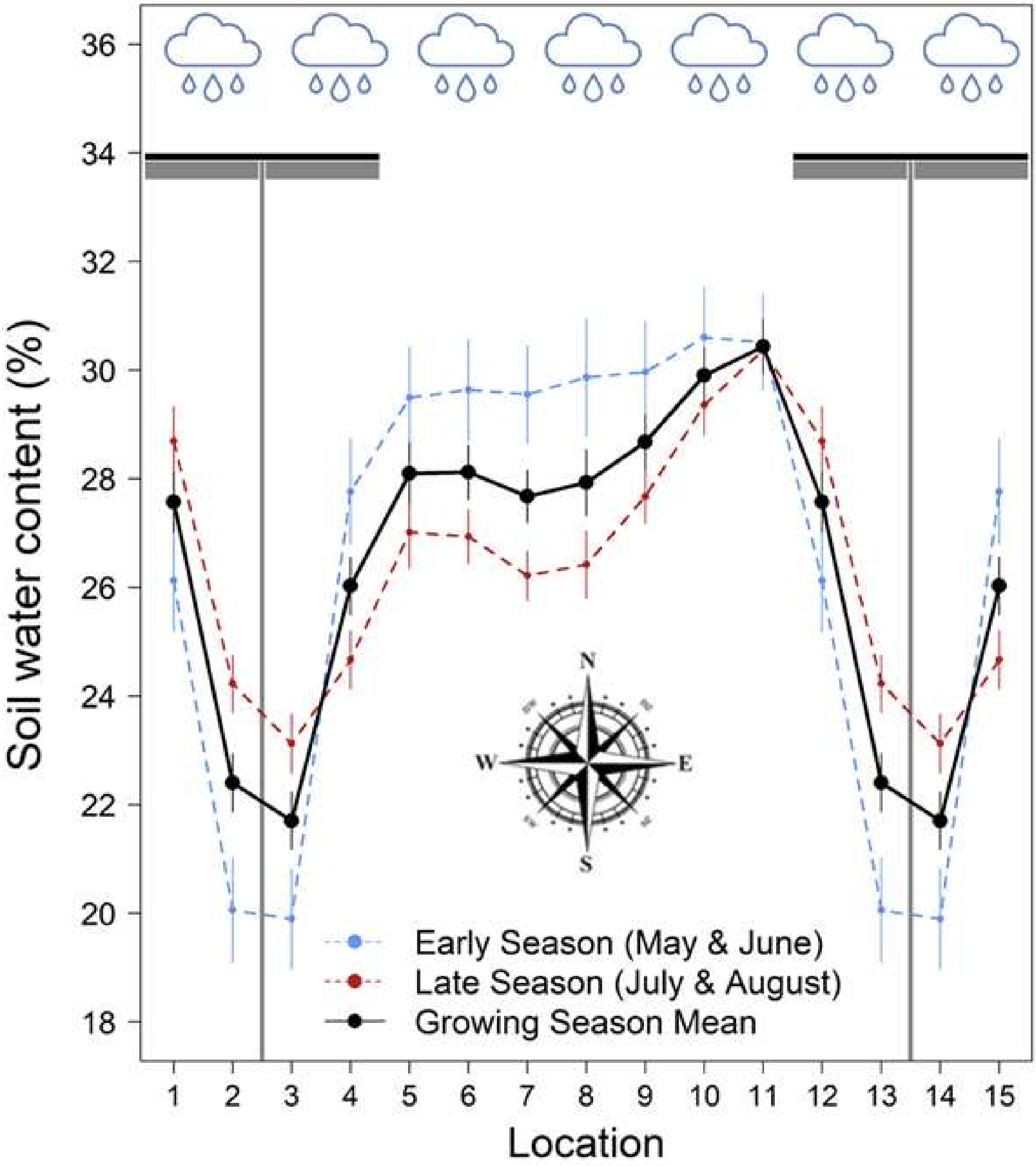


**Figure 2.4.** Spatial patters of early season (blue line) and late season (red line) soil water content (0-20 cm) along a transect perpendicular to rows of PV panels. Overall growing season average (± standard error) is represented by a solid black line. Note that most growing season rainfall occurs after solar noon in this region when PV panels are facing west (as indicated by the purple panel, Fig. 2.1).

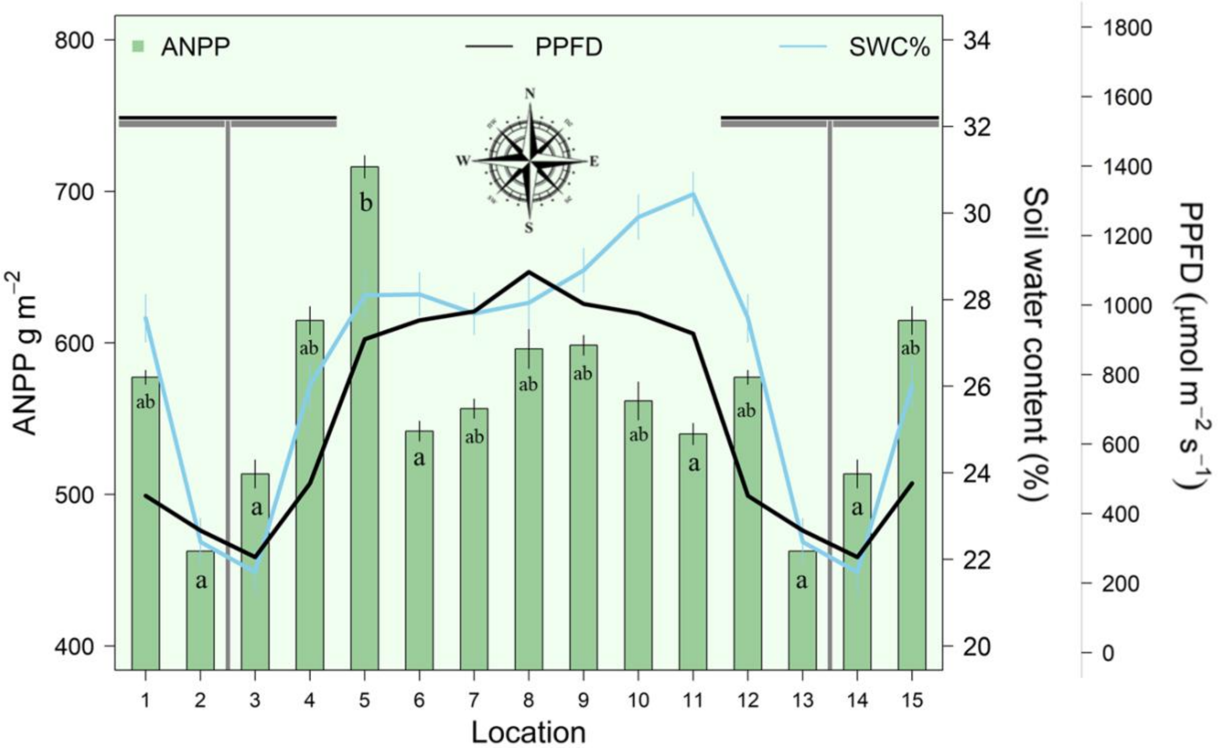


**Figure 2.5.** Spatial patterns of mean (± standard error) ANPP (green bars) along a transect perpendicular to rows of PV panels. The blue line represents mean (± standard error) growing season soil water content at each location. The black line represents mean daily PPFD at each location, presented to demonstrate light patterns simultaneously with SM% and ANPP. Letters a, ab, b, denote levels of significant differences in measurements of ANPP. Bars which share letters are not significantly different from each other.

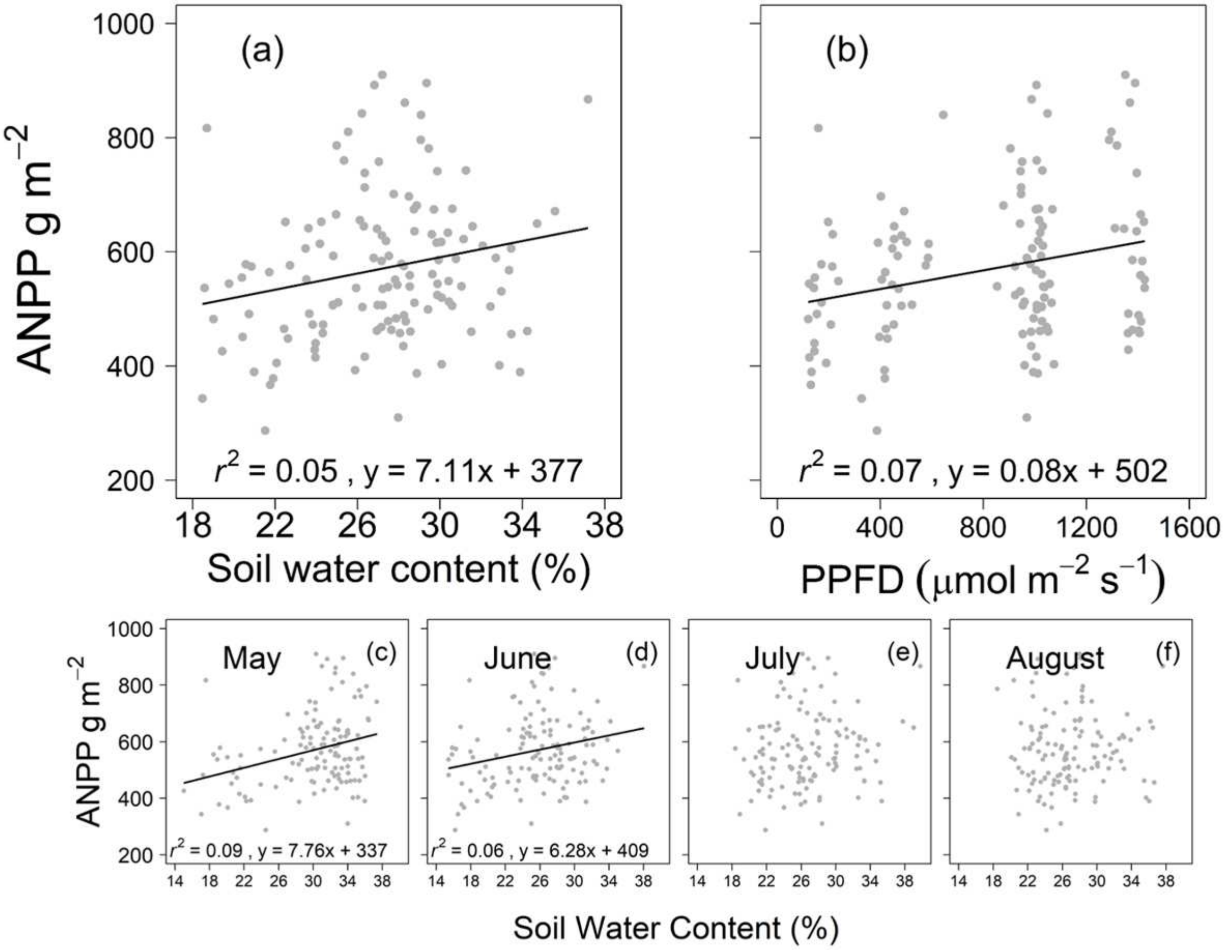


**Figure 2.6.** Plot level relationships (n=128) between ANPP, mean growing season soil moisture (panel a), PPFD (panel b), and monthly averages of SM% (panels c, d, e, f). Black solid lines signify a common relationship across transects. Slopes, intercepts, and r-squared values are displayed for all significant relationships.

# LITERATURE CITED

Adeh, E. H., Selker, J. S., & Higgins, C. W. (2018). Remarkable agrivoltaic influence on soil moisture, micrometeorology, and water-use efficiency. *PloS one*, *13*(11), e0203256.

Adeh, E. H., Good, S. P., Calaf, M., & Higgins, C. W. (2019). Solar PV power potential is greatest over croplands. *Scientific reports*, *9*(1), 1-6.

Aguirre-Gutiérrez, C.A., Holwerda, F., Goldsmith, G.R., Delgado, J., Yepez, E., Carbajal, N., Escoto-Rodríguez, M. and Arredondo, J.T. (2019). The importance of dew in the water balance of a continental semiarid grassland. Journal of Arid Environments, 168, pp.26-35.

Amaducci, S., Yin, X., & Colauzzi, M. (2018). Agrivoltaic systems to optimize land use for electric energy production. *Applied energy*, *220*, 545-561.

Anderson JM & Osmond CB. (1987). Sun-shade responses: compromises between acclimation And photoinhibition. In: Kyle DJ, Osmond CB, Arntzen CJ, eds. *Photoinhibition*. Amsterdam: Elsevier, 1–38.

Andrew, A. C., Higgins, C. W., Smallman, M. A., Graham, M., & Ates, S. (2021). Herbage yield, lamb growth and foraging behavior in agrivoltaic production system. *Frontiers in Sustainable Food Systems*, *5*, 126.

Armstrong A., Waldron S., Whitaker J., Ostle N.J. (2014). Wind farm and solar park effects on plant–soil carbon cycling: uncertain impacts of changes in ground-level microclimate *Glob. Change Biol.* **20** 1699–706

Armstrong, A., Ostle, N. J., & Whitaker, J. (2016). Solar-park microclimate and vegetation management effects on grassland carbon cycling. *Environmental Research Letters*, *11*(7), 074016.

Burkhardt III, J. J., Heath, G., & Cohen, E. (2012). Life cycle greenhouse gas emissions of trough and tower concentrating solar power electricity generation: Systematic review and harmonization. *Journal of Industrial Ecology*, *16*, S93-S109.

Barron-Gafford, G. A., Pavao-Zuckerman, M. A., Minor, R. L., Sutter, L. F., Barnett-Moreno, I., Blackett, D. T., ... & Macknick, J. E. (2019). Agrivoltaics provide mutual benefits across the food–energy–water nexus in drylands. *Nature Sustainability*, *2*(9), 848-855.

Bevan, G. (2012). Renewable energy and climate change. *Significance*, *9*(6), 8-12.

Boardman, N. T. (1977). Comparative photosynthesis of sun and shade plants. *Annual review of plant physiology*, *28*(1), 355-377.

Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., ... &

Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature,* 508(7497), 517-520.

Chen, M., Parton, W.J., Del Grosso, S.J., Hartman, M.D., Day, K.A., Tucker, C.J., Derner, J.D., Knapp, A.K., Smith, W.K., Ojima, D.S. and Gao, W. (2017). The signature of sea surface temperature anomalies on the dynamics of semiarid grassland productivity. *Ecosphere*, 8(12), p.e02069.

Choi, C. S., Cagle, A. E., Macknick, J., Bloom, D. E., Caplan, J. S., & Ravi, S. (2020). Effects of revegetation on soil physical and chemical properties in solar photovoltaic infrastructure. *Frontiers in Environmental Science*, 140.

Cioni, G., & Hohenegger, C. (2017). Effect of soil moisture on diurnal convection and precipitation in large-eddy simulations. *Journal of Hydrometeorology*, *18*(7), 1885-1903.

Derner, J. D., B. W. Hess, R. A. Olson, and G. E. Schuman. (2008). Functional group and species responses to precipitation in three semi-arid rangeland ecosystems. *Arid Land Research and Management* 22:81–92.

Ding, J., Yang, T., Zhao, Y., Liu, D., Wang, X., Yao, Y., ... & Piao, S. (2018). Increasingly important role of atmospheric aridity on Tibetan alpine grasslands. *Geophysical Research Letters*, *45*(6), 2852-2859.

Dupraz C., Marrou H., Talbot G., Dufour L., Nogier A., Ferard Y. (2011). Combining solar photovoltaic panels and food crops for optimising land use: towards new agrivoltaic schemes. *Renewable Energy* 36:2725–2732. https://doi.org/10.1016/j.renene.2011.03.005

Edenhofer, O. et al. *Renewable energy sources and climate change mitigation: Special report of the Intergovernmental Panel on Climate Change* (Cambridge University Press, 2011).

Fahey, T. J., & Knapp, A. K. (Eds.). (2007). Principles and standards for measuring primary production. Oxford University Press.

Gherardi, L. A., & Sala, O. E. (2019). Effect of interannual precipitation variability on dryland productivity: A global synthesis. *Global Change Biology*, *25*(1), 269-276.

Givnish, T. J. (1988). Adaptation to sun and shade: a whole-plant perspective. *Functional Plant Biology*, *15*(2), 63-92.

Goetzberger A., Zastrow A. (1982). On the coexistence of solar-energy conversion and plant cultivation. *Int J Solar Energy* 1:55–69. https://doi.org/10.1080/01425918208909875

Graham, M., Ates, S., Melathopoulos, A. P., Moldenke, A. R., DeBano, S. J., Best, L. R., & Higgins, C. W. (2021). Partial shading by solar panels delays bloom, increases floral abundance during the late-season for pollinators in a dryland, agrivoltaic ecosystem. *Scientific reports*, *11*(1), 1-13.

Griffin-Nolan, R.J., Slette, I.J. and Knapp, A.K. (2021). Deconstructing precipitation variability: Rainfall event size and timing uniquely alter ecosystem dynamics. *Journal of Ecology*, 109(9), 3356-3369.

Hernandez, R. R., Easter, S. B., Murphy-Mariscal, M. L., Maestre, F. T., Tavassoli, M., Allen, E. B., ... & Allen, M. F. (2014). Environmental impacts of utility-scale solar energy. *Renewable and sustainable energy reviews*, *29*, 766-779.

Hernandez, R. R., Hoffacker, M. K., & Field, C. B. (2015). Efficient use of land to meet sustainable energy needs. *Nature Climate Change*, *5*(4), 353-358.

Hoover, D. L., W. K. Lauenroth, D. G. Milchunas, L. M. Porensky, D. J. Augustine, and J. D. Derner. (2021). Sensitivity of productivity to precipitation amount and pattern varies by topographic position in a semiarid grassland. *Ecosphere* 12(2):e03376. 10.1002/ecs2.3376

Huang, J., Ji, M., Xie, Y., Wang, S., He, Y. and Ran, J. (2016). Global semi-arid climate change over last 60 years. *Climate Dynamics*, 46(3-4), pp.1131-1150.

Karn, J.F., Ries, R.E. and Hofmann, L. (1999). Season-long grazing of seeded cool-season pastures in the Northern Great Plains.

Knapp, A.K. and Gilliam, F.S. (1985). Response of *Andropogon gerardii* (Poaceae) to fire-induced high vs. low irradiance environments in tallgrass prairie: leaf structure and photosynthetic pigments. *American Journal of Botany*, 72(11), pp.1668-1671.

Knapp, A.K., (1985). Effect of fire and drought on the ecophysiology of Andropogon gerardii and *Panicum virgatum* in a tallgrass prairie. *Ecology*, 66(4), pp.1309-1320.

Knapp, A.K. and Seastedt, T.R. (1986). Detritus accumulation limits productivity of tallgrass prairie. *BioScience*, 36(10), pp.662-668.

Knapp, A.K., Fahnestock, J.T., Hamburg, S.P., Statland, L.B., Seastedt, T.R. and Schimel, D.S. (1993). Landscape patterns in soil-plant water relations and primary production in tallgrass prairie. *Ecology*, 74(2), pp.549-560.

Knapp, A. K., Fay, P. A., Blair, J. M., Collins, S. L., Smith, M. D., Carlisle, J. D., ... & McCarron, J. K. (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, *298*(5601), 2202-2205.

Konings, A. G., & Gentine, P. (2017). Global variations in ecosystem-scale isohydricity. *Global change biology*, *23*(2), 891-905.

La Pierre, K. J., Blumenthal, D. M., Brown, C. S., Klein, J. A., & Smith, M. D. (2016). Drivers of variation in aboveground net primary productivity and plant community composition differ across a broad precipitation gradient. *Ecosystems*, *19*(3), 521-533.

Liu, M., Cen, Y., Wang, C., Gu, X., Bowler, P., Wu, D., Zhang, L., Jiang, G. and Beysens, D. (2020). Foliar uptake of dew in the sandy ecosystem of the Mongolia Plateau: A life-sustaining and carbon accumulation strategy shared differently by C3 and C4 grasses. *Agricultural and Forest Meteorology*, 287, p.107941.

Marrou, H., Guilioni, L., Dufour, L., Dupraz, C., & Wery, J. (2013a). Microclimate under agrivoltaic systems: Is crop growth rate affected in the partial shade of solar panels?. *Agricultural and Forest Meteorology*, *177*, 117-132.

Marrou, H., Dufour, L., & Wery, J. (2013b). How does a shelter of solar panels influence water flows in a soil–crop system? *European Journal of Agronomy*, *50*, 38-51.

Maia, A. S. C., de Andrade Culhari, E., Fonsêca, V. D. F. C., Milan, H. F. M., & Gebremedhin, K. G. (2020). Photovoltaic panels as shading resources for livestock. *Journal of Cleaner Production*, *258*, 120551.

Macknick, J., Beatty, B., & Hill, G. (2013). *Overview of opportunities for co-location of solar energy technologies and vegetation* (No. NREL/TP-6A20-60240). National Renewable Energy Lab. (NREL), Golden, CO (United States).

Marshall, B., & Briscoe, P. V. (1980). A model for C3 leaves describing the dependence of net photosynthesis on irradiance. *Journal Experimental Botany, 31*, 29–39.

Messier, C., Parent, S., & Bergeron, Y. (1998). Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *Journal of Vegetation Science*, *9*(4), 511-520.

Murchie E.H., Horton P. (1997). Acclimation of photosynthesis to irradiance and spectral quality in British plant species: chlorophyll content, photosynthetic capacity, and habitat preference. *Plant, Cell and Environment* 20, 438–448.

Nippert, J. B., & Knapp, A. K. (2007). Linking water uptake with rooting patterns in grassland species. *Oecologia*, *153*(2), 261-272.

Novick, K. A., Ficklin, D. L., Stoy, P. C., Williams, C. A., Bohrer, G., Oishi, A. C., ... & Phillips, R. P. (2016). The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. *Nature climate change*, *6*(11), 1023-1027.

Parton, W., Morgan, J., Smith, D., Del Grosso, S., Prihodko, L., LeCain, D., Kelly, R. and Lutz, S. (2012). Impact of precipitation dynamics on net ecosystem productivity. *Global Change Biology*, 18(3), pp.915-927.

Pascaris, A. S., Schelly, C., & Pearce, J. M. (2020). A first investigation of agriculture sector perspectives on the opportunities and barriers for agrivoltaics. *Agronomy*, *10*(12), 1885.

Post, A. K., & Knapp, A. K. (2021). How big is big enough? Surprising responses of a semiarid grassland to increasing deluge size. *Global Change Biology*, *27*(6), 1157-1169.

Ravi, S., Macknick, J., Lobell, D., Field, C., Ganesan, K., Jain, R., ... & Stoltenberg, B. (2016). Colocation opportunities for large solar infrastructures and agriculture in drylands. *Applied Energy*, *165*, 383-392.

Raturi, A. K. (2019). Renewables 2019 global status report.

Sala, O. E., & Lauenroth, W. K. (1982). Small rainfall events: an ecological role in semiarid regions. *Oecologia*, *53*(3), 301-304.

Sala, O. E., Parton, W. J., Joyce, L. A., & Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. *Ecology*, *69*(1), 40-45

Schindler, B. Y., Blank, L., Levy, S., Kadas, G., Pearlmutter, D., & Blaustein, L. (2016). Integration of photovoltaic panels and green roofs: review and predictions of effects on electricity production and plant communities. *Israel Journal of Ecology and Evolution*, *62*(1-2), 68-73.

Smeal, D., O'Neill, M.K. and Arnold, R.N., 2005. Forage production of cool season pasture grasses as related to irrigation. Agricultural water management, 76(3), pp.224-236.

Stinziano, J. R., Roback, C., Sargent, D., Murphy, B. K., Hudson, P. J., & Muir, C. D. (2021). Principles of resilient coding for plant ecophysiologists. *AoB Plants*, *13*(5), plab059.

Taylor, C. M., de Jeu, R. A., Guichard, F., Harris, P. P., & Dorigo, W. A. (2012). Afternoon rain more likely over drier soils. *Nature*, *489*(7416), 423-426.

Trainor, A. M., McDonald, R. I. & Fargione, J. Energy sprawl is the largest driver of land use change in United States. *PLoS ONE* **11**, 7896–7906 (2016).

Thieurmel, B., Elmarhraoui, A., & Thieurmel, M. B. (2019). Package "suncalc".

Tsoutsos, T., Frantzeskaki, N., & Gekas, V. (2005). Environmental impacts from the solar energy technologies. *Energy policy*, *33*(3), 289-296.

Valle, B., Simonneau, T., Sourd, F., Pechier, P., Hamard, P., Frisson, T., ... & Christophe, A. (2017). Increasing the total productivity of a land by combining mobile photovoltaic panels and food crops. *Applied energy*, *206*, 1495-1507.

Walters, R. G. (2005). Towards an understanding of photosynthetic acclimation. *Journal of experimental botany*, *56*(411), 435-447.

