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ARTICLE

Agroecosystems

Grassland productivity responds unexpectedly to dynamic light and soil water environments induced by photovoltaic arrays

Matthew A. Sturchio[1] | **Jordan E. Macknick**[2] | **Greg A. Barron-Gafford**[3,4] | **Anping Chen**[1] | **Cavin Alderfer**[1] | **Kathleen Condon**[1] | **Olivia L. Hajek**[1] | **Benjamin Miller**[1] | **Benjamin Pauletto**[1] | **J. Alexander Siggers**[1] | **Ingrid J. Slette**[1,5] | **Alan K. Knapp**[1]

[1]Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado, USA

[2]National Renewable Energy Laboratory, Golden, Colorado, USA

[3]School of Geography, Development and Environment, University of Arizona, Tucson, Arizona, USA

[4]Biosphere 2, University of Arizona, Tucson, Arizona, USA

[5]Long Term Ecological Research Network, National Center for Ecological Analysis and Synthesis, University of California Santa Barbara, Santa Barbara, California, USA

Correspondence
Matthew A. Sturchio
Email: matthew.sturchio@colostate.edu

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Abstract

Agrivoltaic (AV) systems are designed to coproduce 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 (photosynthetic photon flux density [PPFD]) in a single-axis-tracking AV system established in a formerly managed semiarid 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 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

(ϕCO_2) differed for plants growing directly beneath (lowest PPFD) versus between (highest PPFD) PV panels. Overall, the AV system established in this semiarid 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 versus high periods of PPFD incident on plants is an important determinant of productivity patterns in grasslands.

KEYWORDS
agrivoltaic, dryland agriculture, dryland ecology, light response of photosynthesis, plant physiology

INTRODUCTION

The carbon emissions advantages of renewable solar-generated electricity for meeting global energy demands are well known (Bevan, 2012; Burkhardt et al., 2012; Edenhofer et al., 2011; Raturi, 2019; Tsoutsos et al., 2005). 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 versus food and forage production can be alleviated by colocating solar infrastructure and agriculture (Dupraz et al., 2011; Goetzberger & Zastrow, 1982; Macknick et al., 2013; Ravi et al., 2016) with potential benefits and trade-offs associated with such "agrivoltaic" (AV) systems now emerging (Barron-Gafford et al., 2019; Maia et al., 2020; Pascaris et al., 2020).

Semiarid regions cover approximately 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 with more humid productive regions. Further, the current use of these expansive ecosystems for forage production may be more compatible with the colocation 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 semiarid ecosystems, is strongly limited by precipitation inputs (Gherardi & Sala, 2019; Sala et al., 1988; Sala & Lauenroth, 1982), 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 (Borer et al., 2014; Knapp et al., 1993; Knapp & Seastedt, 1986). 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 (SM) 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 SM patterns within PV arrays can vary dramatically—with reports of reduced as well as increased SM levels directly beneath versus between PV panels (Adeh et al., 2018; Andrew et al., 2021; Graham et al., 2021; Weselek, Bauerle, Hartung, et al., 2021; Weselek, Bauerle, Zikeli, et al., 2021). 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 semiarid grasslands can be expected to shift these ecosystems from being characterized by relatively limited spatial variability in SM 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 SM and diurnal variation in incident sunlight in a formerly managed semiarid 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 SM 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.

MATERIALS AND METHODS

Study site

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; Appendix S1: Figure S1a). 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 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 inermis*) 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 2 m (east–west) × 1 m (north–south) and are mounted in series on a single-axis-tracking system (tracking east–west, Figure 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 (Figure 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.