Welty, J., Stillman, S., Zeng, X., & Santanello Jr, J. (2020). Increased likelihood of appreciable afternoon rainfall over wetter or drier soils dependent upon atmospheric dynamic influence. *Geophysical Research Letters*, *47*(11), e2020GL087779.

Weselek, A., Ehmann, A., Zikeli, S., Lewandowski, I., Schindele, S., & Högy, P. (2019). Agrophotovoltaic systems: applications, challenges, and opportunities. A review. *Agronomy for Sustainable Development*, *39*(4), 1-20.

Weselek, A., Bauerle, A., Zikeli, S., Lewandowski, I., & Högy, P. (2021a). Effects on crop development, yields and chemical composition of celeriac (*Apium graveolens L. var. rapaceum*) cultivated underneath an agrivoltaic system. *Agronomy*, *11*(4), 733.

Weselek, A., Bauerle, A., Hartung, J., Zikeli, S., Lewandowski, I., & Högy, P. (2021b). Agrivoltaic system impacts on microclimate and yield of different crops within an organic crop rotation in a temperate climate. *Agronomy for Sustainable Development*, *41*(5), 1-15.

Yamori, W. (2016). Photosynthetic response to fluctuating environments and photoprotective strategies under abiotic stress. *Journal of Plant Research*, *129*(3), 379-395.

# CHAPTER 3: ECOVOLTAIC PRINCIPLES FOR A MORE SUSTAINABLE, ECOLOGICALLY INFORMED SOLAR ENERGY FUTURE[2]

## 3.1 Summary

The majority of power generated by photovoltaic energy infrastructure is derived from ground mounted solar arrays that prioritize energy production, minimize operating costs and, at best, accommodate limited ecosystem services. We argue that co-prioritizing ecosystem services and energy generation via an ecologically informed, Ecovoltaics approach to solar array design and operation will have multiple benefits for climate, biodiversity, and the restoration of degraded lands.

## 3.2 Introduction

Transitioning to renewable energy is key to a sustainable future for humanity, and of the available options, ground-mounted photovoltaic (PV) arrays have tremendous potential for reducing near-term net $CO_2$ emissions. Yet for solar power to supply electricity at a meaningful scale, PV infrastructure is estimated to require ~20x more land area than current fossil fuel infrastructure (van Zalk and Behrens 2018). This land use requirement is a serious challenge for solar proponents from economic, socio-political, and ecological perspectives, especially because ground mounted utility-scale solar facilities often prioritize energy production at the expense of ecosystem services (Hernandez et al. 2014). Here we argue that in many settings, PV arrays should be designed based on ecological principles in order to underpin a more sustainable energy future: an approach we term Ecovoltaics.

---

[2] Sturchio, M. A., & Knapp, A. K. (2023). Ecovoltaic principles for a more sustainable, ecologically informed solar energy future. Nature Ecology & Evolution, 1-4.

### 3.3 Alternatives to utility-based photovoltaic infrastructure

Utility-scale solar installations can vary widely in their impact on ecosystem services (Hernandez et al. 2019) with land grading and removal of vegetation beneath PV panels having the strongest and most obvious negative effects. As a mitigation strategy, Agrivoltaics (AV), the co-location of agriculture and energy production, has emerged as an increasingly popular way to maintain some level of ecosystem services (i.e., producing specialty crops or forage, or providing pollinator habitat) beneath PV arrays. Although there is some evidence for potential crop yield, water use, and energy production benefits from AV systems, particularly for crops grown beneath elevated panels (Barron-Gafford et al. 2019), most large (>10 MW) AV systems prioritize electricity generation and are designed based on utility-scale PV principles (e.g., generating the most electricity per unit land area). In other words, most AV systems are still designed for energy production and secondarily rely on management to facilitate additional ecosystem services (Fig. 3.1)

In contrast, Ecovoltaic approaches co-prioritize energy production and ecosystem services during both the design and management phases of PV arrays. Central to Ecovoltaics is an ecological understanding of the abiotic and biotic consequences of various arrangements of PV panels and their potential impact on ecosystems (Randle Boggis et al. 2020). With this knowledge, Ecovoltaic systems can be designed to facilitate a wide range of ecological processes, interactions, and outcomes.

In addition to contributing to a more sustainable energy future, Ecovoltaic approaches for solar energy generation would offer ecologists new opportunities to test the predictive value of key ecological principles. Indeed, restoration ecology has long been viewed as an “acid test” for ecological theory (Young et al. 2005). Designing photovoltaic (PV) arrays based on ecological theory represents a similar opportunity to apply, and ultimately test, foundational ecological principles while mitigating losses of ecosystem services as part of the global renewable energy transition.

### 3.4 How Ecovoltaics can enhance ecosystem services and promote biodiversity

PV panels generate significant small scale (~1m) environmental heterogeneity in sunlight, soil water, and temperature across space and over time (Armstrong et al. 2016) (Fig. 3.2). In particular, variability in light and the redistribution of precipitation shed from PV panels can strongly influence ecological processes below. For example, PV arrays have been shown to alter patterns of grassland plant productivity (Adeh et al. 2018, Sturchio et al. 2022), phenology (Graham et al. 2021), and nutrient content of the plants beneath arrays (Andrew et al. 2021). Furthermore, well-established ecological theory predicts that increasing environmental heterogeneity, including spatial and temporal variability in resources, can increase biodiversity and alter ecosystem functioning. Thus, Ecovoltaic designs would alter the spacing and operation of PV panels, based on ecological principles, to target specific habitat modifications and generate environmental heterogeneity as a tool to restore, maintain, and perhaps even enhance ecosystem services of the ecosystems beneath. In this way, Ecovoltaics could build on past ecosystem restoration research (Baer et al. 2003) that has assessed the value of increasing environmental heterogeneity as a means of increasing biodiversity (Baer et al. 2020). Further, because environmental heterogeneity has been proposed to improve resilience to climate extremes such as droughts and heat waves (Holl et al. 2022), Ecovoltaics approaches might assist in achieving climate change mitigation goals.

### 3.5 Land use opportunities

Ecovoltaic-induced environmental heterogeneity may be able to assist in the restoration of many degraded land cover types in need of remediation. Ecovoltaic arrays specifically targeted on these lands will not only allow for more rapid implementation of solar energy, but also provide alternatives to PV development in native ecosystems (Barron-Gafford et al. 2019). Below, we identify several land cover types as candidates for an Ecovoltaic approach.

Water-limited agroecosystems including rangelands (e.g., those in warm and dry environments where potential evapotranspiration meets or exceeds precipitation) are prone to over-utilization (e.g., poor grazing management, Bardgett et al. 2021) and may benefit the most from the strategic design of PV arrays (Ravi et al. 2016). These short-statured ecosystems are generally not light-limited and thus partial shading may have minimal impacts whereas reduced evaporative demand may be beneficial (Kannenberg et al. 2023). For example, in these grasslands, where both aridity and drought are predicted to become more severe, the concentration of rainfall via runoff from PV panels can emulate large rainfall events that play a disproportionately important role in controlling aridland ecosystem processes (Post and Knapp 2020) and may even partially rescue these ecosystems from drought (Hoover et al. 2022). As noted above, the structural complexity imparted by PV panels may also provide the habitat amelioration necessary for facilitating increased plant diversity at small spatial scales in these ecosystems.

Many lands with short-statured vegetation amenable for PV deployment are grazed by domestic livestock, but grazing is common in most grasslands. Broadly speaking, the homogenization of grazing lands (Fig. 3.2) can increase their sensitivity to climatic pressures (Fuhlendorf et al. 2012) and thus, there have been calls for increasing environmental heterogeneity in rangelands to promote diverse seedling establishment, enhance plant diversity and stabilize livestock production over time (Allred et al. 2014). The dynamic microenvironments within an Ecovoltaic array can help serve this purpose, increasing the diversity of forage species available to grazers, as well as enabling a wider range of plant phenological strategies to persist (Graham et al. 2021) with the potential to extend the growing/grazing season overall.

The role of the grazer is just as meaningful. In managed and unmanaged grasslands, domesticated and native grazers play an important role in determining plant community structure (Koerner et al. 2018), and in solar arrays there are potential reciprocal benefits of grazers for energy generation. Grazers can facilitate PV performance by reducing plant height which minimizes shade on panels, while shade from PV panels can reduce heat stress in large animals, positively influencing their physiology and well-being (Hernandez et al. 2019). There are, however, concerns about PV installations disrupting migratory movements of native ungulates (Sawyer et al. 2022). Designing arrays that are dispersed more widely, incorporate transit corridors, or include fencing that retain habitat connectivity could facilitate migratory movements of native ungulates (Moore-O'Leary et al. 2017).

Finally, severely degraded or abandoned agricultural lands are obvious candidates for an Ecovoltaic approach (Hernandez et al. 2019). Environmental heterogeneity imposed by Ecovoltaics could facilitate the recovery of diverse biotic communities that typically require decades to recover after abandonment and degradation. Indeed, biodiversity may require more than 80 years to recover after agricultural abandonment when compared to native undisturbed ecosystems (Ladouceur et al. 2023). This is particularly true for meters-scale spatial turnover of plant community dynamics (β-diversity), the scale at which PV panels increase environmental heterogeneity (Fig. 3.2). Both Europe and the US offer substantial amounts of abandoned agricultural land, ideal for the deployment of PV arrays designed and operated with an Ecovoltaic approach. Indeed, industrially degraded lands (i.e., brownfields, and retired mining lands) could similarly benefit from Ecovoltaic installations, where the concentration of resources might accelerate the establishment of plants used for phytoremediation (Fig. 3.2).

### 3.6 Ecovoltaic design options

PV arrays can themselves be somewhat diverse in their design, with clear differences in microclimatic consequences for the plants beneath. Fixed axis panel arrays provide deep shade for shade tolerant species and redistribute rainfall to a single panel edge, effectively concentrating this resource in consistent microsites. In contrast, single axis tracking arrays (i.e., where panels move east-west to track diurnal solar movements) provide more dynamic microenvironmental patterns (Sturchio et al. 2022). Here even plants directly beneath panels receive periods of direct sunlight daily (Kannenberg et al. 2023). In ecosystems where the dominant vegetation requires longer periods of full sunlight, panel rows can be spaced further apart to reduce the amount of shade on the landscape. Conversely, in systems where reduced water loss from evapotranspiration is the goal, Ecovoltaic designs that maximize shading at key times of the day could be more advantageous. Finally, panel angle is another parameter of Ecovoltaic interest because it has direct implications for the redistribution of precipitation. For example, designs that align panels perpendicular to the ground during rain events will result in very different soil moisture patterns than fixed or single axis tracking arrays.

### 3.7 Conclusion

We contend that ground-mounted solar arrays *designed and managed* based on ecological principles can provide a more sustainable approach to future PV energy expansion. The Ecovoltaics approach we describe above represents an extension of Agrivoltaics, which primarily relies upon agricultural management to provide limited ecosystem services beneath PV arrays designed for maximal energy generation. In contrast, we argue that a more ecologically informed design strategy should enhance ecosystem services much more than agrivoltaic approaches. Moreover, such designs can be deployed on a wide range of degraded land cover types. Ecovoltaics has the potential to be used as a restoration tool for such lands, to promote desired biotic communities and interactions that support ecosystem function as well as potentially improve resilience to climate extremes. Indeed, in particularly harsh ecosystems, Ecovoltaic designs could provide refuge from droughts and heatwaves, while the spatiotemporally dynamic microenvironments promote resource complementarity, niche differentiation, and habitat conservation that goes beyond the static protection of plant communities.

### 3.8 Figures

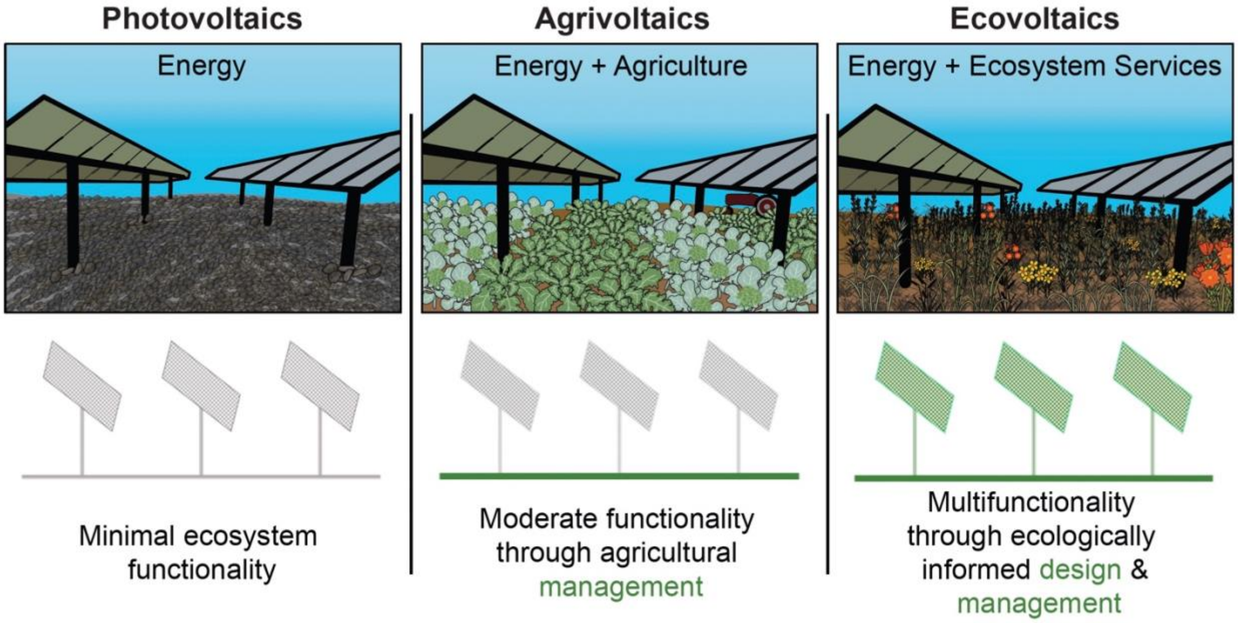


**Figure 3.1.** Solar array design and management goals. The vast majority of power generated by PV infrastructure globally is from utility-scale solar installations (https://www.seia.org/solar-industry-research-data) designed to maximize energy production per unit land area, while minimizing cost and maintenance. As a result, the ecosystems in which they are placed are often minimally valued, resulting in negative impacts to, or a total loss of, natural ecosystem integrity[3] (see left panel). Agrivoltaics (AV) allow for ecosystem functionality through agricultural management but are typically also energy-prioritized and thus use the same array designs as utility scale PV. Ecovoltaic approaches, are designed and managed to co-prioritize ecosystem services with energy generation, and thus could be targeted for lands that might benefit from the presence of PV panels (see text). Therefore, Ecovoltaics is both a grid level electricity solution for reaching emissions goals, and a land use solution that may support recovery of ecosystem services on degraded lands. At the bottom of this figure, green highlighting indicates that ecosystem services are being prioritized. For example, Ecovoltaic approaches prioritize ecosystem services during both the design and management phase of ground mounted solar installations.

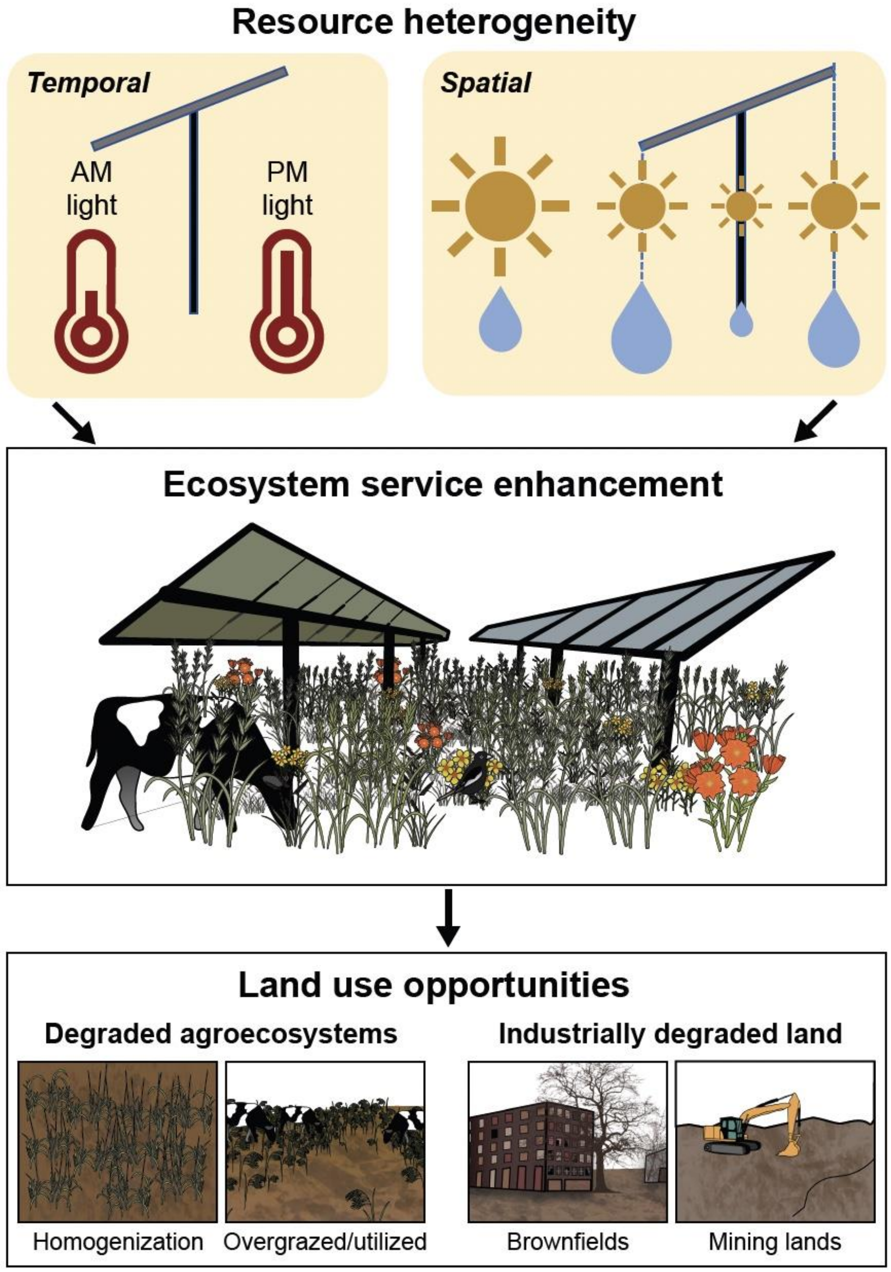


**Figure 3.2.** How ecosystem services and attributes in degraded agroecosystems, rangelands or other low statured ecosystems might be enhanced by an Ecovoltaic approach. Strategic deployment of PV panels can increase both spatial (sunlight and water, upper right) and temporal (sunlight and temperature, upper left) environmental and resource heterogeneity. Critically, cool-shaded, cool-wet, and warm- wet microsites can be created by PV panels in areas where environment homogeneity previously dominated. Size of icons in the top panels depict magnitude of a featured resource. Depicted in the lower panels is an example of how increased resource heterogeneity promotes ecosystem services, as well as potential land uses that might benefit from the physical presence of solar infrastructure.

# LITERATURE CITED

Adeh, E.H., Selker, J. S., & Higgins, C. W. (2018). Remarkable agrivoltaic influence on soil moisture, micrometeorology, and water-use efficiency. *PloS one*, 13(11), e0203256.

Allred, B. W., Scasta, J. D., Hovick, T. J., Fuhlendorf, S. D., & Hamilton, R. G. (2014). Spatial heterogeneity stabilizes livestock productivity in a changing climate. *Agriculture, ecosystems & environment*, 193, 37-41.

Andrew, A. C., Higgins, C. W., Smallman, M. A., Graham, M., & Ates, S. (2021). Herbage yield, lamb growth and foraging behavior in agrivoltaic production system. *Frontiers in Sustainable Food Systems*, 5, 659175.

Armstrong, A., Ostle, N.J. and Whitaker, J., (2016). Solar park microclimate and vegetation management effects on grassland carbon cycling. *Environmental Research Letters*, 11(7), p.074016.

Baer, S.G., Blair, J.M., Collins, S.L. and Knapp, A.K. (2003). Soil resources regulate productivity and diversity in newly established tallgrass prairie. *Ecology*, 84(3), pp.724-735.

Baer, S.G., Adams, T., Scott, D.A., Blair, J.M. and Collins, S.L. (2020). Soil heterogeneity increases plant diversity after 20 years of manipulation during grassland restoration. *Ecological Applications*, 30(1), p.e02014.

Bardgett, R. D., Bullock, J. M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., ... & Shi, H. (2021). Combating global grassland degradation. *Nature Reviews Earth & Environment*, *2*(10), 720-735.

Barron-Gafford, G. A., Pavao-Zuckerman, M. A., Minor, R. L., Sutter, L. F., Barnett-Moreno, I., Blackett, D. T., ... & Macknick, J. E. (2019). Agrivoltaics provide mutual benefits across the food–energy–water nexus in drylands. *Nature Sustainability*, *2*(9), 848-855.

Fuhlendorf, S. D., Engle, D. M., Elmore, R. D., Limb, R. F., & Bidwell, T. G. (2012). Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangeland Ecology & Management*, 65(6), 579-589.

Graham, M., Ates, S., Melathopoulos, A. P., Moldenke, A. R., DeBano, S. J., Best, L. R., & Higgins, C. W. (2021). Partial shading by solar panels delays bloom, increases floral abundance during the late-season for pollinators in a dryland, agrivoltaic ecosystem. *Scientific Reports*, 11(1), 1-13.

Hernandez, R. R., Easter, S. B., Murphy-Mariscal, M. L., Maestre, F. T., Tavassoli, M., Allen, E. B., et al. (2014). Environmental impacts of utility-scale solar energy. *Renew. Sustain. Energy Rev.* 29, 766–779. https://doi:10.1016/j.rser.2013.08.041

Hernandez, R. R., Armstrong, A., Burney, J., Ryan, G., Moore-O'Leary, K., Diédhiou, I., ... & Kammen, D. M. (2019). Techno–ecological synergies of solar energy for global sustainability. *Nature Sustainability*, 2(7), 560-568.

Holl, K. D., Luong, J. C., & Brancalion, P. H. (2022). Overcoming biotic homogenization in ecological restoration. *Trends in Ecology & Evolution*, 37(9), 777-788.

Hoover, D.L., Hajek, O.L., Smith, M.D., Wilkins, K., Slette, I.J. and Knapp, A.K., (2022). Compound hydroclimatic extremes in a semi-arid grassland: Drought, deluge, and the carbon cycle. *Global Change Biology*, *28*(8), pp.2611-2621.

Kannenberg, SA, MA Sturchio, MD Venturas, A.K. Knapp. (2023). Grassland carbon- water cycling is minimally impacted by a photovoltaic array. *Nature Communications Earth & Environment,* 4 (238). https://doi.org/10.1038/s43247-023-00904-4

Koerner, S. E., Smith, M. D., Burkepile, D. E., Hanan, N. P., Avolio, M. L., Collins, S. L., ... & Zelikova, T. J. (2018). Change in dominance determines herbivore effects on plant biodiversity. *Nature Ecology & Evolution*, 2(12), 1925-1932.

Ladouceur, E., Isbell, F., Clark, A.T., Harpole, W.S., Reich, P.B., Tilman, G.D. and Chase, J.M., (2023). The recovery of plant community composition following passive restoration across spatial scales. *Journal of Ecology*. 111: 814–829.

Moore-O'Leary, K. A., Hernandez, R. R., Johnston, D. S., Abella, S. R., Tanner, K. E., Swanson, A. C., ... & Lovich, J. E. (2017). Sustainability of utility-scale solar energy–critical ecological concepts. *Frontiers in Ecology and the Environment*, 15(7), 385-394.

Post, A.K. and Knapp, A.K., (2020). The importance of extreme rainfall events and their timing in a semi-arid grassland. *Journal of Ecology*, *108*(6), pp.2431-2443.

Randle-Boggis, R.J., White, P.C.L., Cruz, J., Parker, G., Montag, H., Scurlock, J.M.O. and Armstrong, A. (2020). Realising co-benefits for natural capital and ecosystem services from solar parks: a co-developed, evidence-based approach. *Renewable and Sustainable Energy Reviews*, 125, p.109775.

Ravi, S., Macknick, J., Lobell, D., Field, C., Ganesan, K., Jain, R., ... & Stoltenberg, B. (2016). Colocation opportunities for large solar infrastructures and agriculture in drylands. *Applied Energy*, 165, 383-392.

Sawyer, H., Korfanta, N.M., Kauffman, M.J., Robb, B.S., Telander, A.C. and Mattson, T., (2022). Trade-offs between utility-scale solar development and ungulates on western rangelands. *Frontiers in Ecology and the Environment*.