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 (Appendix S1: Figure S1b). Two replicate transects, each comprised of 32 sampling points 0.5 m apart, were delineated in areas with either 1.8- or 2.4-m-tall PV rows (Appendix S1: Figure S1c), ultimately producing 128 total plots. For data visualization purposes, each transect comprised of three panel-gap combinations (starting from the east: panel, gap between panels, panel, gap between panels, panel) that were then averaged by discrete location (Locations 1–11). Data from Locations 1–4 were duplicated (Locations 12–15) to help visualize how factors were distributed under and between PV panels. However, Locations 12–15 were not used for data analysis to avoid pseudo-replication. These transects partially spanned three PV rows, with the easternmost plots located underneath (Location 2; Figure 1) the second panel from a walkway or edge (Appendix S1: Figure S1). We named replicates after the cardinal direction they were oriented (North/South) and based on panel heights (N1.8, S1.8, N2.4, S2.4, numbers refer to meters above the ground; Appendix S1: Figure S1c). Light, SM, and productivity measurements were taken at all 128 plots, while leaf-level physiology was measured only on plants experiencing the highest versus lowest mean daily photosynthetic photon flux density (PPFD). In figures, data from Locations 1–4 were once again duplicated (at Locations 12–15) for artistic effect.

Environmental measurements

Diurnal patterns of air temperature (T_{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, PPFD varies quite predictably beneath PV arrays and has been quantified and successfully modeled in the past (Amaducci et al., 2018; Graham et al., 2021; Lu et al., 2022; Marrou, Guilioni, et al., 2013; Valle et al., 2017). Nonetheless, to confirm patterns specific to JSG, PPFD was measured under full sun conditions on a mostly cloud-free day (August 5) with an AccuPAR LP-80 Ceptometer (Decagon Devices, Pullman, WA), which integrates downwelling diffuse sunlight and direct beam sunlight. PPFD measurements were recorded above grass canopy height (~1 m from soil surface) for each plot, at three key times of day: 3 h before solar noon (10 am), at solar noon (1 pm), and 3 h after solar noon (4 pm) to quantify how light availability changed throughout the day under this single-axis-tracking PV system. 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 integrated from 0 to 20 cm) at all plots at 4–8-day intervals between May 3 and August 30 using a HydroSense II Handheld Soil Moisture Sensor (Campbell Scientific, Logan, UT). 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). Further, SM at this depth strongly correlates with plant activity and aboveground productivity with the strength of these

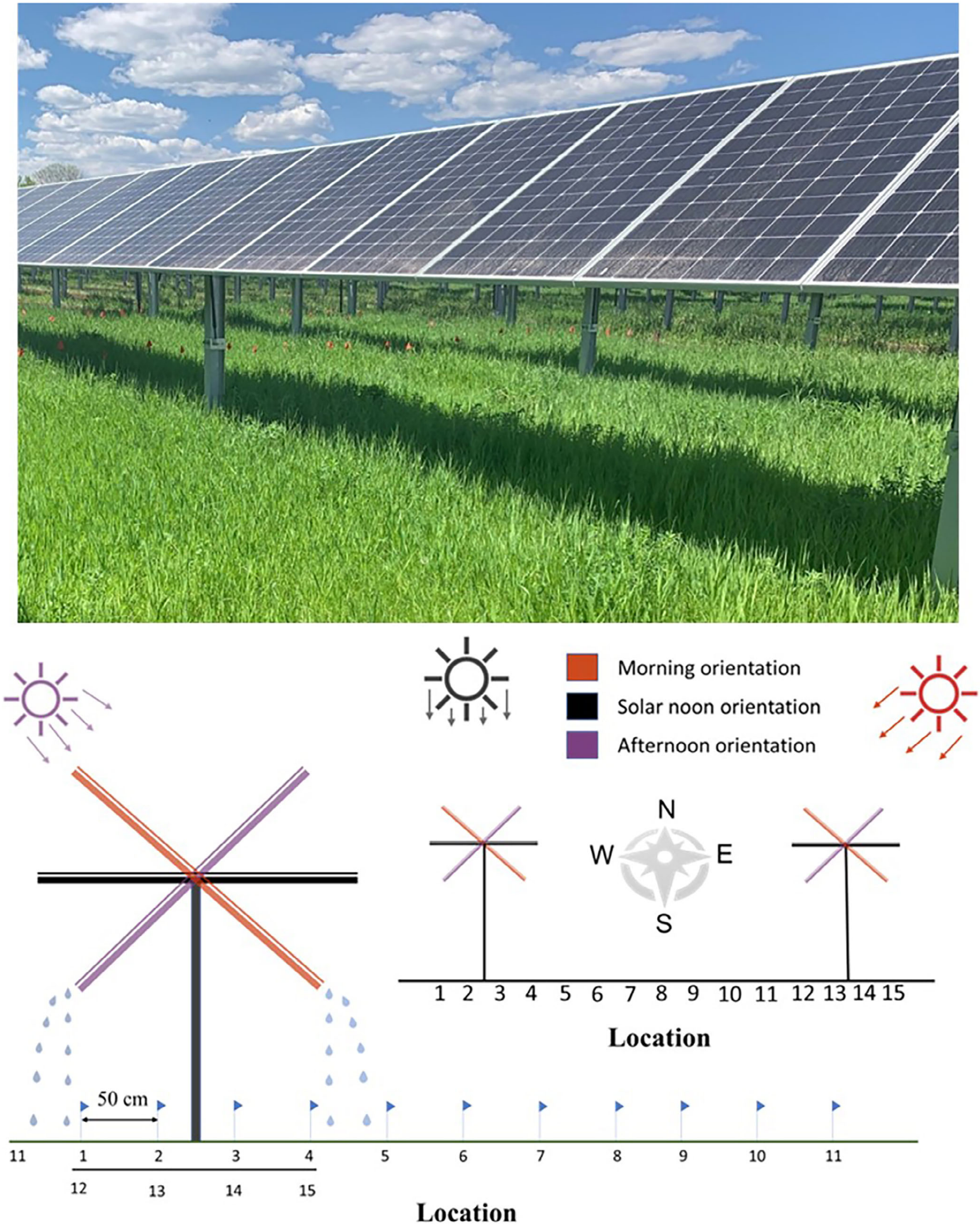

FIGURE 1 Legend on next page.

correlations decreasing with depth (Nippert & Knapp, 2007). Measurements were made during morning hours, typically between 7 am and 10 am local time (US Mountain Time zone). This sampling scheme resulted in 1920 measurements of SM recorded at JSG in 2021.

Measuring and modeling light response of photosynthesis

Plants directly beneath PV panels (between Locations 2 and 3; Figure 1) and plants in the middle of the interspace between panels (Location 8) were used to assess differences in light-saturated photosynthesis (A_{sat}) and the quantum yield of CO_2 assimilation (ϕCO_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 27 and 28 using a portable photosynthesis system (LI-6400, LiCor., 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_{leaf}) of 30.8 ± 1.7°C (standard deviation) across all measurements. Chamber reference CO_2 was set to 410 μmol mol^{-1} and 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 am and 2 pm 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 nine reference (PPFD) values in a descending fashion (2000, 1500, 1200, 900, 600, 400, 200, 100, and 50 μmol m^{-2} s^{-1}; Appendix S1: Figure S2). Each light response curve was parameterized using a nonrectangular parabola (Marshall & Briscoe, 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 the light-saturated net CO_2 assimilation rate (A_{sat}) and quantum yield of CO_2 assimilation (ϕCO_2) derived from the initial slope of the light response curve.

Estimating ANPP

At the end of the growing season (September 19, 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 SM 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 h before being weighed to the nearest 0.01 g.

Data analysis

Our primary goal was to assess spatial patterns of SM and PPFD and their relationship to ANPP. End-of-season biomass accumulation, a standard method for estimating ANPP in ungrazed grasslands (Fahey & Knapp, 2007), is a single measure of seasonally cumulative processes. In contrast, we measured SM as it varied seasonally and PPFD as it varied diurnally. Thus, we initially averaged SM 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 ($L \times H$, $L \times R$, $H \times R$, $L \times H \times R$) 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 ($L \times H$, $L \times R$, $H \times R$, $L \times H \times R$) on photosynthetic parameters obtained from light response measurements (A_{sat}, ϕCO_2).