Sturchio, M. A., Macknick, J. E., Barron-Gafford, G. A., Chen, A., Alderfer, C., Condon, K., ... & Knapp, A. K. (2022). Grassland productivity responds unexpectedly to dynamic light and soil water environments induced by photovoltaic arrays. *Ecosphere*, 13(12), e4334.

Young, T., Petersen, D.A. and Clary, J.J. (2005). The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology letters*, *8*(6), pp.662-673.

van Zalk, J., & Behrens, P. (2018). The spatial extent of renewable and non-renewable power generation: A review and meta-analysis of power densities and their application in the US. *Energy Policy*, 123, 83-91.

# CHAPTER 4: ECOPHYSIOLOGICAL RESPONSE OF A $C_3$ PERENNIAL GRASS TO NOVEL PHOTOVOLTAIC MICROENVIRONMENTS

## 4.1 Summary

As the world transitions to renewable energy generation, land area devoted to ground mounted photovoltaic (PV) solar arrays is expected to increase dramatically, influencing both managed and native ecosystems. These PV arrays impose dynamic shading regimes and redistribute precipitation inputs on the ecosystems beneath, leading to spatial and temporal heterogeneity in plant growth environments. While the presence of PV infrastructure has previously been documented to alter community and ecosystem processes in grass-dominated ecosystems, underlying plant ecophysiological responses to the unique microenvironments generated by PV arrays are largely unexplored. Here, we evaluated how photosynthetic parameters and water relations in a $C_3$ perennial grass (*Bromus inermis*) varied across a range of microsites within a 1.6 ha (1.2 MW) PV array in the semi-arid, high sunlight climate of Colorado, USA. Overall, photosynthetic parameters and leaf water potentials ($\psi_L$) were generally higher for plants growing within the PV array compared to outside, suggesting that solar inputs intercepted by PV panels reduced overall plant water stress. Within the PV array, photosynthetic capacity (i.e., light-saturated photosynthetic rate) was surprisingly consistent spatially, not differing between plants growing in near full sun (between PV rows) *vs.* those growing directly beneath panels in more shaded environments (~28% of full sunlight). We also found that plants located in microsites receiving direct sunlight only in the morning, when air temperature and vapor pressure deficits (VPD) were low, had greater $\psi_L$ and stomatal conductance ($g_{sw}$) than plants receiving direct sunlight primarily in the afternoon, when temperatures and VPD were

higher. The reduction in physiological function in plants receiving primarily afternoon sunlight occurred despite such locations harboring increased soil moisture from PV panel runoff from afternoon rain events. Thus, while soil moisture is a primary control of plant growth in most water-limited grasslands, we found that VPD is a better predictor of the intraday leaf-level gas exchange responses that control patterns of aboveground biomass production in a PV array.

## 4.2 Introduction

As the cost of photovoltaic (PV) energy decreases (Feldman et al. 2021), the deployment of ground mounted PV arrays is expected to expand, covering up to ~ 61,000 km$^2$ in the United States by 2050 (Larson et al. 2020). As a result, an understanding of the potential impacts PV infrastructure has on ecosystems is needed to inform more sustainable array design, management, and siting (Hernandez et al. 2019, Sturchio and Knapp 2023). A well-documented consequence of PV infrastructure is the novel patterns of environmental heterogeneity (e.g., light, temperature, water) induced by the physical presence of rows of PV panels suspended above the ecosystems beneath (Armstrong et al. 2016, Adeh et al. 2018, Choi et al. 2020, Tanner et al. 2020, Sturchio et al. 2022, Choi et al. 2023, Sturchio and Knapp 2023). Indeed, PV-induced modifications in light and water environments have been linked to altered patterns of aboveground primary production (ANPP) in a wide range of ecosystems globally (Armstrong et al. 2016, Adeh et al. 2018, Andrew et al. 2021, Bai et al. 2022, Sturchio et al. 2022, Kannenberg et al. 2023, Sturchio and Knapp 2023, Sturchio et al. 2024, Zhang et al. 2024). Less well-known are the ecophysiological responses of plants to alterations in light and water availability generated by PV arrays. We contend that such responses have the potential to provide unique mechanistic insight for understanding plant growth patterns within PV arrays.

Currently, our understanding of plant physiological responses to different microenvironments within PV arrays are limited to short-term measurements of desert species (Smith et al. 1987, Hernandez et al. 2020, Tanner et al. 2021, Wynne-Sison et al. 2023), as well as seasonal and diurnal ecophysiological responses of irrigated specialty crops (Marrou et al. 2013, Barron-Gafford et al. 2019, Juillion et al. 2022) in Agrivoltaic settings (AV, an approach to solar energy development where the land beneath PV panels is co-utilized for agricultural production, Dupraz et al. 2011, Dinesh & Pearce 2016). However,  the majority of AV land use to date involves perennial agroecosystems, such as restored and managed grasslands, generating ecosystem services in the form of forage production and pollinator habitat (Inspire AV Map). How these long-lived perennial species will respond to the novel environments imposed by PV arrays is unresolved.

Environmental variation in light, temperature, and water are well-known to affect plant physiology at the leaf, whole-plant, and ecosystem levels (Ellsworth and Reich 1992, Atkin and Tjoelker 2003, Wright et al. 2004, Smith and Dukes 2013, Cabon et al. 2022). In the case of PV arrays, dynamic light regimes and the redistribution of precipitation (via panel runoff) result in spatially heterogeneous patterns of soil moisture (SM) that have been shown to weaken (Sturchio et al. 2022) the otherwise robust positive relationship between SM and aboveground net primary production (ANPP) in semi-arid grasslands (Sala et al. 1988, Knapp et al. 2002, La Pierre et al. 2016, Post and Knapp 2021). A proposed explanation for this disruption is that because microsites within PV arrays can vary dramatically in both the amount of sunlight received, as well as the diurnal timing of when direct sunlight is incident, the altered solar radiation regime dampens SM as a driver of plant growth. Ecophysiological evidence consistent with this hypothesis and supporting these patterns of ANPP is lacking, however.

Here, we assessed the physiological response of a $C_3$ perennial grass to PV induced environmental heterogeneity in a formerly managed semi-arid grassland in Colorado, USA. Past research at this site revealed consistent and substantial variation in ANPP depending on the microsite within the PV array (see Sturchio et al. 2022, Sturchio et al. 2024). The goals of this study were to 1) quantify how environmental heterogeneity within an PV array alters *Bromus inermis* photosynthetic capacity and leaf water relations, 2) determine relationships between diurnal patterns of stomatal conductance ($g_{sw}$) and leaf water potential ($\psi_L$) and key environmental drivers, and finally 3), relate ecophysiological patterns in this dominant grass to aboveground productivity.

We expected that 1) the wide variation of spatial and temporal amounts and patterns of light availability within the PV array would lead to diurnal and seasonal physiological responses that differed dramatically from those outside the array, 2) that within the PV array, plants receiving morning light would strongly differ in their rates of gas exchange ($g_{sw}$) and overall water relations than plants receiving afternoon light, and 3) that diurnal patterns of leaf water status and stomatal response, which should relate to productivity, will be better predicted by the atmospheric demand for water (vapor pressure deficit as determined by humidity and temperature) during periods of direct sunlight rather than the supply of water to plants (SM).

## 4.3 Materials and Methods

### 4.3.1 Site Information

Research was conducted at Jack's Solar Garden (JSG), an agrivoltaic research facility (https://www.jackssolargarden.com/) near Longmont, CO (elevation 1508m, 40°07'18.9"N 105°07'49.9"W). JSG is on Mountain Daylight Time (UTC - 06:00) and all references to time of day are reported on a 24-hour clock (00:00-24:00). The climate is semi-arid with a mean annual temperature of 9.8°C and 367 mm of precipitation annually (Colorado Climate Center http://ccc.atmos.colostate.edu/). Historically, the 1.5 ha site was managed for hay production, but active management (mowing) ended in 2019 when the PV array was installed. The grassland at JSG is dominated (>80% cover) by a perennial nonnative $C_3$ grass (*Bromus inermus*) with scattered individuals of *Dactylis glomerata* ($C_3$ Orchard grass), *Medicago sativa* (Alfalfa) and *Tragopogon dubius* ($C_3$ forb) interspersed. This study took place beneath PV panels mounted 1.8 m above the ground (Fig. 4.1a). Individual PV panels at JSG are 2m (east-west) × 1m (north-south) and are mounted in series on a single axis tracking system (tracking east-west, Fig. 4.1a).

### 4.3.2 Experimental Design

We established three 10.4 m transects perpendicular to the rows of PV panels within a portion of JSG that has been maintained as an undisturbed perennial grassland (Fig. 4.1a). Each transect was comprised of 4 replicate sampling points along the environmental gradient created by the PV panels ($E_{edge}$; beneath eastern edge of panel where rainfall is redistributed, $W_{edge}$; beneath western edge of panel where rainfall is redistributed, *Beneath*; directly beneath panel, in line with the panel support beams, and *Between*; between rows of panels, Fig. 4.1a). Each experimental plot was 1 × 0.5 m with a 3 m north-south gap separating transects. Control plots were located ~20 m outside the solar array in a similarly managed portion of the formerly hayed grassland, but not affected by the shade or precipitation redistribution from panels. At the end of the growing season (September 29th), all experimental plots ($n = 52$) were sampled for aboveground net primary production (ANPP, g $m^{-2}$). Because the site had been mowed at the end of the 2021 growing season, aboveground biomass accumulating in 2022 represented ANPP. While harvesting, biomass was sorted by functional group (grass vs. forb). Harvested biomass was dried at 60 °C for 72 hours before being weighed to the nearest 0.01 g.

### 4.3.3 Environmental measurements

Diurnal patterns of air temperature ($T_{air}$), relative humidity (RH%), and Photosynthetic Photon Flux Density (PPFD), were continuously recorded at a meteorological station on site at JSG, May-September 2022, henceforth referred to as the growing season. We recorded PPFD every 15 minutes using CS310 Quantum Sensors (Campbell Scientific, Logan, UT) located in plots directly between PV support posts (Fig. 4.1a, Between), 80cm east of support posts (Fig. 4.1a, $E_{edge}$), directly in line with support posts (Fig. 4.1a, Beneath), and 80cm west of support posts (Fig. 4.1a, $W_{edge}$). $E_{edge}$ and $W_{edge}$ were located 80cm in either direction of support posts to quantify temporal patterns of light availability underneath eastern and western drip edges respectively. PPFD measurements were recorded at grass canopy height which required continuous adjustments as the canopy grew taller throughout the growing season. An on-site meteorological station provided control plot PPFD, $T_{air}$, and RH%.

Volumetric water content (VWC, referred to as SM in the text) was measured every 15 minutes for all experimental microsites and control plots using CS616 Soil Moisture Sensors (Campbell Scientific, Logan, UT). Each plot had paired sensors recording SM at depths of 0-15 (shallow) and 15-30cm (deep), (Fig. 4.1a).

### 4.3.4 Light Response of Photosynthesis

Plants located in each of the microsites indicated in Fig. 4.1a, as well as in the control plot, were used to assess differences in light saturated photosynthesis ($A_{sat}$) and the quantum yield of $CO_2$ assimilation ($\phi CO_2$) in *B. inermis*. Duplicate measurements were made on separate leaves across transects (3 transects, 2 reps, n=6 plants). Light responses of leaf-level photosynthesis were measured bi-weekly during peak growing season (June & July) using a portable photosynthesis system (LI-6800, LiCor., Inc, Lincoln NE, USA). The LI-6800 was fitted with a 3x3 cm cuvette head and a red-blue LED light source. For all measurements, flow rate was held constant at 600 µmol $s^{-1}$. The LI-6800 temperature exchanger was set to the prevailing midday temperature, which resulted in an average leaf temperature ($T_{leaf}$) setting of 31.3 ± 2.1 °C (standard deviation) across all measurements. Chamber reference $CO_2$ was set to 420 µmol $mol^{-1}$ and photosynthetic photon flux density (PPFD) was set to 1800 µmol $m^{-2}$ $s^{-1}$ before leaves were placed into the chamber. Once placed in the chamber, leaves typically reached steady state within 5-10 min, at which time a light response curve was initiated.

All measurements occurred between 09:00 and 13:00 local time and were made on recently matured, fully expanded, upper canopy leaves. One-sided surface area of leaves within the chamber was estimated by measuring leaf length and width. Light response curves were constructed by measuring *A* at 12 reference [PPFD] values between 2000 and 0 µmol $m^{-2}$ $s^{-1}$ in a descending stepwise fashion (Figure A2.1). Each light response curve was parameterized using a non-rectangular parabola (Marshall and Biscoe 1980) through least squared parameter estimation in R version 4.1.2 (R Core Team 2017). The model was fit using the *photosynthesis* package (Stinziano et al. 2021) to estimate light saturated net $CO_2$ assimilation rate ($A_{net}$), quantum yield of $CO_2$ assimilation ($\phi CO_2$), and light compensation point (LCP, light level needed for photosynthesis to exceed respiration).

### 4.3.5 $CO_2$ response of photosynthesis

Similar to light response curves, $CO_2$ response curves of photosynthesis ($A$-$C_i$) were measured bi-weekly during peak growing season (June and July) using a LI-6800. Duplicate measurements were made on separate leaves across transects (n=6). Environmental conditions, leaf position, and timing of $A$-$C_i$ measurements were the same as light response measurements. All $A$-$C_i$ curves were constructed by measuring net photosynthesis ($A_{net}$) at 12 reference [$CO_2$]

values between 0 and 1500 μmol mol$^{-1}$ in a stepwise fashion (420, 300, 250, 150, 100, 50, 0, 420, 650, 800, 1200, 1500, see Figure A2.2). At each reference value, an auto-matching program limited fluctuations of reference $CO_2$ <0.1 μmol mol$^{-1}$ before logging to ensure accurate measurements. Each $A$-$C_i$ curve was parameterized using the Farquhar model of $C_3$ photosynthesis (Farquhar et al. 1980) using non-linear least squared parameter estimation in R version 4.1.2 (R Core Team 2017). The model was fit using the *fitaci* function from the *Plantecophys* package (Duursma 2015). The model estimates the maximum rate of rubisco carboxylation ($V_{cmax}$) and the maximum rate of electron transport for RuBP regeneration ($J_{max}$). The temperature correction function was set to field measurements of $T_{leaf}$ (leaf temperature). Leaf mesophyll conductance to $CO_2$ was not estimated, thus $V_{cmax}$ and $J_{max}$ are apparent values that reflect both biochemical limitations and mesophyll conductance (e.g., Salmon et al. 2020). Spot measurements were selected at chamber PPFD 1800 μmol m$^{-2}$ s$^{-1}$ (i.e., saturating light) and reference $CO_2$ 420 μmol mol$^{-1}$ (i.e., ambient $CO_2$ concentration) to determine relationship between $A$ and $g_s$. Because a strong relationship between the two was evident (see results), we used measurements of $g_s$ to infer responses in $A$.

### 4.3.6 Diurnal measurements of stomatal conductance ($g_s$) and leaf water potential ($\psi_L$)

At two-week intervals, diurnal measurements of stomatal conductance ($g_{sw}$) were made at five times throughout the day (09:00, 11:00, 13:00, 15:00, and 17:00 hrs) using a portable porometer/fluorometer (LI-600, LiCor., Inc, Lincoln NE, USA). Three replicate measurements were taken per experimental plot (between, $E_{edge}$, beneath, $W_{edge}$, and control) per transect, resulting in nine plot level replicates across transects. Grass $g_{sw}$ has been shown to be variable along leaf blades (Ocheltree et al. 2012), so as a precautionary measure, all $g_{sw}$ measurements were taken from a standardized point on *B. inermis* leaves.

Leaf water potential ($\psi_L$) was measured at a similar temporal and spatial frequency diurnally. Three leaves were removed per plot per transect, resulting in nine plot level replicates. Sampled leaves were placed in plastic bags with damp paper towel. $\psi_L$ was measured on site at JSG using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, USA). All leaves were sampled within 40 minutes of diurnal timepoints, and all measurements were made within an hour.

### 4.3.7 Data Analysis

Spatial patterns of aboveground net primary production (ANPP) were similar across all transects, so data were analyzed using a one-way analysis of variance (ANOVA) to test plot level effects. Similarly, sunlight (PPFD) and growing season means of diurnal physiological response ($g_{sw}$ and $\psi_L$) had little variation at the transect level and as a result were analyzed using one-way ANOVA. Two-way ANOVA was used to test for differences between SM at two measurement depths (0-15 and 15-30cm) (Microsite × Depth), and to test how the presence of shade related to diurnal physiological response ($g_{sw}$ × Shade) and ($\psi_L$ × Shade). A relative weight analysis (rwa package in *R*, cran.r-project.org/web/packages/rwa/rwa.pdf) was used to quantify microsite level differences of direction and magnitude for total variance in a regression model for $g_{sw}$ and $\psi_L$ into weights, reflecting the proportional contribution of the predictor variables (SM and VPD). Relative weight analysis allowed us to quantify the proportional influence of covarying environmental drivers on plant physiological processes. Analysis of co-variance (ANCOVA) was then used to determine sensitivity of $g_{sw}$ and $\psi_L$ to SM and VPD via microsite level differences of slope coefficients.

## 4.4 Results

### 4.4.1 Precipitation and Temperature

In 2022, annual precipitation at the site was 11% higher than the long-term average (404 vs. 365 mm, respectively). However, the early growing season (April, May, June) was ∼40% drier than normal (89 mm in 2022 vs. 148 mm average), and the late growing season (July, August) was ∼30% wetter than the long-term average (96 mm vs. 65 mm, Colorado Climate Center; http://ccc.atmos.colostate.edu/). Mean annual temperature (10.2 °C) was slightly above the 30-year average (9.8 °C).

### 4.4.2 Light

Compared to open field conditions, light within the array was reduced by ~38.3% during the growing season averaged across all microsites (Fig. 4.2a, b). As expected, plants *Between* rows of panels received the most sunlight within the PV array (72.3% of control), followed by $E_{edge}$ (52%), $W_{edge}$ (37%), and *Beneath* panel (28%). Differences between PPFD on a single cloudless day (Fig. 4.2a, b insets) and means over the growing season highlight the reduced magnitude of afternoon sunlight available to $W_{edge}$ and *Beneath* panel microsites by ~10% and ~6%, respectively. Reduced $W_{edge}$ PPFD in the afternoon was likely a result of increased cloud cover that consistently developed over nearby mountains.

### 4.4.3 Soil Moisture

Measurements of SM revealed that $E_{edge}$ and $W_{edge}$ microsites were, on average, wetter than all experimental microsites at depths of 0-15cm (Fig. 4.2, Fig. A2.3). The amplification of precipitation events at panel edges increased shallow SM ~2-4 times more for $E_{edge}$ and $W_{edge}$ compared to controls (Fig. 4.2c, d). Statistically significant differences between shallow and deep SM were only apparent in PV microsites where rainfall was concentrated ($W_{edge}$ and $E_{edge}$) or impeded (*Beneath*), see Fig. 4.2 and A2.3. At these microsites, deep soils were typically wetter than shallow, apart from $E_{edge}$ where shallow soils were consistently wetter than deep (Fig. 4.2f, A2.3). The *Beneath* microsite was relatively unaffected by rainfall events (e.g., did not increase in direct response to precipitation events), yet maintained seasonally consistent moisture status likely through a combination of belowground hydrological processes, lateral moisture transfer from adjacent areas, and reduced evapotranspiration.

### 4.4.4 Productivity

Although a few species other than *B. inermis* persist at the study site, none were present in PV sampling transects, and because of this, ANPP statistical analyses only account for *B. inermis* production. Patterns of ANPP were consistent across transects, however results of a one-way-ANOVA indicated there were statistically significant differences between microsites ($p < 0.001$, Fig. 4.1b). We found that plants in the $E_{edge}$ microsite were on average 30% (± 5 SE) more productive ($p < 0.01$) than control, while *Beneath* plants were 22% (± 4 SE) less productive than controls. To infer how these results might scale to the landscape level, we standardized ANPP by plot area (following Kannenberg et al. 2023). Averaged across plots and standardized by microsite area, we estimated that ANPP within the array overall was not statistically different from control ANPP ($p = 0.28$), although the calculated mean ANPP in the array was ~6.1% lower than the control.

### 4.4.5 Photosynthetic Capacity

On average, we found that $A_{\mathrm{sat}}$ and $\phi\mathrm{CO_2}$ were significantly ($p < 0.05$, see Fig. 4.3) higher for plants within the PV array (18.1 ± 1.02 SE, 0.056 ± 0.002 SE, respectively), compared to control plants outside the array (9.7 ± 1.4 SE, 0.038 ± 0.003 SE, respectively). Although differences in $V_{\mathrm{cmax}}$, and $J_{\mathrm{max}}$ were not statistically different between PV microsites and control ($p = 0.24$ and 0.11, respectively), means of $V_{\mathrm{cmax}}$ and $J_{\mathrm{max}}$ were ~32% and 40% higher respectively

(See Fig. A2.4). The strong relationship between $A$ and $g_s$ (Fig. 4.3c) at an ambient concentration of $CO_2$ indicates that measurements of $g_{sw}$ can reliably be inferred as reflective of responses in $A$.

### 4.4.6 Diurnal Physiology

Differences in $g_{sw}$ and $\psi_L$ varied throughout the diurnal cycle, but temporal differences in these traits depended upon spatial, microsite level differences (significant Time of Day × Microsite interactions). Based on seasonally averaged diurnal patterns, $E_{edge}$ plants had significantly higher $g_{sw}$ than plants located in all other experimental microsites ($p < 0.001$) at the first measurement period (9:00 am local time). This pattern continued throughout the morning (11:00), when $g_{sw}$ for $E_{edge}$ and *Beneath* plants were significantly higher than all other plants (Fig. 4.4a). By midday (13:00) control plants had significantly lower $g_{sw}$ compared to all plants located within the PV array, and this trend was sustained for much of the day.

To determine how variation among microsite-level diurnal measurements differed throughout the growing season, a one-way ANOVA was used to compare daily averages of $g_{sw}$ between microsites. The results of this analysis show that $E_{edge}$ had significantly higher $g_{sw}$ than all other PV (+18-45%) and control plots (+115%) (Fig. 4.4b). Additional one-way ANOVAs were used to determine how the presence of shade altered microsite specific response of $g_{sw}$ throughout the growing season. Only experimental microsites in the array were used for this analysis because control plots never experienced PV shade. As expected, the presence of shade significantly reduced $g_{sw}$ across all microsites except for $W_{edge}$, where plants had $18 \pm 4\%$ higher $g_{sw}$ in the shade (Fig. 4.4b inset).

At the first diurnal measurement period, plants located in $W_{edge}$ and *Between* microsites had significantly ($p < 0.001$) higher $\psi_L$ than those located in *Control* and *Beneath* microsites. Mid-morning measurements at 11:00, indicated that $E_{edge}$ plants had significantly lower $\psi_L$ than those located in *W<sub>edge</sub>* and *Beneath*, however, by midday (13:00), microsite level differences in $\psi_L$ were no longer statistically different. However, in the early afternoon (15:00) *Control* $\psi_L$ decreased significantly below all other microsites (Fig. 4.4c), and by late afternoon when final diurnal measurements were taken, $\psi_L$ for *Beneath* and *Control* plants were significantly lower than plants in all other experimental microsites.

Mid-day $\psi_L$ is often assumed to estimate maximum daily water stress, so to better illustrate variation in measurement means of this key physiological variable, a separate one-way ANOVA (Fig. 4.4d) was used to analyze a subset of measurements at mid-day (i.e., solar noon, 13:00). This analysis revealed that $E_{edge}$ and *Beneath* plants had significantly higher mid-day $\psi_L$ than $W_{edge}$, *Between*, and *Control* plants. As with $g_{sw}$ analyses, additional one-way ANOVAs were used to determine how the presence of shade related to diurnal response of $\psi_L$ (Fig. 4.4d inset). $\psi_L$ was only significantly higher for *Beneath* and *Between* plants when PV shade was present. The large variation of sun and shade $\psi_L$ for *Between* plants is likely a result of early morning shade (09:00, Fig. 4.4d) delaying stomatal opening and thus $\psi_L$ was more reflective of soil water potential at the site.

### 4.4.7 Relationships between environmental drivers and physiology

Through relative weight analysis, we determined that SM and VPD had substantially different effects on $g_{sw}$ and $\psi_L$ across the growing season and these effects varied in direction and magnitude between plots (Fig. A2.5). For example, SM contributed to most of the variation in $g_{sw}$ for $W_{edge}$ and *Between* plants, but VPD contributed to most of the variation in $\psi_L$. However, at the $E_{edge}$ VPD was responsible for variation in $g_{sw}$, and SM for $\psi_L$. *Beneath* physiological responses were equally impacted by SM and VPD, while variation in *Control* plant $g_{sw}$, and $\psi_L$ were both driven by VPD. The relative contribution of variation attributed to VPD in *Control* plants, however, may also be due to the lack of early season SM measurements in control plots (e.g., Fig. 4.2c).

There was a consistently positive relationship between SM and $g_{sw}$ across plots ($r^2 = 0.54$, Fig. 4.5e), but no significant pattern between SM and $\psi_L$ (Fig. 4.5f). In contrast, both $g_{sw}$ and $\psi_L$ displayed negative relationships in response to increased VPD, with the slopes of those relationships differing between microsites (VPD × Microsite interaction, Fig. 4.5, panel b, d), indicating that some plots responded more strongly to VPD. Indeed, comparison of $E_{edge}$ and $W_{edge}$ (Fig. 4.5b, d) highlights the control of VPD on plant water status and thus $g_{sw}$ response, despite both microsites experiencing wetter soils and similar amounts of light availability.

Overall, slopes of relationships between $\psi_L$ and VPD were higher for plants in *Control*, $W_{edge}$, and *Between* microsites, indicating greater sensitivity to VPD throughout the growing season compared to $E_{edge}$ and *Beneath* plants (Fig. 4.5a, b). In contrast, slopes of relationships between $g_{sw}$ and VPD were more negative for $E_{edge}$ and *Between* plants, indicating more sensitivity in stomatal response to increasing VPD (Fig. 4.5c, d).

## 4.5 Discussion

Our goal was to determine how microsites with different environmental conditions within PV arrays can alter physiological responses that underly patterns of productivity in a $C_3$ grass. Consistent with previous work (Sturchio et al. 2022, Sturchio et al. 2024), we found that plants located on the $E_{edge}$ of PV panels, exposed to morning sunlight and afternoon shade, had the highest ANPP despite receiving less direct sunlight (Fig. 4.2b) than control plants. Surprisingly, photosynthetic parameters ($A_{sat}$, $\phi CO_2$) were similar across microsites within the array but were significantly lower for plants growing in control plots outside of the array. These control plants also had consistently lower $\psi_L$ throughout the growing season and were presumably more water stressed. We found that plants exposed to primarily morning light consistently had the higher $g_{sw}$ and $\psi_L$ throughout the growing season (Fig. 4.4). Additionally, $E_{edge}$ plants had the highest sensitivity of stomatal response to changes in VPD (Fig. 4.5d), but $\psi_L$ was relatively unchanged by changes in VPD (Fig. 4.5b).

### 4.5.1 The importance of the diurnal timing of direct sunlight

Strong positive relationships between SM and $g_{sw}$ highlight the importance of SM as a determinant of productivity in water limited grasslands. However, variation in SM happens at coarser time scales and is less consistent than diurnal fluctuations of VPD. Diurnal patterns of $g_{sw}$ and $\psi_L$ are more dependent upon changes in VPD, evidenced by the contrasting relationships between $E_{edge}$ and $W_{edge}$ plants which receive direct sunlight in the morning or afternoon, respectively (Fig. 4.5a, b). Therefore, SM is likely more physiologically important in PV arrays than previously reported (i.e., Sturchio et al. 2022), however, diurnal patterns of physiological response indicate that VPD is more important for controlling diurnal patterns of plant water balance and potentially the apparent differences in end of season production across microsites.

The ability of $E_{edge}$ plants to maintain a consistent $\psi_L$ regardless of changes in VPD is likely due to afternoon shading, reducing physiological stress when atmospheric demand is at its highest. This is in stark contrast to the physiological response of $W_{edge}$ plants that receive a majority of sunlight in the afternoon, where $g_{sw}$ is limited by high VPD (Fig. 4.5d) and $\psi_L$ responds more dynamically (Fig. 4.5c). Although $E_{edge}$ and $W_{edge}$ plants exist just two meters apart and receive nearly identical amounts of direct sunlight daily, the association between time of day and VPD (Fig. 4.6) drastically impacts their diurnal physiology. The relationship between $g_{sw}$ and SM illustrates this point by showing that $E_{edge}$ and $W_{edge}$ plants are capable of similar $g_{sw}$ maximums, but that $E_{edge}$ achieved those at much lower levels of soil moisture (Fig. 4.5f).

However, the relative importance of SM and VPD as limiting factors of production might be expected to change during drought conditions. Future studies that quantify how these relationships change under severe water limitation will help determine the potential water savings benefits of photovoltaic colocation in water limited ecosystems.

### 4.5.2 Photosynthetic response to novel PV light regimes

Dynamic photosynthetic parameters and their response to alterations in sunlight availability have been well documented across leaf, plant, and ecosystem levels (Thornley 1974, Chazdon and Pearcy 1991, Kull and Kruijt 1998, Emmel et al. 2020). In this unique environment, we found that despite a ~40% reduction in photosynthetically active light within the array, $A_{\mathrm{sat}}$ and $\phi CO_2$ were both significantly higher for plants inside the PV array compared to control plants (Fig. 4.3). Control plants also had consistently lower midday plant water potential than those within the array. These responses indicate that reductions in the availability of direct sunlight might negligibly impact the overall capacity of photosynthesis in $C_3$ grasses and a reduction in solar radiation may even help alleviate water stress in dry climates. This finding has important implications for the future design of PV arrays that co-prioritize ecosystem services and energy production (i.e., Ecovoltaics, see Sturchio and Knapp 2023). If light is not a sizeable limitation to photosynthesis in vegetation under the panels, numerous management options could be applied while minimally impacting vegetation carbon uptake and growth.

Temperature is an environmental variable that has demonstrated considerable control on instantaneous and seasonal fluctuations of photosynthetic response (Atkin and Tjoelker 2003, Yamori et al. 2014, Smith and Dukes 2017). As previously stated, patterns of stomatal conductance were much different for $E_{edge}$ and $W_{edge}$ plants (morning light vs. afternoon light) (Fig. 4.4, A2.6), however these differences had no discernable effect on light and $CO_2$ response

($A_{sat}$, $\phi CO_2$, $V_{cmax}$, and $J_{max}$, Fig. 4.3, Fig. A2.4) of all plants grown in PV microsites. This result is in contrast to the lower rates of $A_{sat}$ in control plants (Fig. 4.3, Fig. A2.4) which could be the result of a combination of longer exposure to direct sunlight and elevated leaf temperatures (~ 4 °C higher for control plants than PV plants, Figure A2.7), therefore promoting greater water stress. Temperature response of photosynthesis was not directly tested in this study, but further inquiry may be useful in determining whether biochemical limitation via temperature stress varies between plants grown in PV shade and control plants.

### 4.5.3 Building an ecological understanding of PV agroecosystems

As first noted by Smith et al. (1987) more than 30 years ago, in arid and semi-arid systems, reductions in solar irradiance from PV panels may be offset by the benefits of higher plant water potential during times of limited water availability. Indeed, the mechanistic importance of *when* light is available might help inform ecologically informed approaches to solar development that prioritize plant water relations over energy production during the hottest and driest days of the growing season (Sturchio and Knapp 2023). These dynamic PV microenvironments shift the nature of resource limitation in space and time, enabling potential applications related to water stress abatement.

Future work that tests the efficacy of these principles in more diverse grasslands will play an essential role in determining where large-scale solar projects are developed and how they are managed. For example, in more diverse rangelands there will be more opportunities to test how plants from different functional groups (i.e., $C_3$ grass, $C_4$ grass, forb, shrubs) alter their patterns of physiological response to the unique microenvironmental conditions in an PV array. Of particular interest is determining if $C_4$ plants (i.e., “warm season” species) respond differently to the unique PV-generated microenvironments. Distinct temporal shifts in phenology (Graham et al. 2021) and seasonality (Sturchio et al. 2024) of key ecosystem services (e.g., floral resources and forage quality) have been reported in other PV arrays. A physiologically rooted investigation for how environmental heterogeneity contributes to phenological patterns of floral production, forage quality, and water use, will enable us to better predict ecosystem response and the overall sustainability of PV co-location.

### 4.6 Conclusion

In conclusion, we found that microenvironmental conditions created by PV panels altered patterns of photosynthetic response, water balance, and productivity of a $C_3$ grass in semi-arid Colorado. We found that photosynthetic parameters ($A_{sat}$, $\phi CO_2$, $V_{cmax}$, and $J_{max}$) were similar for plants in PV microsites, but consistently lower in control plants outside the array. This reduction was also present, although muted, in patterns of ANPP, and were likely a result of a combination of higher overall water stress (i.e., coupled response of $g_{sw}$ and $\psi_L$) and perhaps temperature stress from prolonged exposure to direct sunlight. In fact, the relationship between timing of light availability and atmospheric water demand (i.e., morning vs. afternoon see Fig. 4.6) limited $g_{sw}$ for plants growing in afternoon sunlight when temperatures were hotter and drier. This work provides mechanistic insight into the physiological processes that underly function in these novel ecosystems. The apparent physiological benefits of shade highlight the compatibility of water limited grasslands and PV cover, at least for $C_3$ grasses. Further work that identifies the contribution of environmental conditions to physiological variability across species and biomes is needed to inform sustainable PV co-location.

### 4.7 Figures

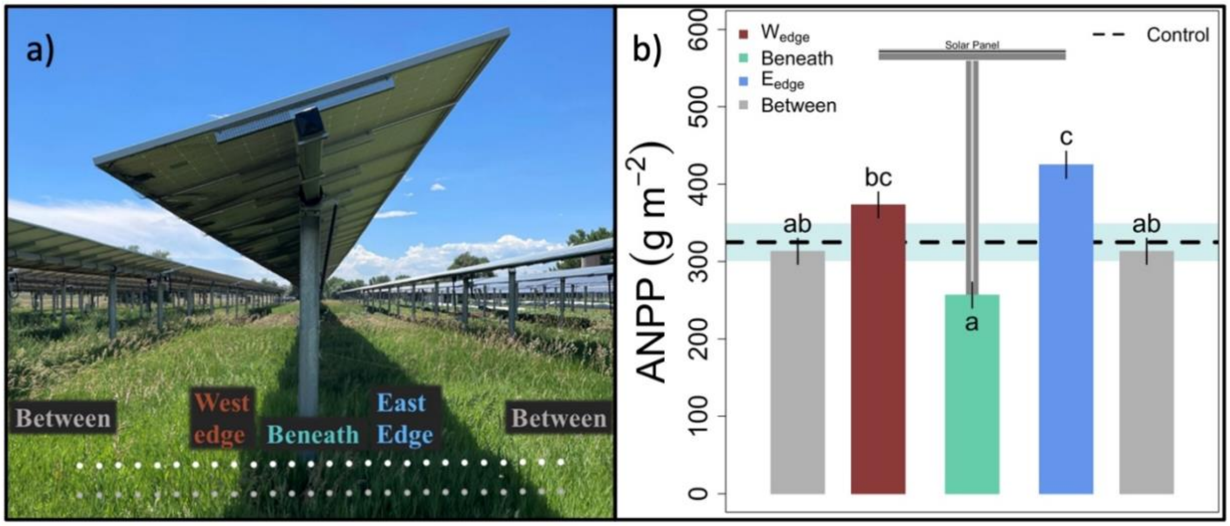


**Figure 4.1.** Left: Annotated photograph depicting the experimental microsites (between, $E_{edge}$, beneath, and $W_{edge}$) used for physiological measurements and end of season plant productivity sampling. Soil moisture sensor layout (20cm between sensors, E-W) at two depths is shown using white and grey dots. Right: Spatial patterns of mean aboveground net primary productivity (ANPP) for 2022 for experimental microsites are shown in bars. Patterns of production are comparable to those reported previously at the same site (Sturchio et al. 2022, Sturchio et al. 2024). Lines on vertical bars represent standard error from the mean. Letters above bars denote statistical differences ($p<0.05$). The control microsite mean ANPP is depicted by a dashed horizontal line with a light blue shadow representing standard error from the mean.

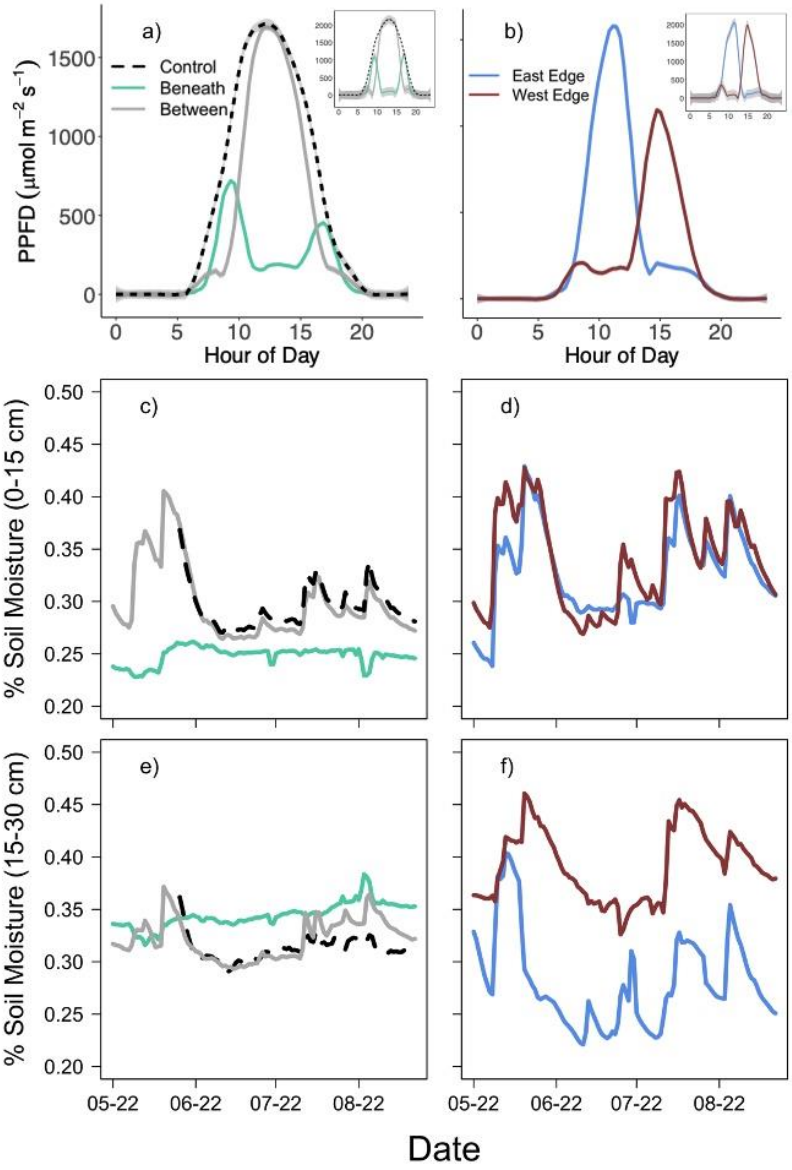


**Figure 4.2. (a)** Mean growing season patterns of diurnal photosynthetic photon flux density (PPFD) in a control site (with no influence of the PV array) and in the two PV microsites that differed dramatically in incident solar radiation (directly beneath and in-between panels. **(b)** PPFD patterns in two PV microsites that experience opposing diurnal patterns of PPFD (morning vs. afternoon sun) as well as unequal amount precipitation due to redistribution (runoff) of precipitation occurring primarily in the afternoon from late day thunderstorms. Insets in both (a) and (b) show diurnal patterns of PPFD on a cloudless day with grey shadowing on lines representing standard error from the mean. In **(c-f)**, growing season soil moisture is similarly shown, illustrating the concentration of precipitation at panel edges. Note the differences between 0-15cm (c and d) and 15-30cm (e and f). Plot level statistical differences between shallow and deep soil moisture are shown in supplemental Figure 3.

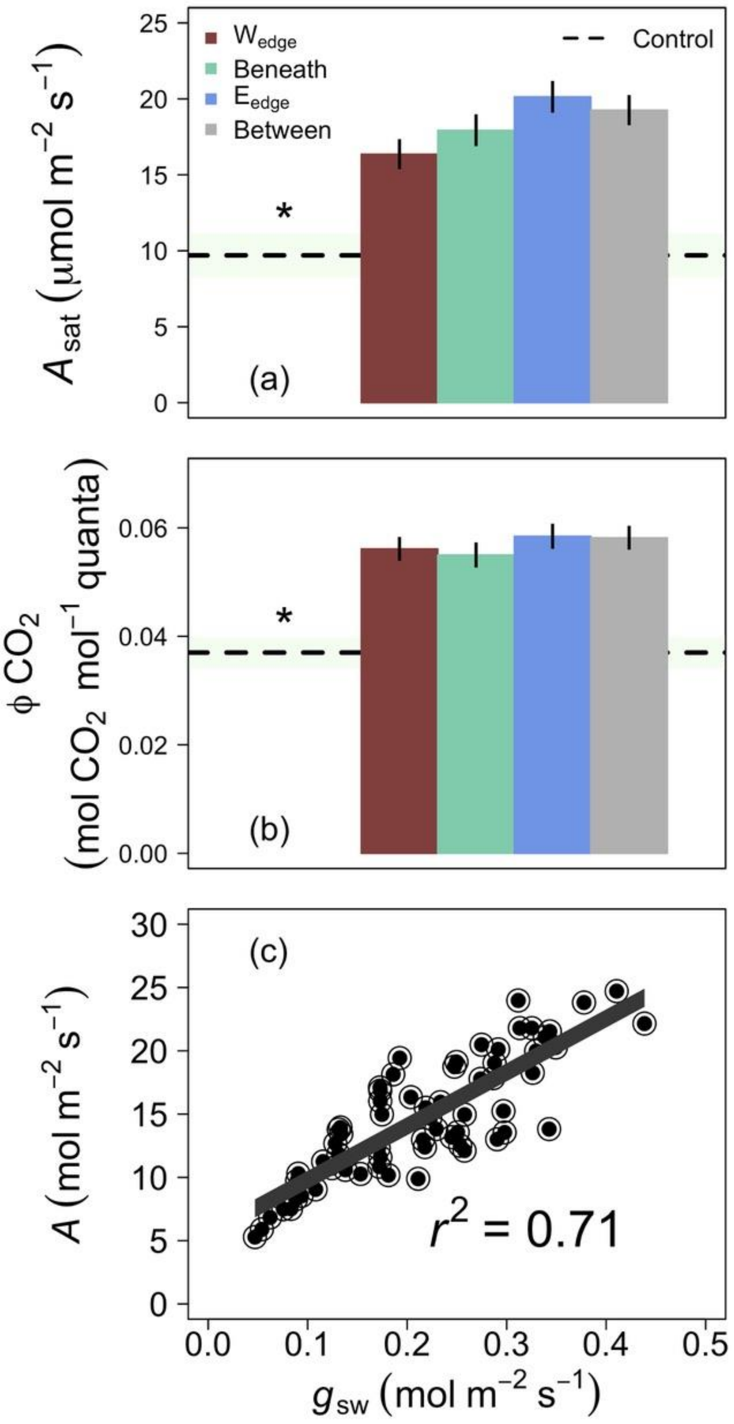


**Figure 4.3.** Light saturated photosynthesis ($A_{sat}$, see panel a) and quantum yield of $CO_2$ assimilation ($\Phi$ $CO_2$, see panel b). PV microsite means are shown using vertical bars with vertical lines indicating standard error from the mean. The control microsite mean is depicted by a dashed horizontal line with a light green shadow representing standard error from the mean. Star indicates significant difference between control microsite and all PV microsites (* < 0.05). Relationship between A (assimilation of $CO_2$) and $g_{sw}$ (stomatal conductance to water vapor) combined for plants in all microsites combined is shown in panel c.

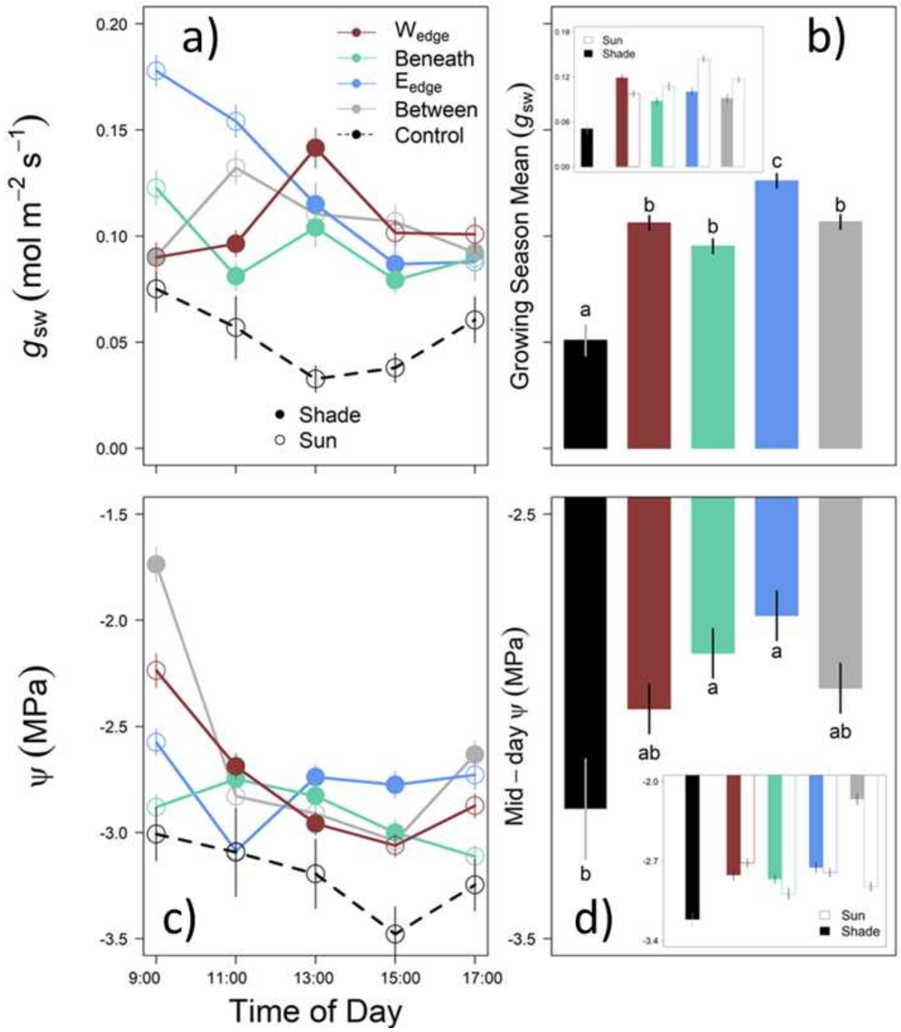


**Figure 4.4.** Growing season means (n= 8 timepoints) of stomatal conductance to water ($g_{sw}$) and leaf water potential ($\psi_L$) over time (diurnally, panels a and c) and across space (microsites, panels b and d). Open circles indicate timepoints when plants receive direct sunlight, and closed circles indicate when plants are shaded by PVs. Letters above bars represent statistical similarity, where shared letters indicate statistical similarity. Insets in panels b and d indicate the variable patterns of plant physiology when leaves of different plots experience sun vs. shade.