FIGURE 1 Top: late spring view of a row of photovoltaic (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, and west facing—note color coding). Water drops show the approximate location of the eastern drip edge (between Locations 4 and 5) and the western drip edge (between Locations 11 and 1) where rain would be shed in the morning and afternoon, respectively. The compass is three-dimensionally oriented to indicate that rows of panels run in series north–south. Note that for data analyses, only true replicates of plot Locations 1–11 were used, but to more clearly illustrate spatial patterns within the agrivoltaic system, figures show two PV panels where data for Locations 12–15 are identical to Locations 1–4.

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 values for the entire growing season, relationships between monthly SM values (May, June, July, and August) and ANPP (one time point) were assessed to determine which month of SM had the strongest relationship with productivity. All analyses were performed using R version 4.1.2 (R Core Team, 2017).

RESULTS

In 2021, annual precipitation at the site was 10% higher than the long-term average (401 vs. 365 mm, respectively). Seasonally, the early growing season (April, May, and June) was approximately 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 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 vs. 9.7°C).

Light

As expected for a single-axis-tracking system (Graham et al., 2021; Valle et al., 2017), mean daily PPFD was significantly lower under PV panels compared with between panels with spatial patterns varying predictably among morning, solar noon, and afternoon sampling periods (Figure 2). Averaged across time of day and locations, PPFD levels were slightly lower within 1.8- versus 2.4-m PV arrays (1126 vs. 1190 μmol m^{-2} s^{-1}, respectively; Table 1), but the ecophysiological significance of this for C_3 grasses is likely small. Overall, plots between panels (Location 8) receive approximately 7 h of direct sunlight versus <2 h underneath, while plots near the edges of panels (Locations 4 and 11) received approximately 4 h of direct sun (M. Sturchio, unpublished data).

Light saturation and quantum yield of photosynthesis

The results of a three-way ANOVA indicated no significant differences between A_{sat} or ϕCO_2 in *B. inermis* grown directly beneath or between PVs, across panel heights (1.8 and 2.4 m), across replicates, or their interactions (Figure 3). Differences beneath and between panels were more pronounced for A_{sat} in 1.8-m plots while differences in ϕCO_2 were similar across panel height.

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 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 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 (Figure 4, Locations 10–11; July–August SM = 29.8%) relative to between PV panels (Figure 4, Locations 7–8; July–August SM = 26.5%). In contrast, SM directly beneath the PV panels (Locations 2–3) was consistently low with growing season mean SM approximately 8% lower than along the western edge of PV panels (Figure 4).

Productivity

There were no statistical differences between panel heights (Table 1) or in patterns of forb and grass production across locations (Appendix S1: Figure S3); 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 1) with ANPP at the eastern edge of PV panels (Figure 5, Location 5) significantly higher (by ~33%) than at the western edge (Figure 5, Location 11, 716.2 and 539.8 g m^{-2}, respectively). In contrast, ANPP directly beneath PV panels (Figure 5, Locations 2 and 3 mean = 488.2 g m^{-2}) was reduced ($p < 0.05$) by approximately 20% relative to those locations least impacted by PV panels (Locations 8 and 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, Figure 5) in this grassland. This magnitude of spatial variability is approximately 40% of the mean ANPP in locations least impacted by PV panels (Locations 8 and 9).

Light and SM relationships with ANPP

Results of separate one-way ANOVAs indicated that SM and PPFD were both significantly related to patterns of