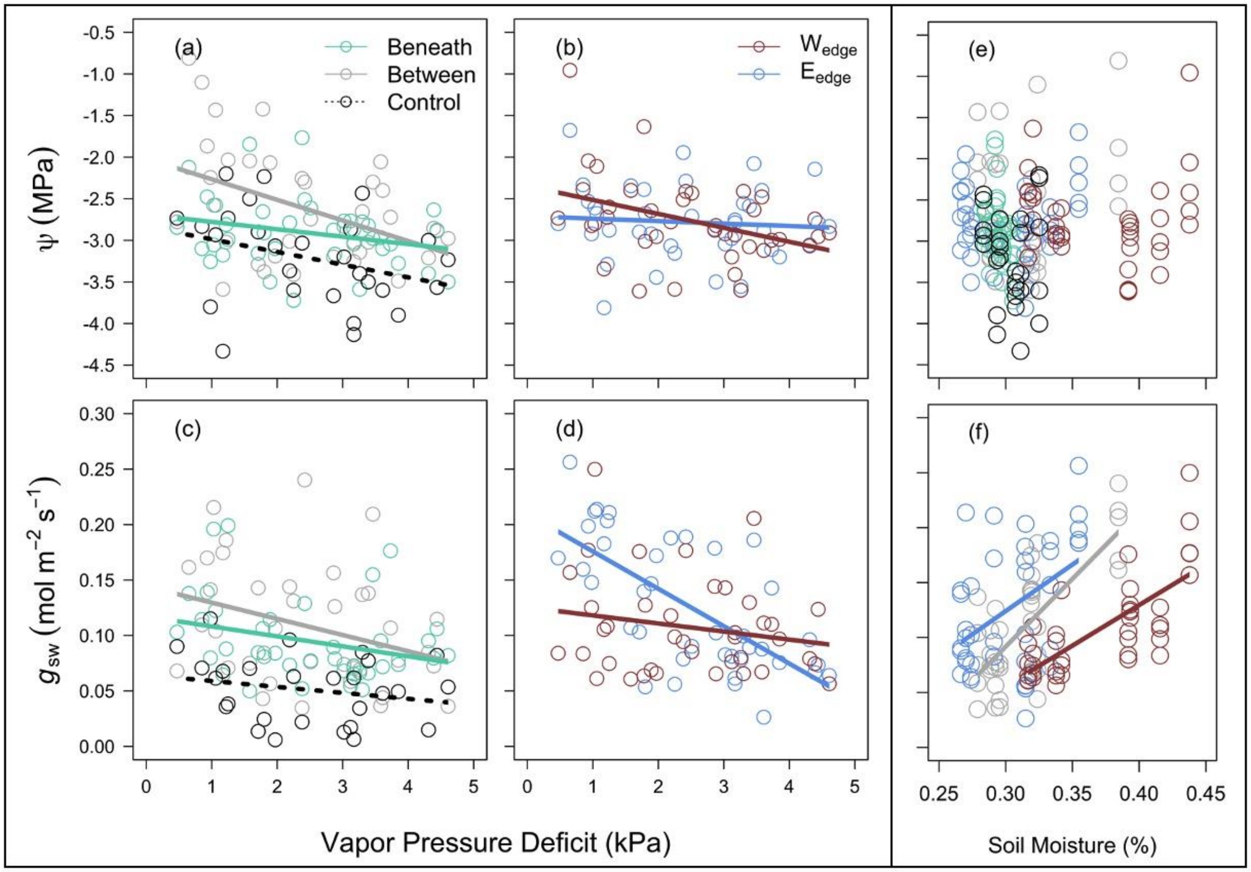


**Figure 4.5.** *Relationships between VPD and leaf physiological traits ($g_{sw}$ and $\psi_L$) contrasting PV microsites as in Fig. 2. Relationships between soil moisture and leaf physiological traits (e and f) were not split in this way because slopes of relationships were consistent across plots. Note that control and beneath plots are not shown in (f) due to the small range in soil moisture encountered during sampling dates.*

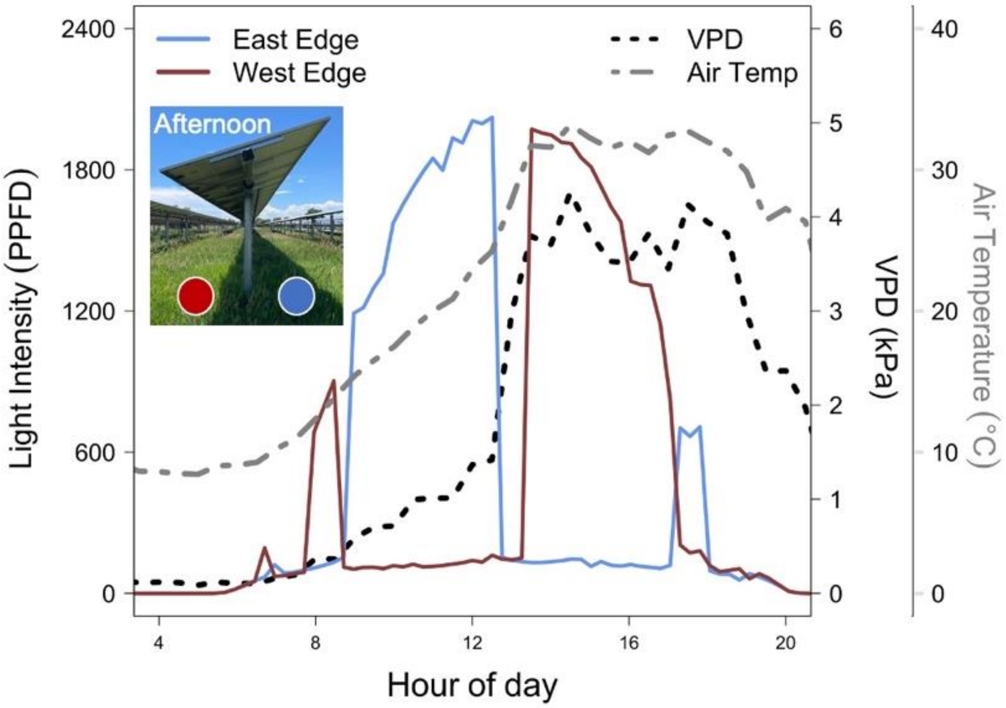


**Figure 4.6.** Single day example for the diurnal patterns of environmental drivers of photosynthesis. Red and blue lines indicate light intensity (PPFD) for plots located identical distance from PV support pole on east and west edges respectively. Dashed black line indicates diurnal pattern of vapor pressure deficit (VPD). Grey line represents air temperature.

# LITERATURE CITED

Adeh, E. H., Selker, J. S., & Higgins, C. W. (2018). Remarkable agrivoltaic influence on soil moisture, micrometeorology and water-use efficiency. PloS one, 13(11), e0203256.

Andrew, A. C., Higgins, C. W., Smallman, M. A., Graham, M., & Ates, S. (2021). Herbage yield, lamb growth and foraging behavior in agrivoltaic production system. Frontiers in Sustainable Food Systems, 126.

Armstrong, A., Ostle, N. J., & Whitaker, J. (2016). Solar park microclimate and vegetation management effects on grassland carbon cycling. Environmental Research Letters, 11(7), 074016.

Atkin, O. K., & Tjoelker, M. G. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. Trends in plant science, 8(7), 343-351.

Bai, Z., Jia, A., Bai, Z., Qu, S., Zhang, M., Kong, L., ... & Wang, M. (2022). Photovoltaic panels have altered grassland plant biodiversity and soil microbial diversity. Frontiers in Microbiology, 13, 1065899.

Barron-Gafford, G. A., Pavao-Zuckerman, M. A., Minor, R. L., Sutter, L. F., Barnett-Moreno, I., Blackett, D. T., ... & Macknick, J. E. (2019). Agrivoltaics provide mutual benefits across the food–energy–water nexus in drylands. *Nature Sustainability*, *2*(9), 848-855.

Cabon, A., Kannenberg, S. A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., ... & Anderegg, W. R. (2022). Cross-biome synthesis of source versus sink limits to tree growth. Science, 376(6594), 758-761.

Chazdon, R. L., & Pearcy, R. W. (1991). The importance of sunflecks for forest understory plants. BioScience, 41(11), 760-766.

Choi, C. S., Cagle, A. E., Macknick, J., Bloom, D. E., Caplan, J. S., & Ravi, S. (2020). Effects of revegetation on soil physical and chemical properties in solar photovoltaic infrastructure. Frontiers in Environmental Science, 8, 140.

Choi, C. S., Macknick, J., Li, Y., Bloom, D., McCall, J., & Ravi, S. (2023). Environmental Co-Benefits of Maintaining Native Vegetation With Solar Photovoltaic Infrastructure. Earth's Future, 11(6), e2023EF003542.

Dinesh, H., & Pearce, J. M. (2016). The potential of agrivoltaic systems. *Renewable and Sustainable Energy Reviews*, *54*, 299-308.

Dupraz, C., Marrou, H., Talbot, G., Dufour, L., Nogier, A., & Ferard, Y. (2011). Combining solar photovoltaic panels and food crops for optimising land use: Towards new agrivoltaic schemes. *Renewable energy*, *36*(10), 2725-2732.

Duursma, R. A. (2015). Plantecophys-an R package for analysing and modelling leaf gas exchange data. PloS one, 10(11), e0143346.

Ellsworth, D. S., & Reich, P. B. (1992). Leaf mass per area, nitrogen content and photosynthetic carbon gain in Acer saccharum seedlings in contrasting forest light environments. Functional Ecology, 423-435.

Emmel, C., D'Odorico, P., Revill, A., Hörtnagl, L., Ammann, C., Buchmann, N., & Eugster, W. (2020). Canopy photosynthesis of six major arable crops is enhanced under diffuse light due to canopy architecture. Global change biology, 26(9), 5164-5177.

Farquhar, G. D., von Caemmerer, S. V., & Berry, J. A. (1980). A biochemical model of photosynthetic CO 2 assimilation in leaves of C 3 species. planta, 149, 78-90.

Feldman, D., Ramasamy, V., Fu, R., Ramdas, A., Desai, J., & Margolis, R. (2021). US solar photovoltaic system and energy storage cost benchmark (Q1 2020) (No. NREL/TP-6A20-77324). National Renewable Energy Lab.(NREL), Golden, CO (United States).

Graham, M., Ates, S., Melathopoulos, A. P., Moldenke, A. R., DeBano, S. J., Best, L. R., & Higgins, C. W. (2021). Partial shading by solar panels delays bloom, increases floral abundance during the late-season for pollinators in a dryland, agrivoltaic ecosystem. Scientific reports, 11(1), 7452.

Hernandez, R. R., Armstrong, A., Burney, J., Ryan, G., Moore-O'Leary, K., Diédhiou, I., ... & Kammen, D. M. (2019). Techno–ecological synergies of solar energy for global sustainability. Nature Sustainability, 2(7), 560-568.

Hernandez, R. R., Tanner, K. E., Haji, S., Parker, I. M., Pavlik, B. M., & Moore-O'Leary, K. A. (2020). Simulated photovoltaic solar panels alter the seed bank survival of two desert annual plant species. Plants, 9(9), 1125.

Juillion, P., Lopez, G., Fumey, D., Lesniak, V., Génard, M., & Vercambre, G. (2022). Shading apple trees with an agrivoltaic system: Impact on water relations, leaf morphophysiological characteristics and yield determinants. Scientia Horticulturae, 306, 111434.

Kannenberg, S. A., Sturchio, M. A., Venturas, M. D., & Knapp, A. K. (2023). Grassland carbon-water cycling is minimally impacted by a photovoltaic array. Communications Earth & Environment, 4(1), 238.

Knapp, A. K., Fay, P. A., Blair, J. M., Collins, S. L., Smith, M. D., Carlisle, J. D., ... &

McCarron, J. K. (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science, 298(5601), 2202-2205.

Kull, O., & Kruijt, B. (1998). Leaf photosynthetic light response: a mechanistic model for scaling photosynthesis to leaves and canopies. Functional Ecology, 12(5), 767-777.

La Pierre, K. J., Blumenthal, D. M., Brown, C. S., Klein, J. A., & Smith, M. D. (2016). Drivers of variation in aboveground net primary productivity and plant community composition differ across a broad precipitation gradient. Ecosystems, 19, 521-533.

Larson, E. (2020). Net-zero America: potential pathways, infrastructure, and impacts. Princeton University.

Marrou, H., Guilioni, L., Dufour, L., Dupraz, C., & Wery, J. (2013). Microclimate under agrivoltaic systems: Is crop growth rate affected in the partial shade of solar panels?. *Agricultural and Forest Meteorology*, *177*, 117-132.

Marshall, B., & Biscoe, P. V. (1980). A model for C3 leaves describing the dependence of net photosynthesis on irradiance. Journal of Experimental Botany, 31(1), 29-39.

Ocheltree, T. W., Nippert, J. B., & Prasad, P. V. V. (2012). Changes in stomatal conductance along grass blades reflect changes in leaf structure. Plant, cell & environment, 35(6), 1040-1049.

Post, A. K., & Knapp, A. K. (2021). How big is big enough? Surprising responses of a semiarid grassland to increasing deluge size. Global Change Biology, 27(6), 1157-1169.

R Core Team. 2017. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Sala, O. E., Parton, W. J., Joyce, L. A., & Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. Ecology, 69(1), 40-45.

Salmon, Y., Lintunen, A., Dayet, A., Chan, T., Dewar, R., Vesala, T., & Hölttä, T. (2020). Leaf carbon and water status control stomatal and nonstomatal limitations of photosynthesis in trees. New phytologist, 226(3), 690-703.

Smith, S.D., Patten, D.T. and Monson, R.K., (1987). Effects of artificially imposed shade on a Sonoran Desert ecosystem: microclimate and vegetation. Journal of Arid Environments, 13(1), pp.65-82.

Smith, N. G., & Dukes, J. S. (2013). Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO 2. Global change biology, 19(1), 45-63.

Smith, N. G., & Dukes, J. S. (2017). Short-term acclimation to warmer temperatures accelerates leaf carbon exchange processes across plant types. Global change biology, 23(11), 4840-4853.

Stinziano, J. R., Roback, C., Sargent, D., Murphy, B. K., Hudson, P. J., & Muir, C. D. (2021). Principles of resilient coding for plant ecophysiologists. AoB Plants, 13(5), plab059.

Sturchio, M. A., Macknick, J. E., Barron-Gafford, G. A., Chen, A., Alderfer, C., Condon, K., ... & Knapp, A. K. (2022). Grassland productivity responds unexpectedly to dynamic light and soil water environments induced by photovoltaic arrays. *Ecosphere*, *13*(12), e4334.

Sturchio, M. A., & Knapp, A. K. (2023). Ecovoltaic principles for a more sustainable, ecologically informed solar energy future. Nature Ecology & Evolution, 1-4.

Sturchio, M. A., Kannenberg, S. A., & Knapp, A. K. (2024). Agrivoltaic arrays can maintain semi-arid grassland productivity and extend the seasonality of forage quality. *Applied Energy*, 356, 122418.

Tanner, K. E., Moore-O'Leary, K. A., Parker, I. M., Pavlik, B. M., & Hernandez, R. R. (2020). Simulated solar panels create altered microhabitats in desert landforms. Ecosphere, 11(4), e03089.

Tanner, K. E., Moore-O’Leary, K. A., Parker, I. M., Pavlik, B. M., Haji, S., & Hernandez, R. R. (2021). Microhabitats associated with solar energy development alter demography of two desert annuals. Ecological Applications, 31(6), e02349.

Thornley, J. H. M. (1974). Light fluctuations and photosynthesis. Annals of Botany, 38(2), 363-373.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... & Villar, R. (2004). The worldwide leaf economics spectrum. Nature, 428(6985), 821-827.

Wynne-Sison, T., Devitt, D. A., & Smith, S. D. (2023). Ecovoltaics: Maintaining Native Plants and Wash Connectivity inside a Mojave Desert Solar Facility Leads to Favorable Growing Conditions. Land, 12(10), 1950.

Yamori, W., Hikosaka, K., & Way, D. A. (2014). Temperature response of photosynthesis in C3, C4, and CAM plants: temperature acclimation and temperature adaptation. Photosynthesis research, 119, 101-117.

Zhang, B., Zhang, R., Li, Y., Wang, S., Zhang, M., & Xing, F. (2024). Deploying photovoltaic arrays in degraded grasslands is a promising win-win strategy for promoting grassland restoration and resolving land use conflicts. Journal of Environmental Management, 349, 119495.

# CHAPTER 5: AGRIVOLTAIC ARRAYS CAN MAINTAIN SEMI-ARID GRASSLAND PRODUCTIVITY AND EXTEND THE SEASONALITY OF FORAGE QUALITY[3]

## 5.1 Summary

The co-location of photovoltaic energy generation and agricultural land use (Agrivoltaics, AV) has become increasingly popular in recent years. Although the benefits of AV in croplands have great promise, the development of AV systems has primarily occurred in former grasslands and sites now managed as grasslands, because of their relatively flat topography and consistently high solar irradiation. Evidence is accumulating that grassland productivity can be maintained within solar arrays, but how grassland productivity responds to grazing within solar arrays is largely unknown, despite the prevalence of grazing as a vegetation management option. Here, we report the results of a study aimed at quantifying how a semi-arid $C_3$ grassland growing beneath an AV system in Colorado (USA) responded to simulated grazing treatments (canopy removal in June or July). In the absence of simulated grazing, there were no differences between aboveground primary production in the AV grassland vs. an adjacent control grassland. However, simulated grazing in June and July had a compensatory effect and, in some cases, annual productivity exceeded that in the control grassland. Additionally, we found that simulated grazing increased forage protein content later into the growing season compared to un-grazed AV and control sites. Overall, our results indicate that grazing within a grassland AV array is unlikely to negatively impact forage production, and that forage quality in this semi-arid region may even be increased later into the growing season with grazing.

---

[3] Sturchio, M. A., Kannenberg, S. A., & Knapp, A. K. (2024). Agrivoltaic arrays can maintain semi-arid grassland productivity and extend the seasonality of forage quality. *Applied Energy*, 356, 122418.

## 5.2 Introduction

Increasing energy production from ground mounted photovoltaic (PV) solar arrays is a realistic approach for reducing greenhouse gas emissions in the near term (IPCC 2023). However, the land area required for PV is much greater than that of fossil fuel-based energy systems (US DOE 2021), and the requirements of this land are more stringent. The ideal locations for PV arrays are topographically flat with high annual solar irradiation. However, if water is available, most of this land is currently used for agricultural production (e.g., croplands and forage production, Adeh et al. 2019), which creates a land-use conflict and hinders the widespread deployment of PV.

To alleviate some of this land use tension and improve the sustainability of PV development, agrivoltaic systems (AV), where agriculture and energy production are co-located on the same land, have emerged as a promising solution (Dupraz et al. 2011, Macknick et al. 2013, Dinesh & Pearce 2016, Barron-Gafford et al. 2019, Macknick et al. 2022). In some cases, AV facilities have been shown to improve growing conditions for the plants beneath and reduce the water demand of specialty crops (Barron-Gafford et al. 2019). However, concerns related to the use of farm equipment around PV structures, the long-term productivity of prime agricultural land, and sociopolitical hurdles have limited the expansion of crop producing AV at the gigawatt (GW) scale (Pascaris et al. 2020, 2021). For these reasons and others, AV development co-located with grazing lands and/or pollinator habitat has become the most popular version of AV in the US, currently covering ~100x greater land area than that of crop producing AV arrays (Inspire Agrivoltaics Map, https://openei.org/wiki/InSPIRE/Agrivoltaics_Map). Given this disproportionate interest in non-crop AV development, including interest in “ecovoltaic” approaches where ecosystem services are prioritized within PV arrays (Sturchio and Knapp 2023), it is important that we quantify how PV arrays alter ecosystem function.

Vegetation management is of high importance in AV arrays, in particular reducing the height of vegetation to avoid panel shading. While mowing has traditionally been the means to accomplish this, grazing at AV facilities has recently been deployed as a cost reduction strategy that adds an additional layer of land use functionality (McCall et al. 2023). In the upcoming decade, the number of AV facilities utilizing grazing management is likely to grow, and although operators and practitioners have begun to develop these strategies, there is a clear need to better understand how the unique microenvironments beneath solar panels interact with management strategies to impact forage production and plant nutritional quality throughout the growing season. Past studies of grassland AV facilities (without grazing) have shown that PV panels alter ecological processes that regulate ecosystem health and function (Armstrong et al. 2016, Adeh et al. 2018, Sturchio et al. 2022, Kannenberg et al. 2023). In Oregon, USA, where precipitation inputs are highest during cool winter months (i.e., Mediterranean climate), researchers reported an inverse relationship between productivity and forage quality in a grass dominated pasture, where low productivity microenvironments beneath PV arrays supported higher quality forage (Andrew et al. 2021). In a complementary study, delays in flowering phenology were related to unique AV microenvironments (Graham et al. 2021), with potential implications for extending the grazing season and buffering climate driven pollinator mismatch (Walston et al. 2022, Choi et al. 2023, Sturchio and Knapp 2023). The impacts of grazing on forage productivity and quality, though, have yet to be investigated.

Short-statured grassland ecosystems like those of the semi-arid western US are ideal candidates for PV development because they require minimal management and are generally more limited by water than light (Sturchio and Knapp 2023). In an AV array located in semi-arid Colorado, USA, panel-induced heterogeneity in environmental drivers alter patterns of plant productivity (Sturchio et al. 2022). However, soil moisture, which is typically a strong predictor of productivity in water limited grasslands (Sala and Lauenroth 1982, Sala et al. 1988, Gherardi & Sala 2019), was only weakly related to the patterns of aboveground net primary production (ANPP). This highlights the significant uncertainties that remain with regards to semi-arid grassland AV systems and controls on forage production. For example, grazing in semi-arid rangelands has been shown to promote a compensatory growth response of new tissue that is high in nitrogen (N), and which can enhance overall ANPP (Oesterheld and McNaughton 1991, Van Staalduinen and Anten 2005). Yet, the impacts of different grazing regimes on forage productivity and quality have yet to be investigated in a semi-arid AV ecosystem. Such research is necessary to inform and guide the widespread deployment of AV systems geared towards forage production.

Here, we report the results of a study aimed at understanding how a semi-arid $C_3$ grassland previously managed for hay production, responded to different simulated grazing management strategies within an AV array. Our goals were to 1) quantify how the timing of grazing alters overall productivity, and whether those patterns differ between the distinct microenvironments generated by solar arrays, and 2) determine whether forage quality changes throughout the growing season and if those changes differ between distinct microenvironments. Based on previous work in this solar array (Sturchio et al. 2022) and independent research in grazed grasslands (*e.g.,* Knapp et al. 2012), we expected that 1) more favorable microenvironments (*e.g.,* high soil moisture and afternoon shade) will support increased production consistently throughout the growing season despite reductions in light availability, 2) the heterogeneous AV microclimate will alter the seasonality of forage quality, and 3) grazing treatments will improve overall production, and regrowth forage quality will be higher in grazed plots regardless of grazing timing.

## 5.3 Materials and Methods

### 5.3.1 Experimental Design

The research was conducted at Jack's Solar Garden (JSG), an agrivoltaic learning and research facility (https://www.jackssolargarden.com/) near Longmont, CO (elevation 1508 m, 40°07′18.9″ N, 105°07′49.9″ W). The climate is semiarid with a mean annual temperature of 9.7°C and 365 mm of precipitation annually (Colorado Climate Center; http://ccc.atmos.colostate.edu/). Historically, the 1.5-ha site was irrigated and managed for hay production, but active agricultural management ended in 2019 when the PV array was installed. The grassland section at JSG is a remnant of the non-native grasses and forbs that were originally planted for hay production. The site is dominated (>90% cover) by the perennial $C_3$ grass, Smooth Brome (*Bromus inermis*), with scattered individuals of Orchard Grass (*Dactylis glomerata*, $C_3$ perennial grass), Alfalfa (*Medicago sativa*, $C_3$ legume), and Yellow Salsify (*Tragopogon dubius*, $C_3$ forb) interspersed. These species are all highly palatable forage products that range in terms of quality (e.g., *M. sativa* is a nitrogen fixer and therefore has higher protein content than *B. inermis*). Individual PV panels at JSG are 2 m (east–west) × 1 m (north–south) and are mounted in series on a single-axis-tracking system (tracking east–west, Fig. 5.1). The tracking system is bound to a maximum angle of 45° to the east in the morning and west in the afternoon. When PV panels are parallel with the ground (at solar noon and overnight), there is approximately 3.2 m of interspace between the western edge of one row of panels and the eastern edge of the next row. Because taller panel heights provide greater potential for various management strategies, in this case grazing by sheep or cattle, we chose to utilize the east side of the array which has elevated panels mounted 2.4 m (8 ft) off the ground.

We established four transects perpendicular to rows of PV panels, each comprised of 4 replicate sampling points along the environmental gradient created by the PV panels ($E_{edge}$; beneath eastern edge of panel where rainfall is redistributed, $W_{edge}$; beneath western edge of panel where rainfall is redistributed, *Beneath*; directly beneath panel, in line with the panel support beams, and *Between*; between rows of panels, Fig. 5.2). Each experimental plot was 1 × 0.5 m with a 1 m north-south gap separating transects. Each transect was assigned an aboveground biomass removal treatment (simulating grazing) in June or July, or no biomass removal (un-grazed) and all plots were harvested at the end of the season (EOS, September 29th) to estimate Aboveground Net Primary Productivity (ANPP). We selected June for the first grazing treatment because it aligned with 1) peak inflorescence, and 2) a timepoint when AV managers typically graze to reduce vegetation height. We added a second timepoint (July) to determine whether forage quality would remain consistent or decline throughout the growing season. If "grazed" before EOS, the biomass removed previously was added to the EOS harvest for total annual ANPP estimates. A control transect, with four sampling plots, was located ~10 m outside the array and sampled at EOS. To estimate ANPP, we harvested aboveground biomass to ground level within 0.1-$m^2$ using quadrats centered in experimental plots. We recognize that complete biomass removal at this small scale does not perfectly simulate large herbivore grazing patterns, but it does remove the canopy, providing us with a measure of post-grazing regrowth potential along the varying locations within the PV array. Because the site had been mowed in 2021, aboveground biomass accumulating in 2022 represented ANPP for that year. While harvesting, biomass was sorted by functional group (grass vs. forb), then dried at 60°C for 72 h before being weighed to the nearest 0.01 g. Dried plant tissue was ground and analyzed for total plant N via an elemental analyzer at the Colorado State University Soil, Water, and Plant Testing Laboratory (agsci.colostate.edu/soiltestinglab). Percent plant N values were converted to % crude protein (%CP) by applying the commonly used conversion factor of 6.25 (Krul 2019).