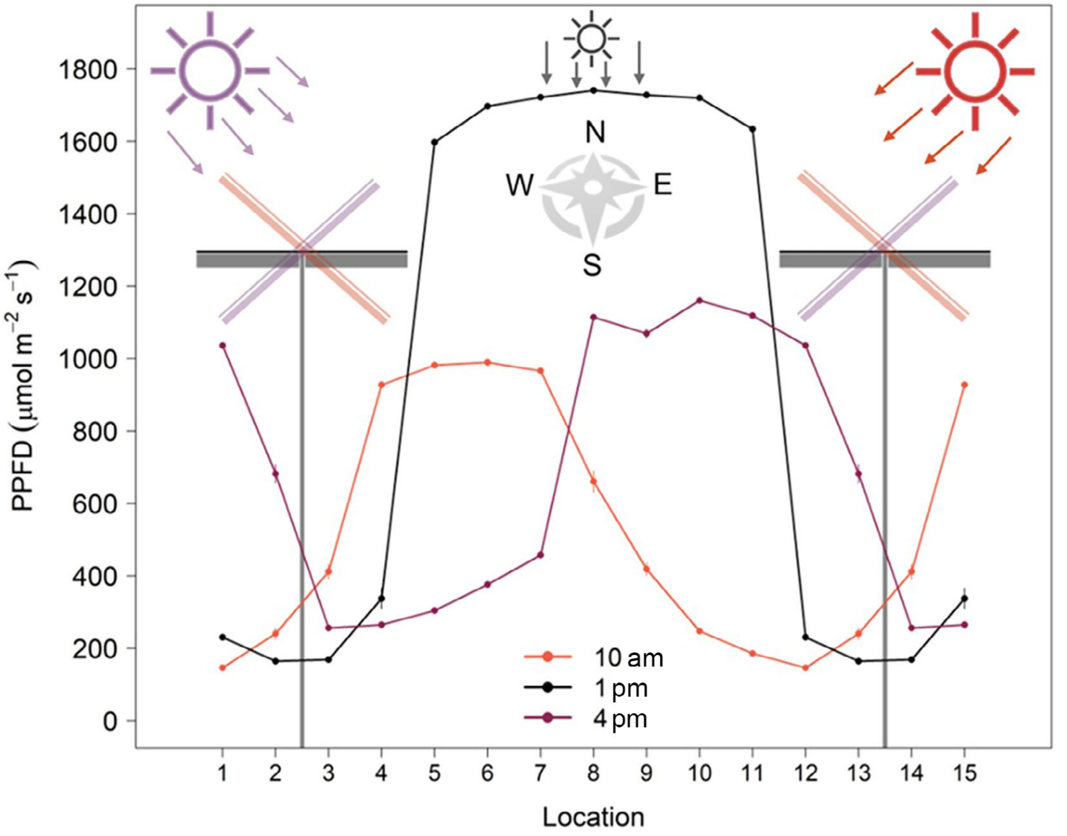

FIGURE 2 Mean photosynthetic photon flux density (PPFD) at 10 am, solar noon or 1 pm, and 4 pm along a transect perpendicular to rows of photovoltaic (PV) panels. Because PV panels track diurnal movements of the sun, the three different panel orientations at the time of measurements are color-coded to match PPFD data.

TABLE 1 Results of three-way ANOVAs to assess how transect location (*L*), height of the photovoltaic panels (*H*), and each replicate (*R*) varied for aboveground net primary production (ANPP; $n = 128$), soil water content (SWC; $n = 2762$), and photosynthetic photon flux density (PPFD; $n = 384$).

Response variable	*L*		*H*		*R*		*L* × *H*		*L* × *R*		*H* × *R*		*L* × *H* × *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

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

ANPP, but surprisingly neither explained >10% of the spatial variation in productivity (Figure 6a,b). Multiple regression analyses that included both SM and PPFD as predictors were not significant. We were also interested if spring (May and June) SM measurements were more strongly related to productivity than time points later in the growing season (July and August). We found weak relationships between ANPP and early growing season SM (Figure 6c,d), and no relationship between ANPP and late growing season SM (Figure 6e,f).