### 5.3.2 Environmental measurements

Air temperature ($T_{air}$) and relative humidity (RH%) were continuously recorded at a meteorological station on site at JSG throughout the growing season (May-September 2022) and were used to calculate vapor pressure deficit (VPD). Previous measurements of photosynthetic photon flux density (PPFD) have documented general trends of light availability within this PV facility (Sturchio et al. 2022, Kannenberg et al. 2023). In summary, *Beneath* plots received only ~30% of diurnal light energy compared to control plots, most of which comes in the form of direct sunlight in the early morning and late afternoon, $W_{edge}$ (~42%) mostly in the afternoon, $E_{edge}$ (~47%) mostly in the morning, and *Between* (~70%) when the sun is at its highest point, typically between the hours of 9:30am-3:30pm.

Volumetric water content (VWC, referred to as SM hereafter) was measured in an adjacent section of JSG every 15 minutes for all experimental and control plots using CS616 Soil Moisture Sensors (Campbell Scientific, Logan, UT). Each plot received a 30cm probe inserted at a 45° angle for integrated measurements of 0-15 cm SM. In most grasslands in this semiarid region and even in more mesic regions, the majority of root biomass is found in the upper 20 cm (see Post & Knapp, 2020), therefore, in Fig 5.2 we reported 0-15 cm SM.

### 5.3.3 Data analysis

Our primary goal was to assess how PV panels altered patterns of ANPP and forage quality across space and in response to different simulated grazing treatments. To do this we used treatment specific (June, July, EOS, June regrowth, July regrowth) one-way analyses of variance (ANOVA) to determine how productivity varied across plot level microsites ($W_{edge}$, *Beneath*, $E_{edge}$, *Between*). Measurements were then weighted by percentage of total field area ($W_{edge}$ = 11.5%, $E_{edge}$ = 11.5%, *Beneath* = 27%, *Between* = 50%) to compare ANPP between AV management treatments and controls at the array-scale. Because forage quality (i.e., plant N) is a spot measurement and cannot be added over time like other accumulative measurements (e.g., ANPP), we used a two-way ANOVA (Microsite × Management Treatment) to compare how % crude protein (%CP) varied across space and seasonally between different management treatments. All analyses were performed in R version 4.1.2 using R stats Package developed by R Core Team (R Core Team, 2017). All data met the normal distribution assumptions of ANOVA, requiring no transformation.

## 5.4 Results

### 5.4.1 Environmental

In 2022, annual precipitation at the site was 11% higher than the long-term average (404 vs. 365 mm, respectively). However, the early growing season (April, May, June) was ~40% drier than normal (89 mm in 2022 vs. 148 mm average), and the late growing season (July, August) was ~30% wetter than the long-term average (96 mm vs. 65 mm, Colorado Climate Center; http://ccc.atmos.colostate.edu/). Because of this pattern in water availability, monthly means of plot level SM were relatively consistent throughout the growing season (Fig. 5.2, bottom). Mean annual temperature (10.2 °C) was lower than in 2021 (10.6 °C), but still slightly above the 30-year average (9.8 °C).

### 5.4.2 Productivity

As predicted, and consistent with results from the same site in 2021 (Sturchio et al. 2022), ANPP measured at the end of the growing season was significantly higher at the $E_{edge}$ of PV panels than all other experimental and control plots ($p < 0.001$, Fig. 5.3). This spatial pattern was consistent across un-grazed and grazed treatments. In addition, *Beneath* panel plots in June grazed and un-grazed treatments were significantly less productive than all other microsites within the array ($p = 0.02$, Fig. 5.3). Patterns of regrowth were proportionally similar across microsites, compensating between 24-36% and 15-24% of ANPP in June and July grazed treatments respectively. For example, EOS re-sampling of June grazed plots (i.e., second sampling, see Fig. 5.3 hatched bars), indicated that re-growth was significantly higher in $E_{edge}$ plots compared to *Beneath* and *Between* plots ($p < 0.001$), with *Beneath* plots having significantly lower re-growth than both $E_{edge}$ and $W_{edge}$.

Area weighted means, an analog for field-level ANPP, revealed that un-grazed AV was ~8% ($p = 0.22$, not significant) less productive when compared to control plots (297 g $m^{-2}$ vs. 326 g $m^{-2}$). However, when the same scaling was applied to total ANPP (including regrowth) from June and July grazed treatments, area weighted ANPP was ~10% ($p = 0.13$, not significant) and ~7% ($p = 0.34$, not significant) higher than un-grazed controls, respectively (Fig. 5.4).

### 5.4.3 Forage quality

In line with our hypothesis, we found consistent declines in forage quality throughout the growing season across all AV microsites (Fig. 5.5). Providing further support for our hypothesis, a two-way ANOVA revealed strong Microsite × Management Treatment interactions ($p < 0.001$), indicating that microsite level differences in forage quality also differed across treatments. For example, control plants, which were only sampled at EOS, had ~30% higher forage quality (crude protein, %CP) when compared to all un-grazed AV plants at EOS. However, %CP was similar for June sampled AV plants and EOS control plants. Furthermore, grazed AV plots re-sampled at EOS had similar %CP values to that of controls, and in the case of July grazed $E_{edge}$ plants, EOS %CP was ~35% higher than that of controls (Fig. 5.5).

## 5.5 Discussion

Forage production (or ANPP) in grasslands is a valuable ecosystem service that is important for the economics of grazing as an agricultural land use (Irisarri et al. 2019). In this study we found that an elevated AV array, built to maximize energy production and accommodate grazing, did not have a significant impact on end of season ANPP totals in the absence of simulated grazing activity. More importantly, re-growth following simulated grazing led to equal or greater ANPP than in un-grazed sites at all microenvironment locations throughout the array. Consistent with predictions informed by previous work (Sturchio et al. 2022, Kannenberg et al. 2023), plants grown on the $E_{edge}$ were the most productive throughout the growing season and in response to simulated grazing treatments. This consistency across the growing season and in response to grazing treatments supports our hypothesis that AV microenvironments with morning sun (when air temperatures and VPD are low) would be more conducive to $C_3$ grass production (Yamori et al. 2013). Although there are still many questions regarding array designs for optimized facilitation of ecosystem services within solar arrays (Randle-Boggis et al. 2020, Blaydes et al. 2021, Sturchio and Knapp 2023), this finding indicates that a previously managed low diversity semi-arid grassland can maintain productivity within an AV array and that the timing of grazing is unlikely to strongly affect total annual productivity.

### 5.5.1 Patterns of forage quality

Patterns of forage quality were consistent across space and over time in AV plots. The observed steady decline in CP throughout the growing season following peak inflorescence (end of June-beginning of July) is consistent with the seasonal translocation of nitrogen out of leaf tissue and into roots and rhizomes as grasslands senesce and enter dormancy (Hayes 1985, Heckathorn and DeLucia 1994). Previous work has demonstrated that AV arrays can delay the phenology (seasonal timing) of flowering (Graham et al. 2021), and we hypothesize that differences in end of season forage quality between AV and control plants might also be due to the influence that solar arrays have on phenological patterns. We did not measure control forage quality throughout the growing season, so we are unable to definitively determine phenological differences between AV and control. However, differences in either direction (i.e., earlier spring, delayed fall) have positive implications for extending the growing and grazing season.

Grazed plots, however, were able to overcome the seasonal decline in CP through the formation of new, CP rich plant material. Indeed, grazing and defoliation have been shown to functionally reset the forage quality clock as new aboveground tissue with high CP form (Nowak and Caldwell 1984, Van Staalduinen and Anten 2005). We found a similar response to our simulated grazing treatments where regrowth was of similar or greater quality than that of early season forage.

Overall, our findings indicate that un-grazed AV pasture had lower forage quality than that of un-grazed control pasture at EOS, however re-growth forage quality exceeded CP levels of un-grazed control pasture, indicating that capacity for high quality forage within AV array might be related to the seasonal timing when sampling occurred. We hypothesize that incorporating ungulate grazers into grassland AV, in addition to adding a layer of functionality to the land beneath PV, could potentially extend the availability of high-quality forage. What remains an untested yet important question, is how the interaction between AV development and grazing unfolds in more diverse native grasslands where $C_3$ and $C_4$ grasses co-exist. Future research that explores this interaction within PV arrays and grazing management is needed to devise effective strategies that improve the sustainability of solar grazing in semi-arid climates. Synergistic efforts that examine animal behavior (Kampherbeek et al. 2022), ungulate forage preference (Pauler et al. 2020), and their influence on grassland AV ecosystem processes will be integral for advising the future of AV grazing management.

### 5.5.2 Implications of AV in managed semi-arid grasslands

Grassland productivity is directly related to animal productivity and reproductive success (Frank et al. 1998, Daskin and Pringle 2016). As grazing becomes more frequently utilized as a strategy for maintaining vegetation in semi-arid grassland AV arrays, careful consideration must be given to the subsequent impact that AV have on forage production and quality. Overall, our results indicate that an AV array designed with row spacing intended to maximize energy production did not significantly reduce forage production or quality in a $C_3$ dominated grassland. Additionally, the system maintained the capacity to recover from simulated grazing through compensatory growth. Indeed, in regions where water scarcity is of concern, the combination of enhanced water savings (Kannenberg et al. 2023) and support of crucial ecosystem services like forage production could make AV a useful water conservation strategy that supports agricultural land use beneath solar arrays.

## 5.6 Figures

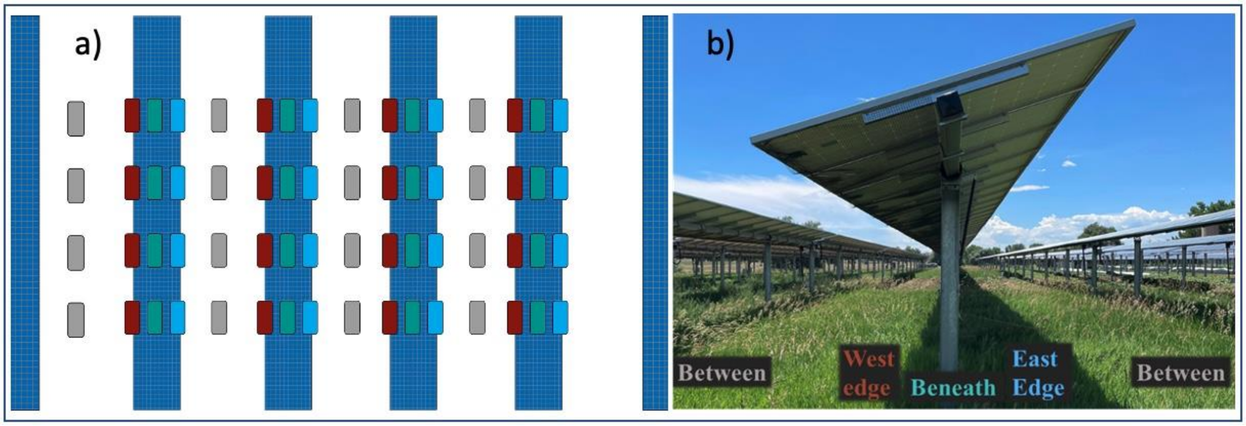


**Figure 5.1.** Conceptual figure of experimental design. Microsites (panel b) are color coded in the transect map (panel a) to demonstrate Microsite × Transect design. Control plots were in part of the field that received no abiotic influence from PV panels.

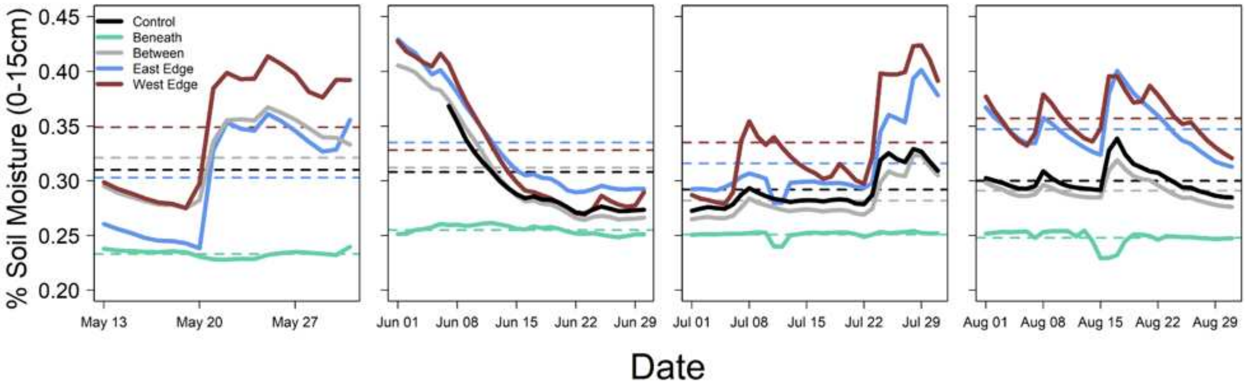


**Figure 5.2.** Soil moisture (SM, 0-15 cm) throughout the growing season, broken up by month, with monthly means shown as dashed horizontal lines.

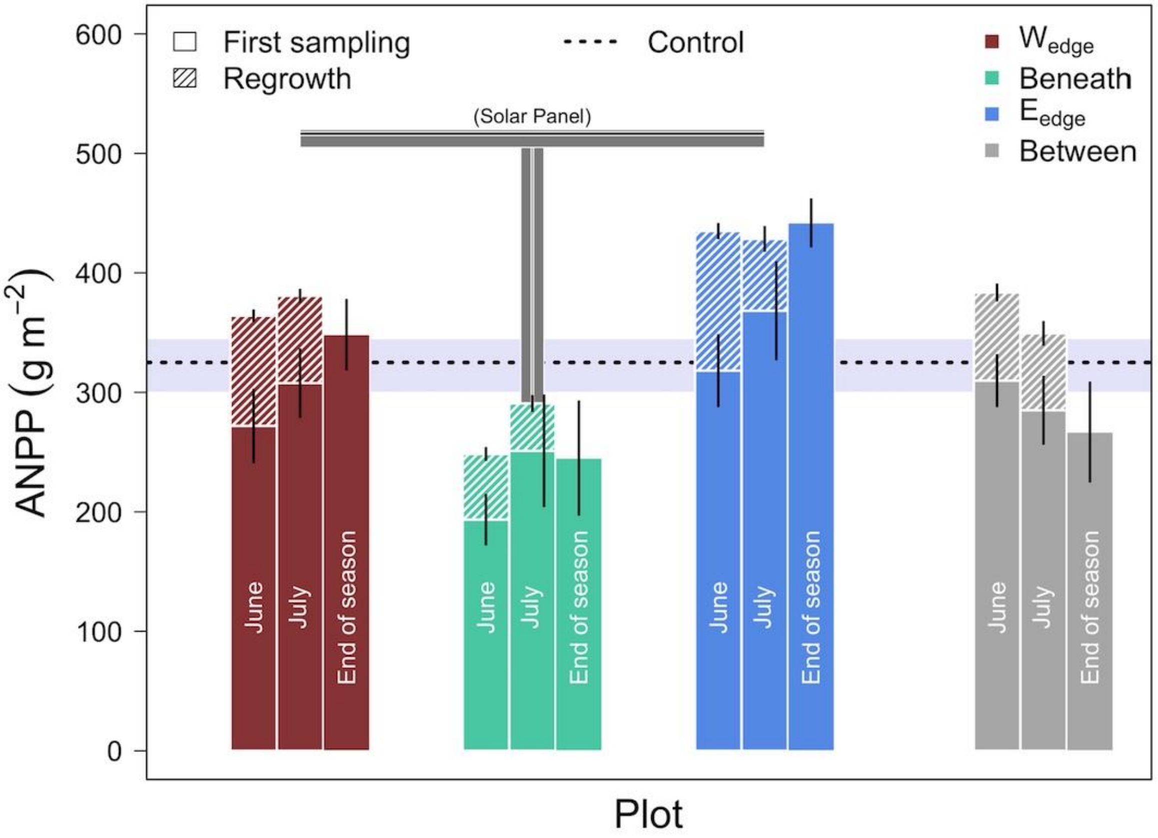


**Figure 5.3.** Means and standard errors of aboveground net primary productivity (ANPP). Text inside of bars denotes timepoint at which first sampling occurred (e.g., June, July, and end of the growing season). Hatched bars represent re-growth biomass sampled at the end of the growing season. Control plot means (sampled once at the end of the growing season) are presented with a dashed line and purple shadow which signifies ± standard error.

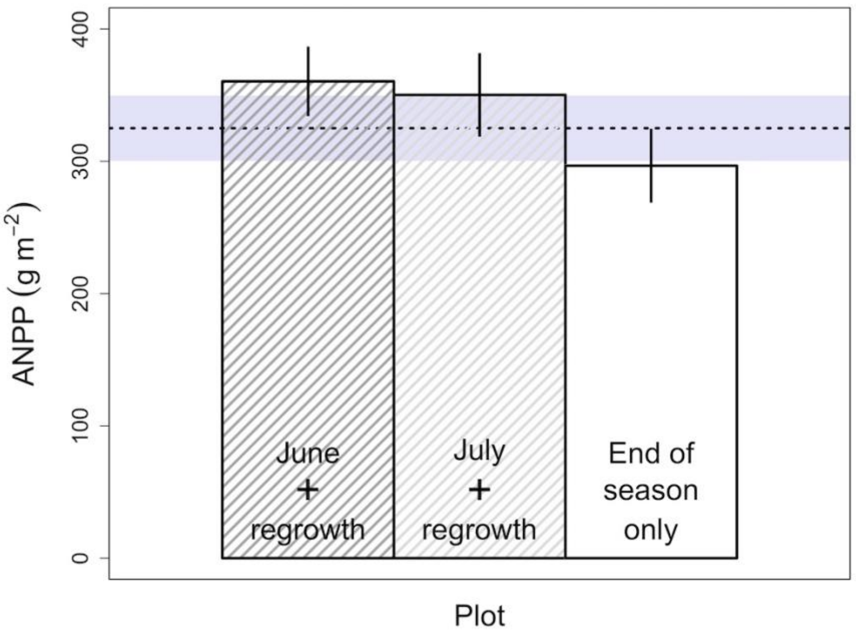


**Figure 5.4.** Management treatments scaled by area weighted means across plots to demonstrate Array level ANPP. As shown in previous figures control plot means sampled once at the end of the growing season are presented with a dashed line and purple shadow which signifies ± standard error.

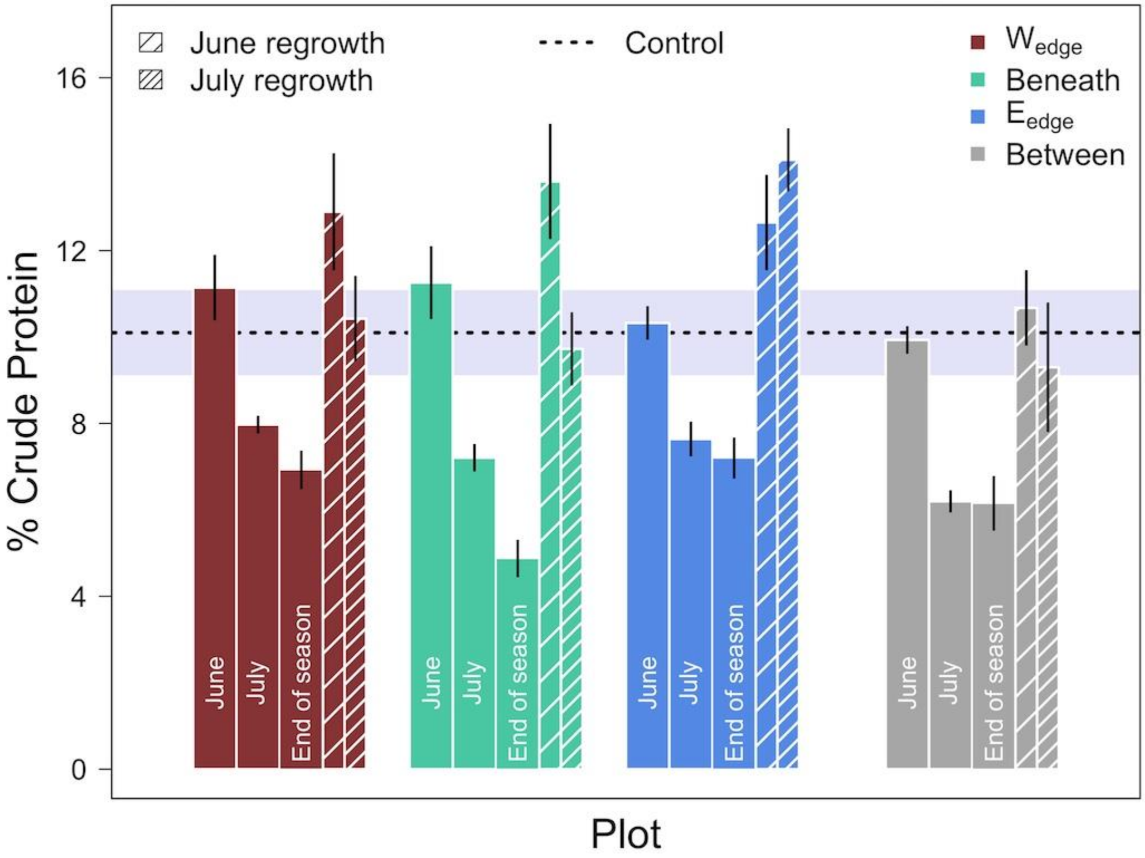


**Figure 5.5.** Means of crude protein analysis. Text inside of bars denotes timepoint when sampling occurred (e.g., June, July, and end of the growing season). Hatched bars represent re-growth biomass sampled at the end of the growing season. Control plot means (sampled once at the end of the growing season) are presented with a dashed line and purple shadow which signifies ± standard error.

# LITERATURE CITED

Adeh, E.H., Selker, J. S., & Higgins, C. W. (2018). Remarkable agrivoltaic influence on soil moisture, micrometeorology, and water-use efficiency. PloS one, 13(11), e0203256.

Adeh, E. H., Good, S. P., Calaf, M., & Higgins, C. W. (2019). Solar PV power potential is greatest over croplands. Scientific reports, 9(1), 11442.

Andrew, A. C., Higgins, C. W., Smallman, M. A., Graham, M., & Ates, S. (2021). Herbage yield, lamb growth and foraging behavior in agrivoltaic production system. Frontiers in Sustainable Food Systems, 5, 659175.

Armstrong, A., Ostle, N. J., & Whitaker, J. (2016). Solar Park microclimate and vegetation management effects on grassland carbon cycling. Environmental Research Letters, 11(7), 074016.

Barron-Gafford, G. A., Pavao-Zuckerman, M. A., Minor, R. L., Sutter, L. F., Barnett-Moreno, I., Blackett, D. T., ... & Macknick, J. E. (2019). Agrivoltaics provide mutual benefits across the food–energy–water nexus in drylands. Nature Sustainability, 2(9), 848-855.

Blaydes, H., Potts, S. G., Whyatt, J. D., & Armstrong, A. (2021). Opportunities to enhance pollinator biodiversity in solar parks. Renewable and Sustainable Energy Reviews, 145, 111065.

Choi, C. S., Macknick, J., Li, Y., Bloom, D., McCall, J., & Ravi, S. (2023). Environmental Co-Benefits of Maintaining Native Vegetation with Solar Photovoltaic Infrastructure. Earth's Future, 11(6), e2023EF003542.

Daskin, J. H., & Pringle, R. M. (2016). Does primary productivity modulate the indirect effects of large herbivores? A global meta-analysis. Journal of Animal Ecology, 85(4), 857-868.

Dinesh, H., & Pearce, J. M. (2016). The potential of agrivoltaic systems. *Renewable and Sustainable Energy Reviews*, 54, 299-308.

Dupraz, C., Marrou, H., Talbot, G., Dufour, L., Nogier, A., & Ferard, Y. (2011). Combining solar photovoltaic panels and food crops for optimising land use: Towards new agrivoltaic schemes. Renewable energy, 36(10), 2725-2732.

Frank D.A., McNaughton S.J., Tracy B.F., (1998). The ecology of the earth's grazing ecosystems: profound functional similarities exist between the serengeti and yellowstone. Bioscience, 48, 514–521.

Gherardi, L. A., & Sala, O. E. (2019). Effect of interannual precipitation variability on dryland productivity: A global synthesis. Global Change Biology, 25(1), 269-276.

Graham, M., Ates, S., Melathopoulos, A. P., Moldenke, A. R., DeBano, S. J., Best, L. R., & Higgins, C. W. (2021). Partial shading by solar panels delays bloom, increases floral abundance during the late-season for pollinators in a dryland, agrivoltaic ecosystem. Scientific Reports, 11(1), 1-13.

Hayes, D. C. (1985). Seasonal nitrogen translocation in big bluestem during drought conditions. Rangeland Ecology & Management/Journal of Range Management Archives, 38(5), 406-410.

Heckathorn, S. A., & DeLucia, E. H. (1994). Drought-induced nitrogen retranslocation in perennial C4 grasses of tallgrass prairie. Ecology, 75(7), 1877-1886.