DISCUSSION

The primary goal of our study was to assess how spatial variability in 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 semiarid grasslands in the western United States. In these water-limited grasslands, as well as in nonirrigated managed pastures, SM responds directly to precipitation amounts and patterns

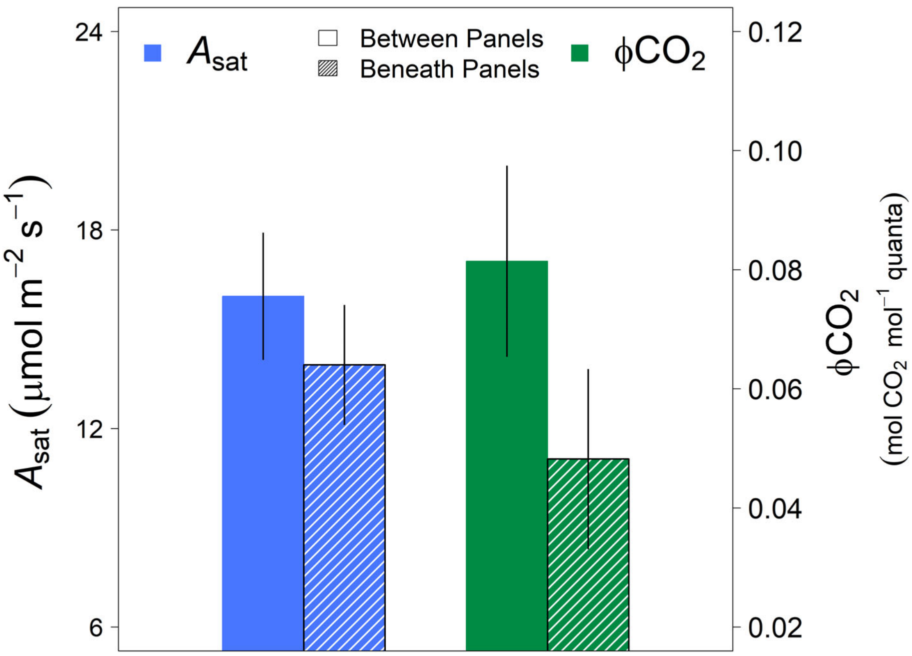

FIGURE 3 Results of a three-way ANOVA on photosynthetic light response measurements. Light-saturated photosynthesis (A_{sat}) and quantum yield of CO_2 assimilation (ϕCO_2) beneath (hashed bars) and between (solid bars) photovoltaic panels. Measurements were averaged (±SE) across panel heights because differences were nonsignificant.

(e.g., Griffin-Nolan et al., 2021; Hoover et al., 2021) and both precipitation inputs and SM are strongly related to ANPP (Knapp et al., 2002; La Pierre et al., 2016; Post & Knapp, 2021; Sala et al., 1988). However, despite substantial variation in SM and PPFD (Figures 2 and 4) within the PV arrays at JSG, spatial variation in ANPP, which was also substantial (~275 g m^{-2} along the transects; Figure 5), was not strongly related to patterns of light and/or water availability (Figure 6). Early season SM was a better predictor of ANPP compared with growing season or late season SM, consistent with other grasslands in the region (Chen et al., 2017; Derner et al., 2008; Parton et al., 2012), 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 (Figure 6). But despite these much-reduced PPFD levels, A_{sat} and ϕCO_2 of *B. inermis* growing directly under PV panels did not differ significantly from plants receiving full sun between rows of PV panels (Figure 3). It is important to note that these results might have been different if panels were fixed in one orientation throughout the day, resulting in consistent shading beneath panels. In contrast, panels that track the sun across the sky result in both shade and sun at all locations (Graham et al., 2021; Valle et al., 2017). This is an example of how single-axis tracking might alter ecosystem processes less than fixed PV panels. Thus, of our initial predictions—that ANPP would be strongly related to SM, 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 (Barron-Gafford et al., 2019; Graham et al., 2021; Marrou, Dufour, & Wery, 2013). The beneficial effects of shading may be particularly important when SM is higher beneath versus between panels (Adeh et al., 2018). This was clearly not the case in the managed grassland we studied, however.