Irisarri, J. G., Derner, J. D., Ritten, J. P., & Peck, D. E. (2019). Beef production and net revenue variability from grazing systems on semiarid grasslands of North America. Livestock Science, 220, 93-99.

Kampherbeek, E. W., Webb, L. E., Reynolds, B. J., Sistla, S. A., Horney, M. R., Ripoll-Bosch, R., ... & McFarlane, Z. D. (2022). A preliminary investigation of the effect of solar panels and rotation frequency on the grazing behavior of sheep (Ovis aries) grazing dormant pasture. Applied Animal Behaviour Science, 105799.

Kannenberg, S. A., Sturchio, M. A., Venturas, M. D., & Knapp, A. K. (2023). Grassland carbon-water cycling is minimally impacted by a photovoltaic array. Communications Earth & Environment, 4(1), 238.

Knapp, A. K., Hoover, D. L., Blair, J. M., Buis, G., Burkepile, D. E., Chamberlain, A., ... & Zinn, A. (2012). A test of two mechanisms proposed to optimize grassland aboveground primary productivity in response to grazing. Journal of Plant Ecology, 5(4), 357-365.

Krul, E. S. (2019). Calculation of nitrogen-to-protein conversion factors: A review with a focus on soy protein. Journal of the American Oil Chemists' Society, 96(4), 339-364.

Macknick, J., Beatty, B., & Hill, G. (2013). Overview of opportunities for co-location of solar energy technologies and vegetation (No. NREL/TP-6A20-60240). National Renewable Energy Lab.(NREL), Golden, CO (United States).

Macknick, J., Hartmann, H., Barron-Gafford, G., Beatty, B., Burton, R., Seok-Choi, C., ... & Walston, L. (2022). The 5 Cs of Agrivoltaic Success Factors in the United States: Lessons From the InSPIRE Research Study (No. NREL/TP-6A20-83566). National Renewable Energy Lab.(NREL), Golden, CO (United States).

McCall, J., Macdonald, J., Burton, R., & Macknick, J. (2023). Vegetation Management Cost and Maintenance Implications of Different Ground Covers at Utility-Scale Solar Sites. Sustainability, 15(7), 5895.

Nowak, R. S., & Caldwell, M. M. (1984). A test of compensatory photosynthesis in the field: implications for herbivory tolerance. Oecologia, 61, 311-318.

Oesterheld, M., & McNaughton, S. J. (1991). Effect of stress and time for recovery on the amount of compensatory growth after grazing. Oecologia, 85, 305-313.

Pascaris, A. S., Schelly, C., & Pearce, J. M. (2020). A first investigation of agriculture sector perspectives on the opportunities and barriers for agrivoltaics. Agronomy, 10(12), 1885.

Pascaris, A. S., Schelly, C., Burnham, L., & Pearce, J. M. (2021). Integrating solar energy with agriculture: Industry perspectives on the market, community, and socio-political dimensions of agrivoltaics. Energy Research & Social Science, 75, 102023.

Pauler, C. M., Isselstein, J., Suter, M., Berard, J., Braunbeck, T., & Schneider, M. K. (2020). Choosy grazers: Influence of plant traits on forage selection by three cattle breeds. Functional Ecology, 34(5), 980-992.

Post, A. K., & Knapp, A. K. (2020). The importance of extreme rainfall events and their timing in a semi-arid grassland. Journal of Ecology, 108(6), 2431-2443.

Randle-Boggis, R. J., White, P. C. L., Cruz, J., Parker, G., Montag, H., Scurlock, J. M. O., & Armstrong, A. (2020). Realising co-benefits for natural capital and ecosystem services from solar parks: a co-developed, evidence-based approach. Renewable and Sustainable Energy Reviews, 125, 109775.

IPCC, 2023: Climate Change 2023: Synthesis Report. A Report of the Intergovernmental Panel on Climate Change. 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, (in press)

R Core Team. 2017. R: A language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Sala, O. E., & Lauenroth, W. K. (1982). Small rainfall events: an ecological role in semiarid regions. Oecologia, 53, 301-304.

Sala, O. E., Parton, W. J., Joyce, L. A., & Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. Ecology, 69(1), 40-45.

Van Staalduinen, M. A., & Anten, N. P. (2005). Differences in the compensatory growth of two co-occurring grass species in relation to water availability. Oecologia, 146, 190-199.

Sturchio, M. A., Macknick, J. E., Barron-Gafford, G. A., Chen, A., Alderfer, C., Condon, K., ... & Knapp, A. K. (2022). Grassland productivity responds unexpectedly to dynamic light and soil water environments induced by photovoltaic arrays. Ecosphere, 13(12), e4334.

Sturchio, M.A., Knapp, A.K. (2023). Ecovoltaic principles for a more sustainable, ecologically informed solar energy future. *Nature Ecology & Evolution*. https://doi.org/10.1038/s41559-023-02174-x

US Department of Energy Solar Energy Technologies Office. (2021). Solar futures study.

Walston, L. J., Barley, T., Bhandari, I., Campbell, B., McCall, J., Hartmann, H. M., & Dolezal, A. G. (2022). Opportunities for agrivoltaic systems to achieve synergistic food-energy-environmental needs and address sustainability goals. Frontiers in Sustainable Food Systems, 6, 932018.

Yamori, W., Hikosaka, K., & Way, D. A. (2014). Temperature response of photosynthesis in C 3, C4, and CAM plants: temperature acclimation and temperature adaptation. Photosynthesis research, 119, 101-117.

# CHAPTER 6: CONCLUSIONS

Of all renewable energy generation options, a transition to solar photovoltaic (PV) has the greatest potential to reduce fossil fuel related emissions by the end of 2030 (Lee et al. 2023). To meet energy needs, ground mounted PV (i.e., the cheapest form of PV energy) must expand dramatically. Some estimates report that PV will require ~61,000 km$^2$ of land area by 2050 (Larson et al. 2020), and a majority of the ideal locations for PV development exist in lands already managed for agriculture (e.g., cropland and grazing, Adeh et al. 2019). This can cause land use tension when productive farm and rangelands are graded, and vegetation removed to prioritize electricity production per unit area. Foundational research on the topic of PV land use and ecological outcomes was mainly focused on the negative impacts of PV development and habitat change (Hernandez et al. 2014, Hernandez et al. 2020, Randle-Boggis et al. 2020, Grodsky and Hernandez 2021). Since then, dual-use approaches to PV like agrivoltaics (AV), where land beneath PV panels is agriculturally managed, have stimulated questions related to solar co-location optimization. In this dissertation I focused on addressing questions related to the ecology of dual-use PV facilities located in rainfed grassland ecosystems in order to inform sustainable PV energy co-location in one of the ecosystems most frequently targeted for PV development.

## 6.1 Research Summary

My research demonstrated that PV arrays create considerable heterogeneity in the abiotic controls of aboveground primary production (ANPP) in a semi-arid C$_3$ perennial grassland. My first study (Chapter 2) reported the result of elevated ANPP in microsites that received direct morning sunlight and afternoon shade, rather than in microsites where rainfall redistribution amplified soil moisture. This was unexpected because water limited ecosystems typically respond positively to larger soil water inputs (Sala et al. 1988, Heisler-White et al. 2008, Post and Knapp 2021). Our findings highlighted the potential importance of diurnal variation in environmental conditions, for example, temperature and evaporative demand (VPD) increase throughout the day and reach maximums in afternoon hours. Therefore, we concluded that plants which received higher soil water inputs also carried out most of their photosynthetic activity in hot and dry afternoons, ultimately limiting ANPP.

Although the high spatial and temporal variation in soil water and sunlight had been well described within PV arrays (Adeh et al. 2018, Choi et al. 2020, Graham et al. 2021, Sturchio et al. 2022), the concept of implementing intentional design and management strategies that utilize PV arrays to facilitate the enhancement of ecosystem services had not. In Chapter 3, I outlined ecological concepts in support of an Ecovoltaic approach to solar development, whereby energy generation and ecosystem services are co-prioritized. The Ecovoltaic approach provides an avenue for applying well-established ecological theories (e.g., heterogeneity begets biodiversity) in PV arrays to promote processes that support biodiversity and enhance ecosystem services. An ecologically informed approach to PV development could potentially improve the restoration of water limited and degraded lands, thus relieving the land use burden on pristine natural and prime agricultural lands.

To test our hypothesis that temporal variation in environmental conditions, specifically the favorability of morning conditions and their relation to increased ANPP, we focused on quantifying the physiological mechanisms underpinning this relationship (Chapter 4). We collected diurnal measurements of leaf water potential ($\psi_L$) and stomatal conductance to water vapor ($g_{sw}$) throughout the growing season to better understand how leaf water balance was affected by the timing of direct sunlight availability. We found that plants receiving morning sunlight and afternoon shade had significantly higher $g_s$ and $\psi_L$ compared to control plants and for plants within the array that received afternoon sunlight and morning shade. This result indicated a clear physiological benefit of reduced water stress in plants receiving morning sunlight rather than exposed to direct sunlight in the hot and dry afternoon. Measurements of photosynthetic capacity (light and $CO_2$ response of photosynthesis) were additionally collected to identify how unique PV microenvironments alter biochemical constraints of photosynthesis. Overall, we found that plants from all PV microsites had significantly higher rates of light saturated photosynthesis ($A_{sat}$) and a higher quantum yield of $CO_2$ assimilation ($\phi CO_2$). While not surprising that plants which received less sunlight had higher $\phi CO_2$, allowing them to reach maximum rates of $CO_2$ assimilation more quickly when light was available, higher overall rates of $A_{sat}$ for plants within the PV array experiencing less direct sunlight were a surprise.

Forage production is one of the most highly valued ecosystem service provided by rangeland ecosystems (Zhao et al. 2020), and as such, a greater understanding of how PV co-location in grasslands alters forage production dynamics is important for future management of these facilities. The final study of my dissertation (Chapter 5) reported that a semi-arid $C_3$ perennial grassland co-located with a single axis tracking PV array, was capable of maintaining levels of forage production and regrowth after simulated grazing when compared to non-AV control grassland. Forage quality was also similar to control grassland, and after simulated grazing regrowth had higher forage quality at the end of the growing season, indicating a shift in the seasonality of forage production.

## 6.2 Implications and Future Directions

Overall, the results of my dissertation provide support for the successful co-location of solar energy generation facilities and grassland ecosystems in the semi-arid west. Grassland productivity, forage quality, and gas exchange were either maintained or improved in response to PV cover, illuminating potential synergies through an Ecovoltaic approach to PV development. Of great importance, but not addressed by this work, is the response of more diverse semi-arid grasslands composed of multiple plant functional groups (e.g., $C_3$, $C_4$, forbs, annuals). To do this, an understanding of the physiological mechanisms underpinning the response of more diverse communities will allow ecologists to predict long term ecosystem dynamics in grassland PV facilities.

The application of Ecovoltaic principles, whether it be during PV site design, management, or both, has yet to be tested. Long term monitoring and evaluation of such strategies will not only help to understand the overall impact of co-locating grassland and PV energy facilities, but also potentially improve our understanding of basic biological processes. PV facilities offer an opportunity to test questions related to resource limitation and amplification like no other field-based study system. Ecologists would do well to use the infrastructure for experiments to test and potentially improve the efficacy of fundamental ecological concepts.

# LITERATURE CITED

Adeh, E. H., Selker, J. S., & Higgins, C. W. (2018). Remarkable agrivoltaic influence on soil moisture, micrometeorology, and water-use efficiency. PloS one, 13(11), e0203256.

Adeh, E. H., Good, S. P., Calaf, M., & Higgins, C. W. (2019). Solar PV power potential is greatest over croplands. *Scientific reports*, *9*(1), 1-6.

Choi, C. S., Cagle, A. E., Macknick, J., Bloom, D. E., Caplan, J. S., & Ravi, S. (2020). Effects of revegetation on soil physical and chemical properties in solar photovoltaic infrastructure. Frontiers in Environmental Science, 140.

Graham, M., Ates, S., Melathopoulos, A. P., Moldenke, A. R., DeBano, S. J., Best, L. R., & Higgins, C. W. (2021). Partial shading by solar panels delays bloom, increases floral abundance during the late-season for pollinators in a dryland, agrivoltaic ecosystem. Scientific Reports, 11(1), 1-13.

Grodsky, S. M., & Hernandez, R. R. (2020). Reduced ecosystem services of desert plants from ground-mounted solar energy development. Nature Sustainability, 3(12), 1036-1043.

Heisler-White, J. L., Knapp, A. K., & Kelly, E. F. (2008). Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia, 158, 129-140.

Hernandez, R. R., Easter, S. B., Murphy-Mariscal, M. L., Maestre, F. T., Tavassoli, M., Allen, E. B., ... & Allen, M. F. (2014). Environmental impacts of utility-scale solar energy. *Renewable and sustainable energy reviews*, *29*, 766-779.

Hernandez, R. R., Tanner, K. E., Haji, S., Parker, I. M., Pavlik, B. M., & Moore-O'Leary, K. A. (2020). Simulated photovoltaic solar panels alter the seed bank survival of two desert annual plant species. Plants, 9(9), 1125.

Larson, E. (2020). Net-zero America: potential pathways, infrastructure, and impacts. Princeton University.

Lee, H., Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P., ... & Park, Y. (2023). IPCC, 2023: Climate Change 2023: Synthesis Report, Summary for Policymakers. 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.

Post, A. K., & Knapp, A. K. (2021). How big is big enough? Surprising responses of a semiarid grassland to increasing deluge size. Global Change Biology, 27(6), 1157-1169.

Randle-Boggis, R.J., White, P.C.L., Cruz, J., Parker, G., Montag, H., Scurlock, J.M.O. and Armstrong, A. (2020). Realising co-benefits for natural capital and ecosystem services from solar parks: a co-developed, evidence-based approach. Renewable and Sustainable Energy Reviews, 125, p.109775.

Sala, O. E., Parton, W. J., Joyce, L. A., & Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. Ecology, 69(1), 40-45.

Sturchio, M. A., Macknick, J. E., Barron-Gafford, G. A., Chen, A., Alderfer, C., Condon, K., ... & Knapp, A. K. (2022). Grassland productivity responds unexpectedly to dynamic light and soil water environments induced by photovoltaic arrays. *Ecosphere*, 13(12), e4334.

Zhao, Y., Liu, Z., & Wu, J. (2020). Grassland ecosystem services: a systematic review of research advances and future directions. Landscape Ecology, 35, 793-814.

# APPENDIX 1

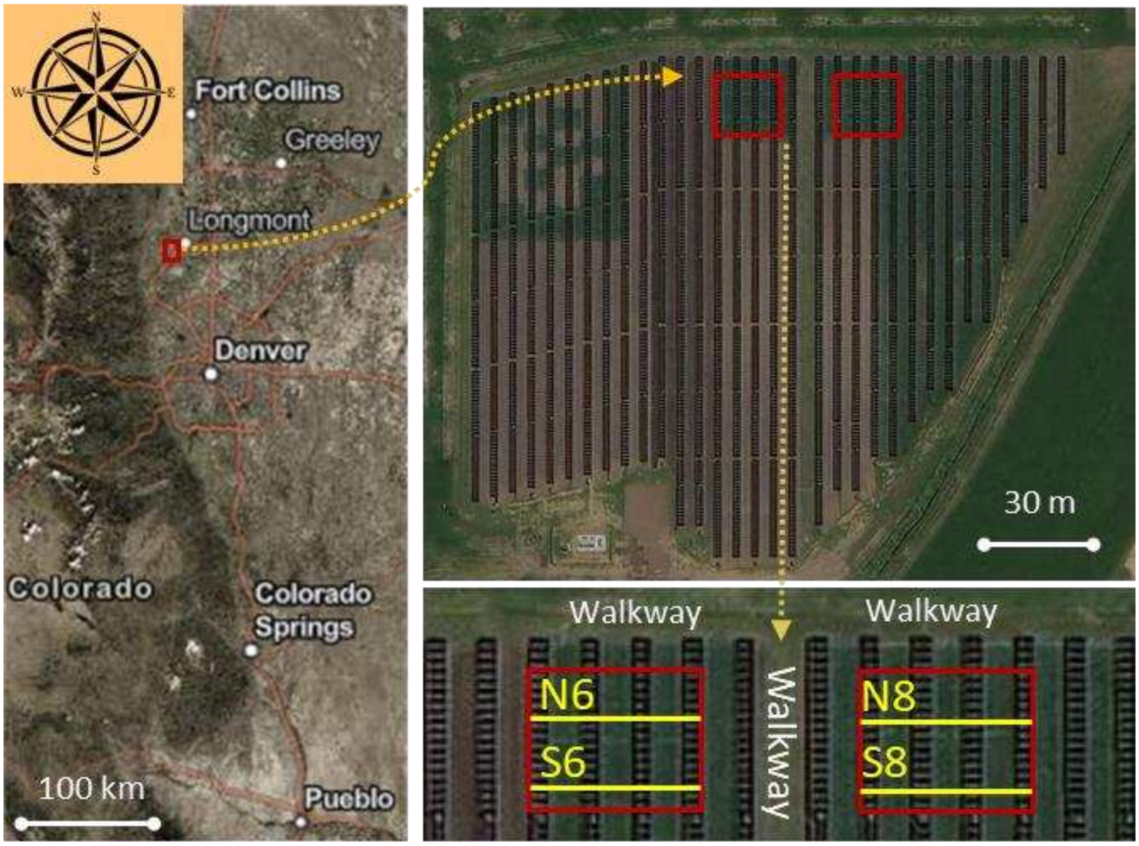


**Figure A1.1.** In panel a, the study site location is highlighted in a red box. In panel b, the location of experimental transects are highlighted in red boxes, and in panel c, individual transects are notated with yellow lines running perpendicular to the solar array. The transect specific alphanumeric code used unique identifiers for direction (N = north, S = south) and feet above the ground (6 (1.8 m) or 8 (2.4 m)).

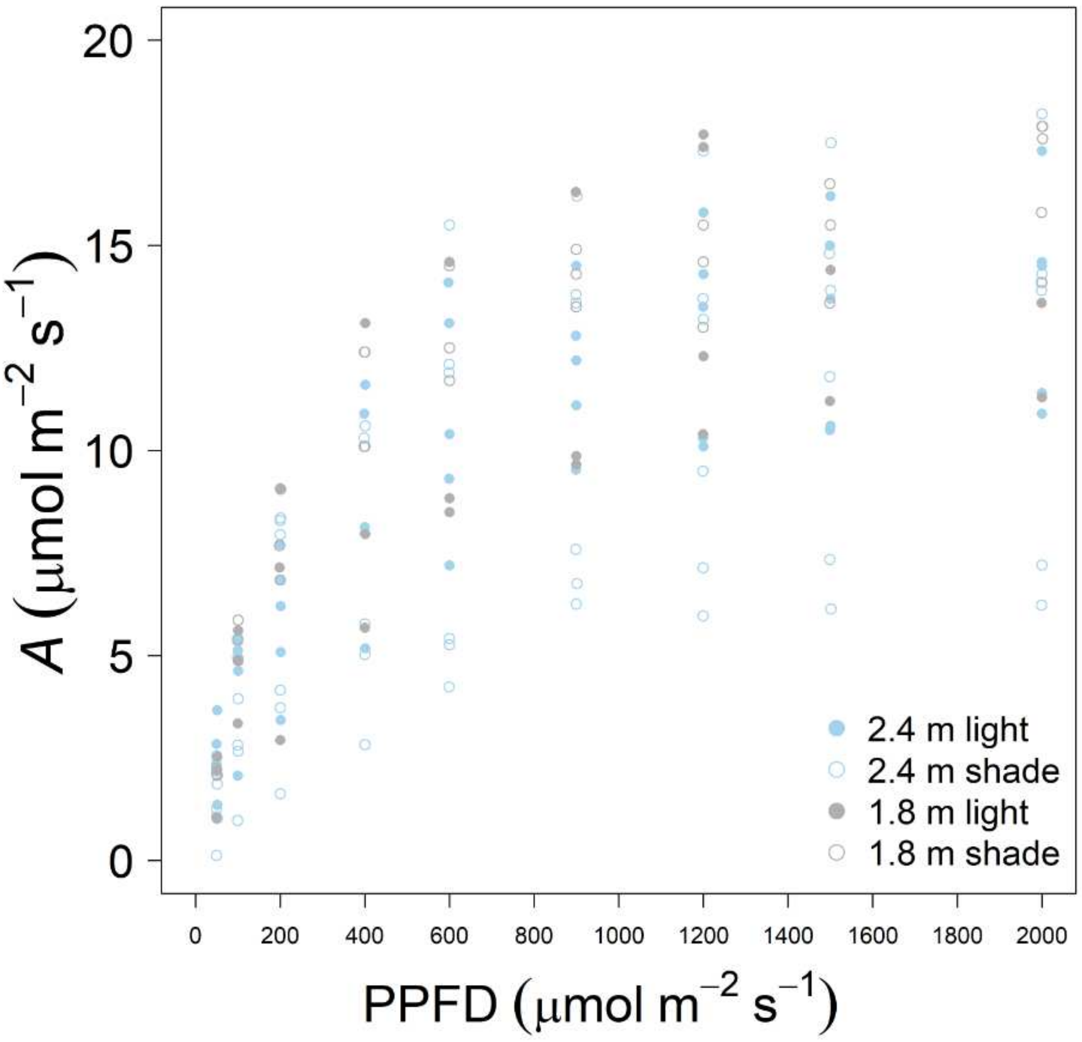


**Figure A1.2.** Raw light response of photosynthesis data.

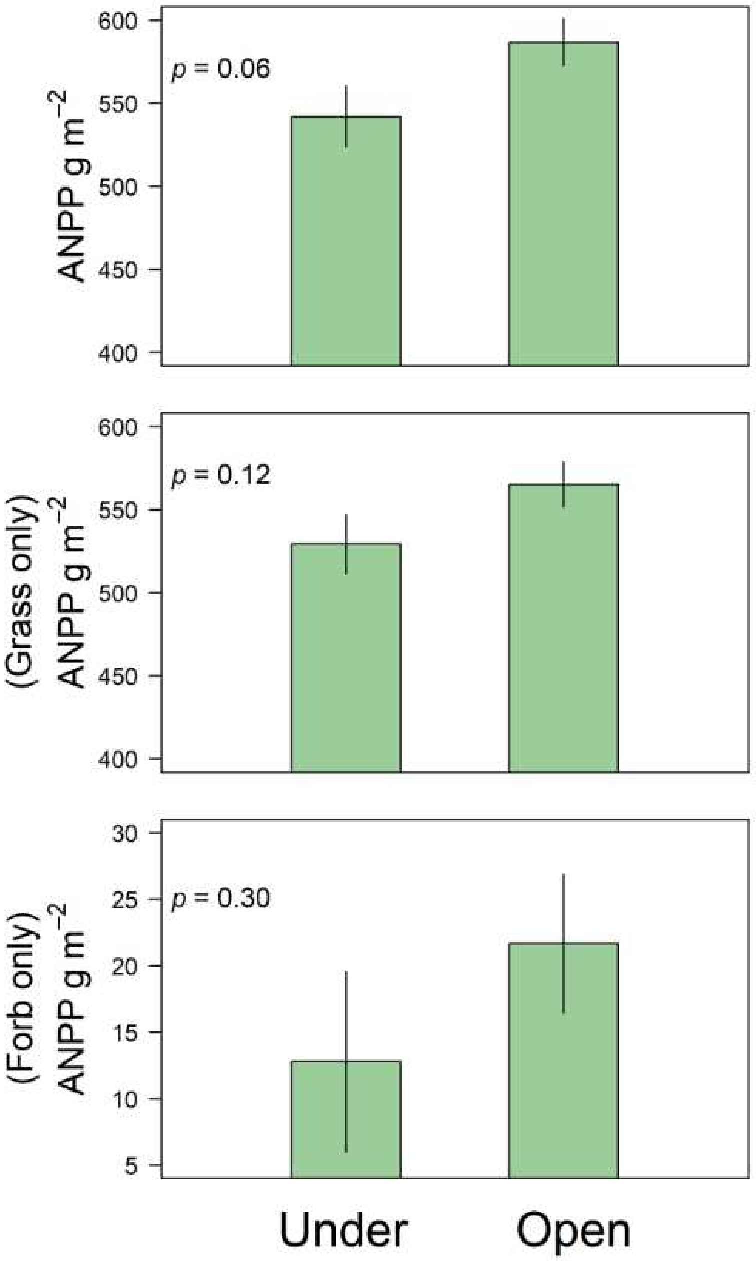


**Figure A1.3.** One-way ANOVA results of mean ANPP under PVs vs. between PVs, across transects. The second panel shows the results of the same ANOVA but only for grass, and the third panel shows ANOVA results for forb only.

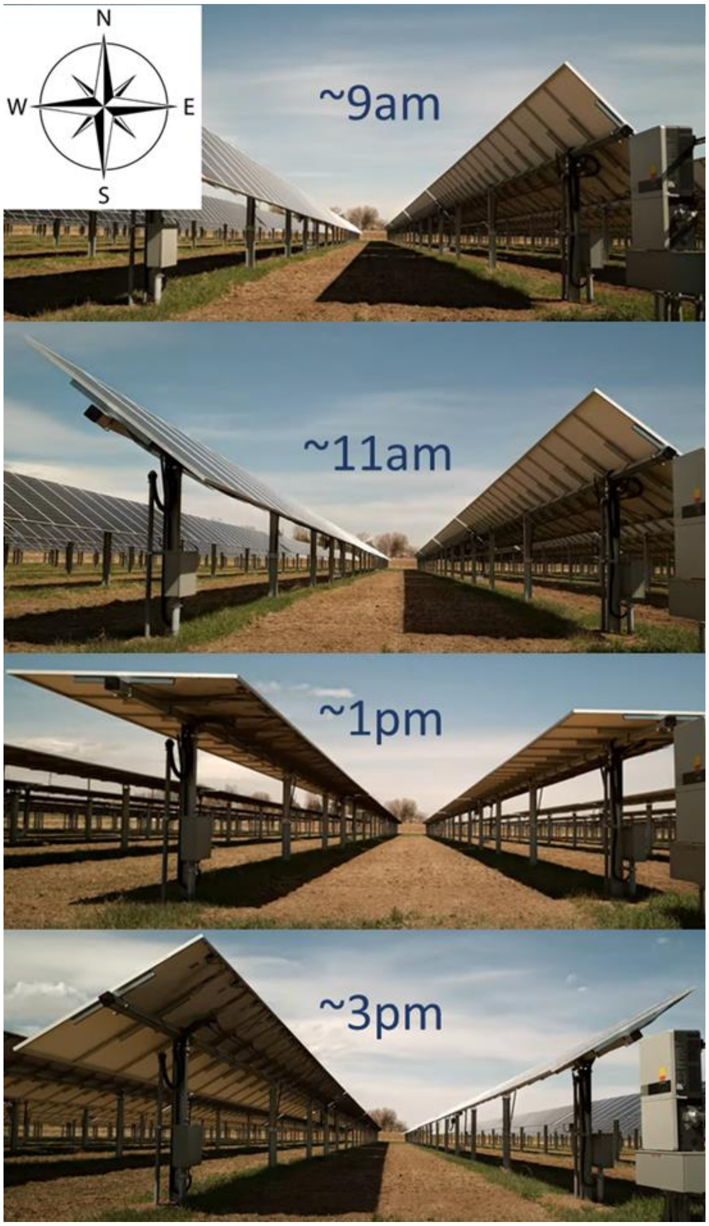


**Figure A1.4.** Light patterns starting mid-morning (9am), captured every two hours until mid-afternoon (3pm).

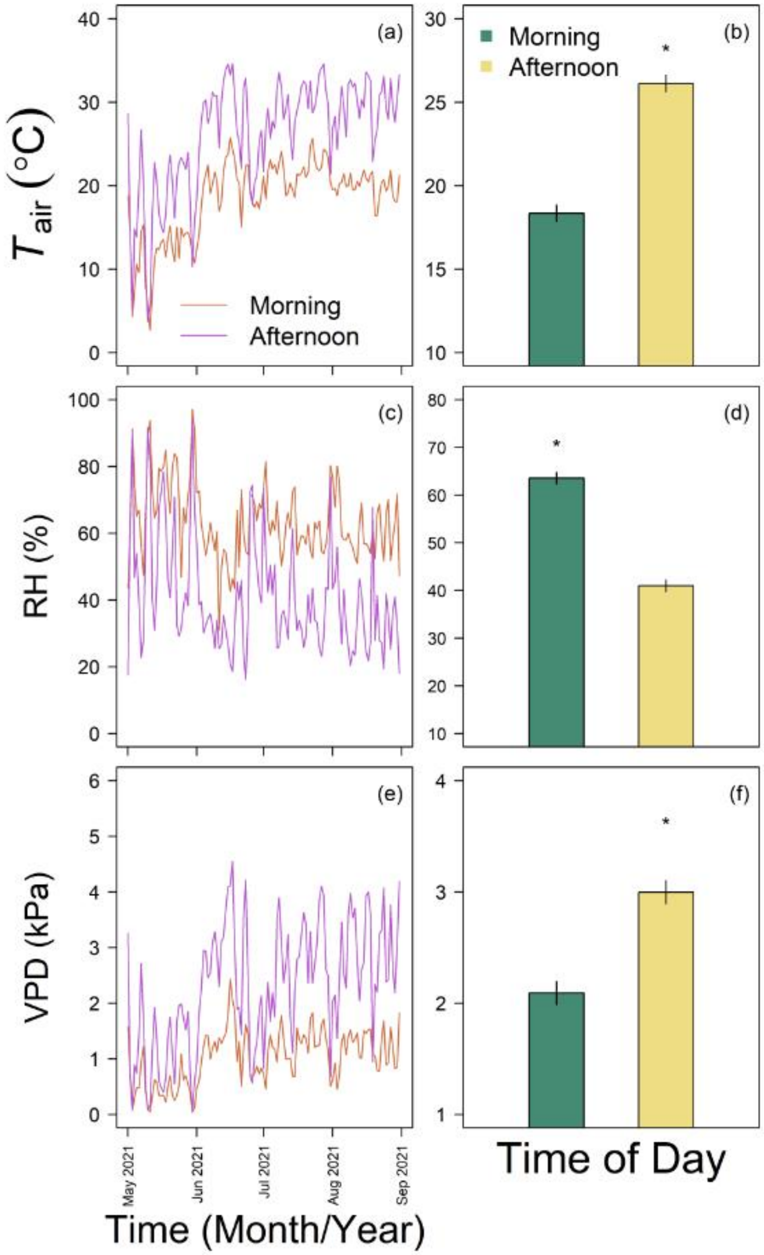


**Figure A1.5**. Environmental parameters separated at solar noon (calculated using *suncalc* package, Thieurmel et al. 2019) and averaged across the growing season. Panels a, c, and e, show patterns throughout the growing season. Panels b, d, and f, show mean growing season values for each parameter.

APPENDIX 2

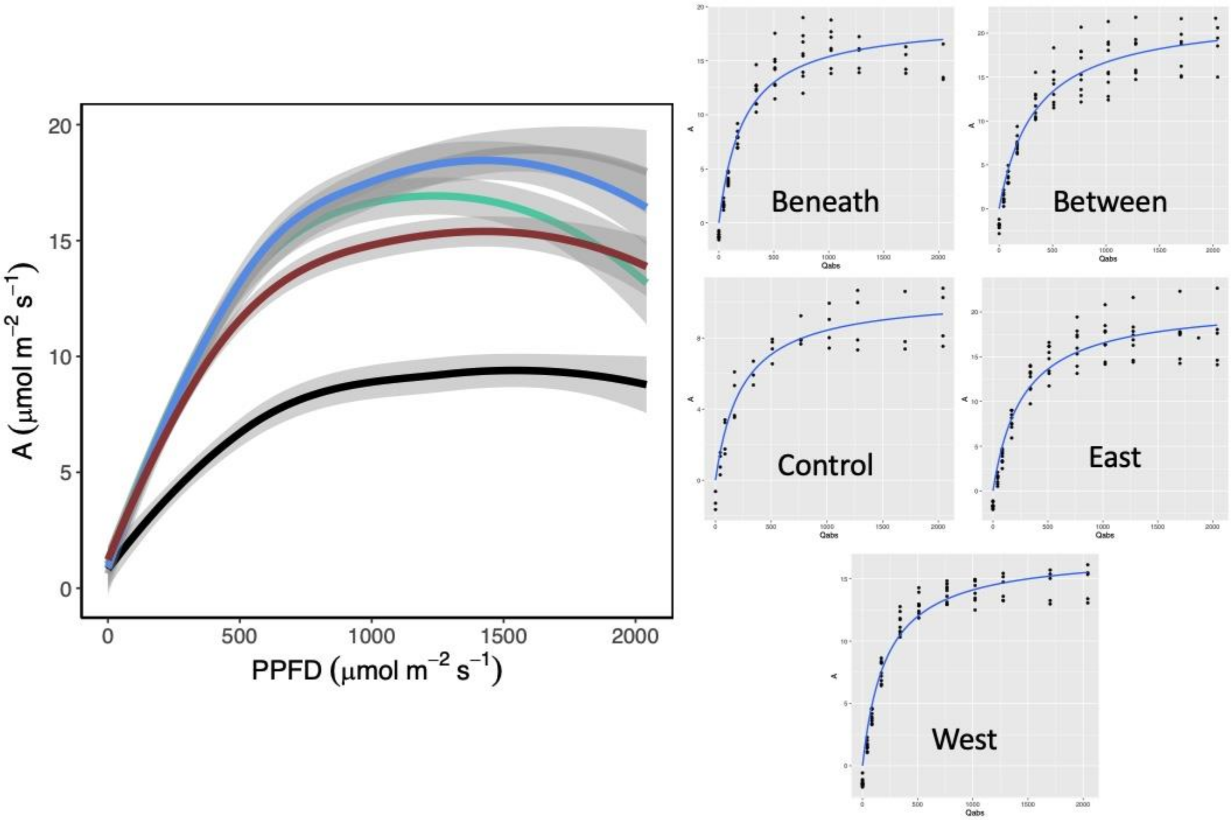


**Figure A2.1.** Mean light response curves separated by microsite. Grey shadowing represents standard errors.

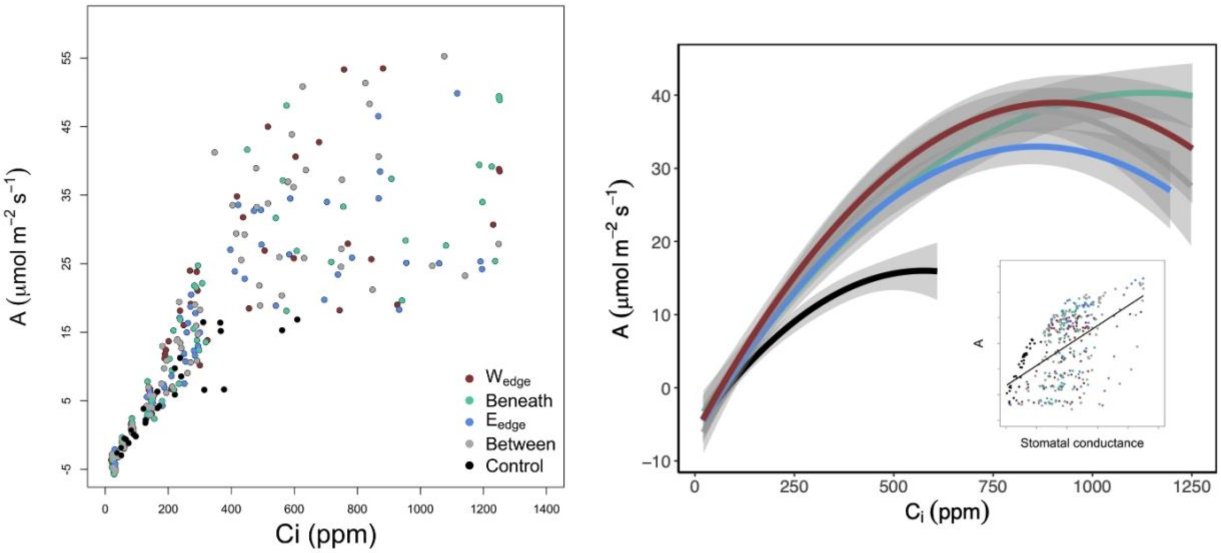


**Figure A2.2.** Mean *A*-$C_i$ response curves separated by microsite. Grey shadowing represents standard errors.

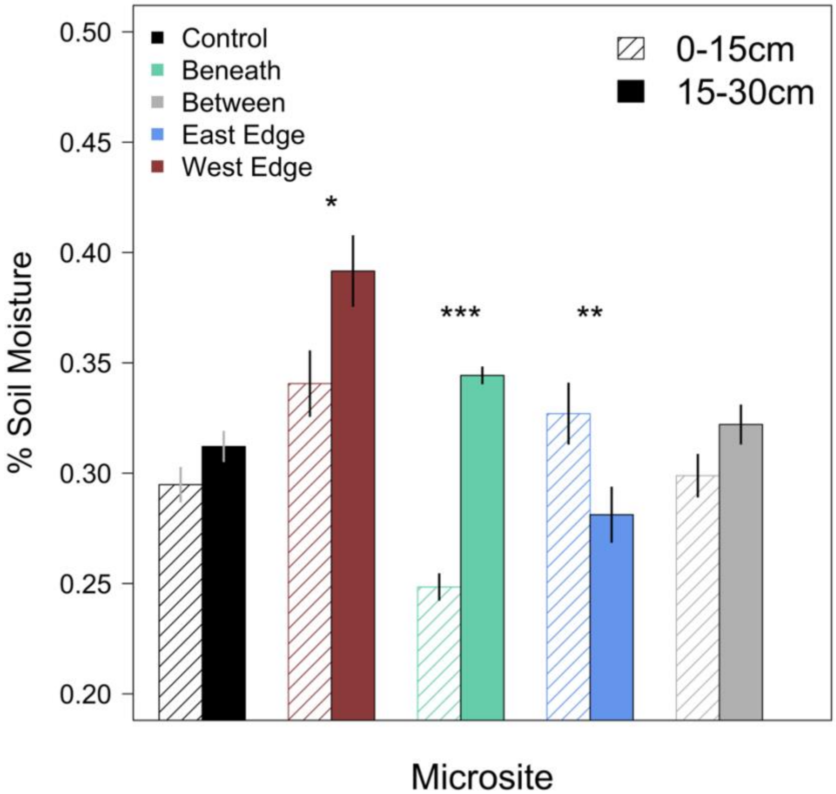


**Figure A2.3.** ANOVA results of soil moisture depth comparison microsite.

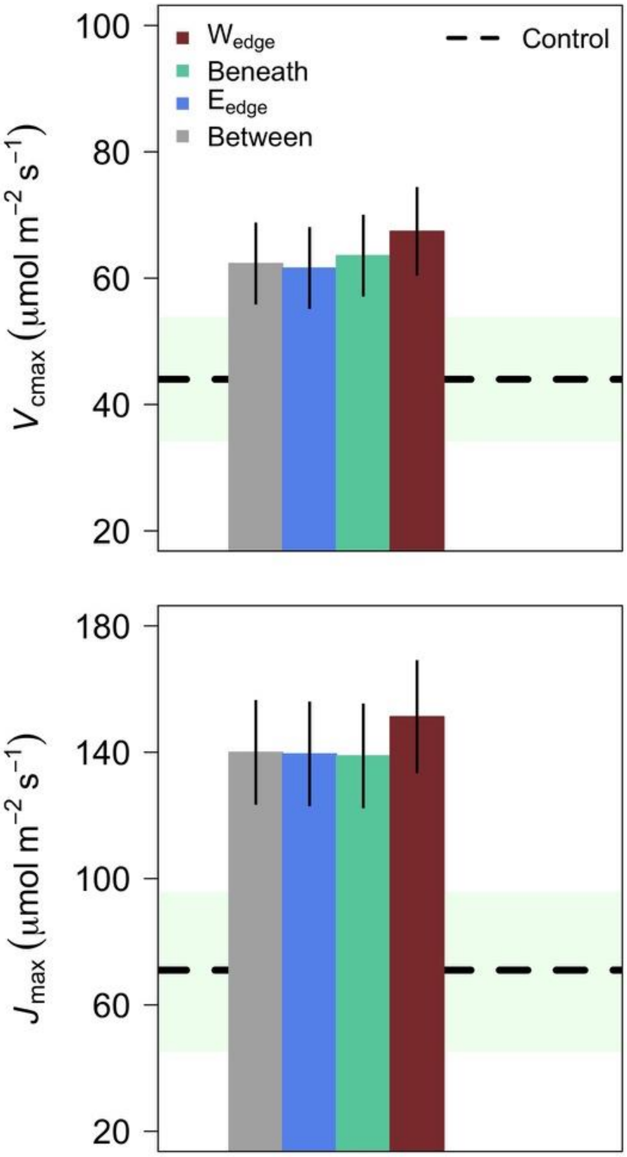


**Figure A2.4.** *A*-$C_i$ response curve model outputs: top) maximum rate of rubisco carboxylation, bottom) maximum rate of electron transport for RUBP regeneration.

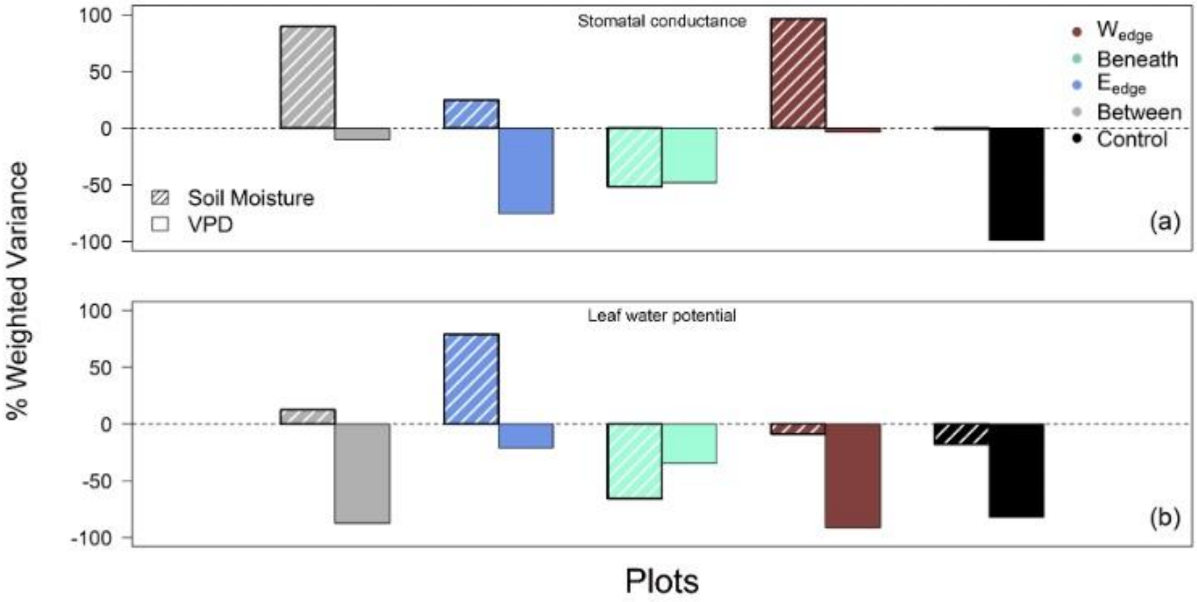


**Figure A2.5.** A relative weight analysis was used to quantify microsite level differences of total variance for $g_{sw}$ (a) and $\psi_L$ (b) into weights, thus capturing the proportional contribution of environmental predictor variables (SM and VPD).

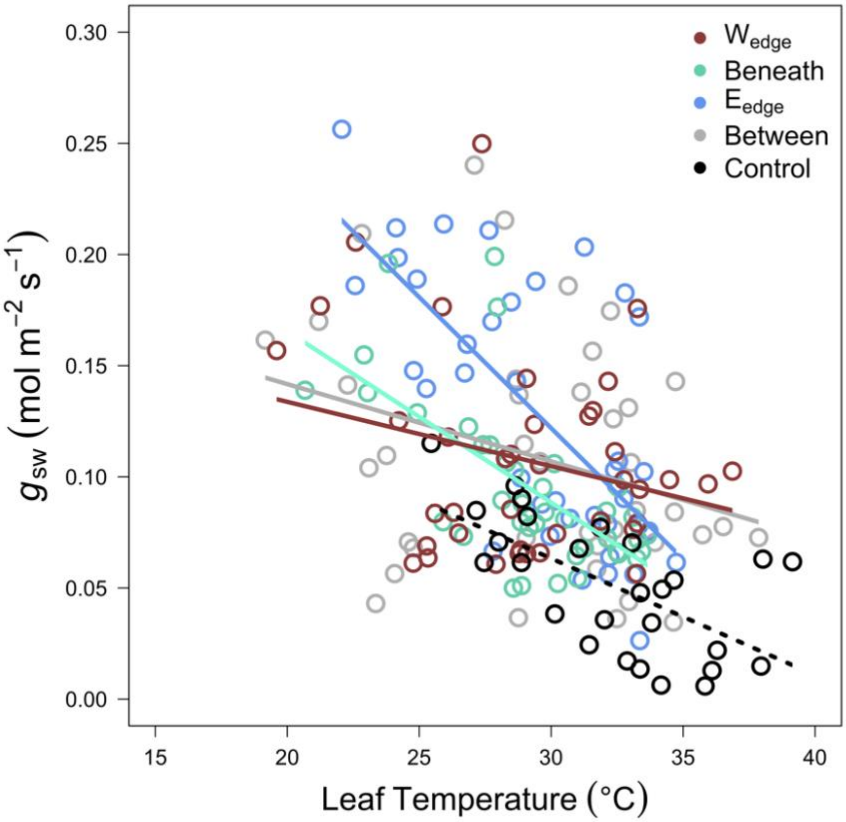


**Figure A2.6.** Relationships between stomatal conductance and leaf temperature separated by microsite.

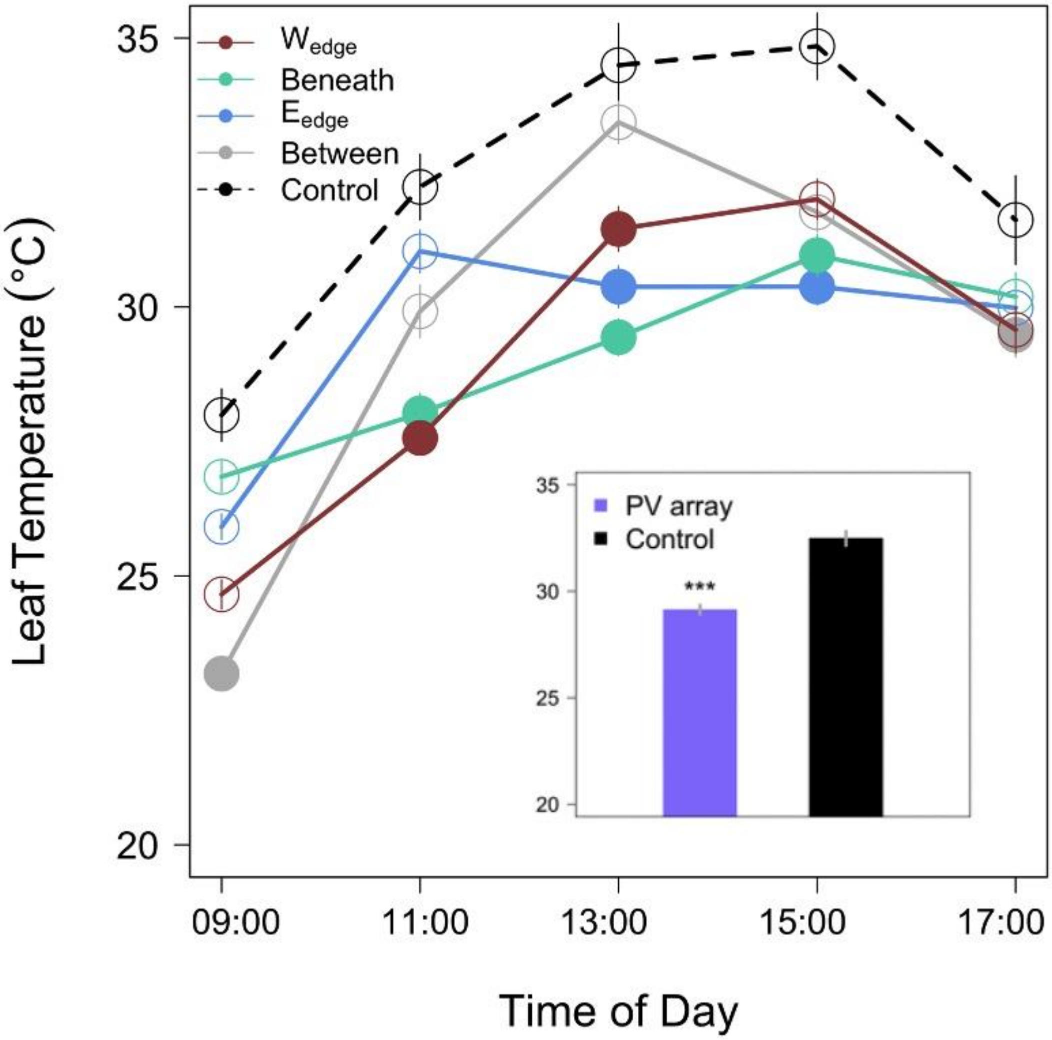


**Figure A2.7.** Mean growing season diurnal leaf temperature separated by microsite. The inset figure shows area weighted means for leaves in control and PV microsites.