At JSG, SM 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 versus beneath PV panels (Figure 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 (Figure 3), we expected to see clear evidence of physiological acclimation to this low-light environment, consistent with past studies of sun versus shade plants in forest understories (Anderson & Osmond, 1987; Boardman, 1977; Givnish, 1988; Murchie & Horton, 1997),

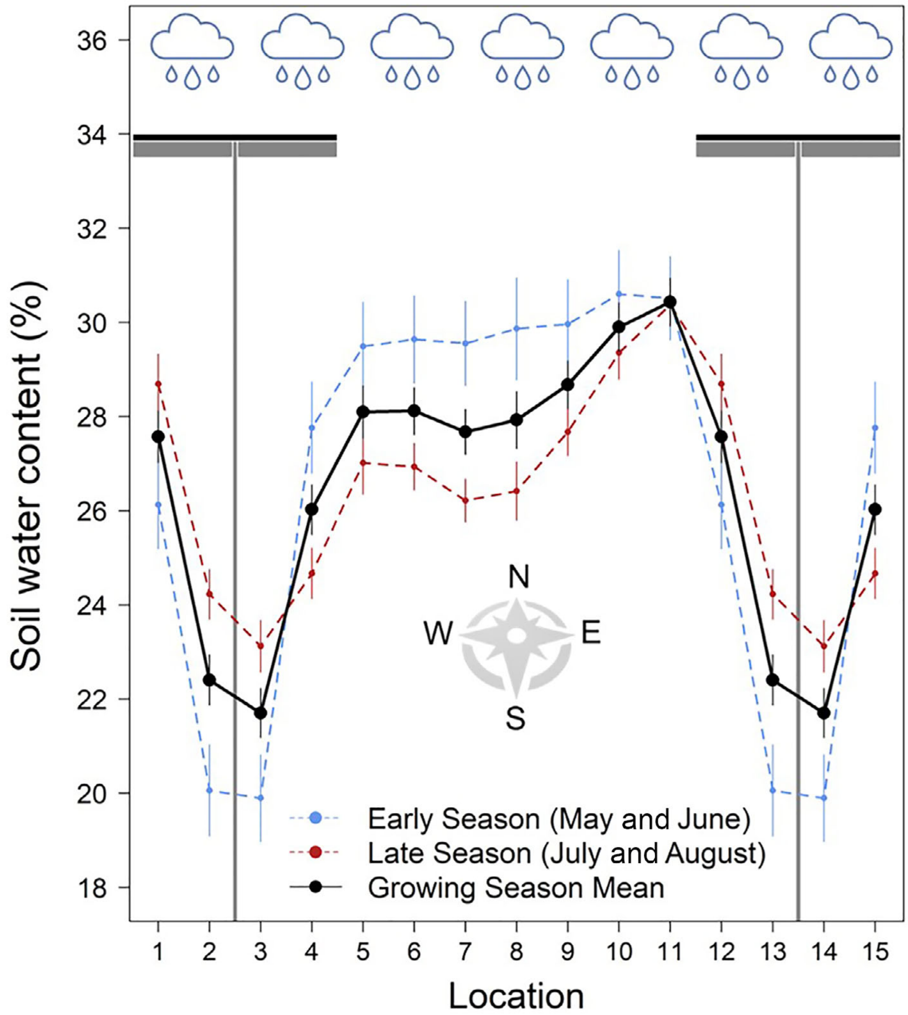

FIGURE 4 Spatial patterns of early season and late season soil water content (0–20 cm) along a transect perpendicular to rows of photovoltaic (PV) panels. Overall growing season average (±SE) is represented by a solid black line. Note that most growing season rainfall occurs after solar noon in this region when PV panels are facing west (as indicated by the purple panel in Figure 1).

as well as in productive grasslands (Knapp, 1985; Knapp & Gilliam, 1985). Specifically, we predicted that A_{sat} would be reduced in grasses beneath PV panels, whereas ϕCO_2 would be increased in shaded leaves (suggesting an increase in photosynthetic efficiency; Walters, 2005; Yamori, 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), SM was highest at the western drip edge of PV panels (Figures 4 and 5), which can be attributed to the high proportion of summer precipitation occurring in the afternoon in Colorado (Cioni & Hohenegger, 2017; Taylor et al., 2012; 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 (Figure 5). We consider two, nonexclusive 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 & Knapp, 2007) and dew inputs can positively affect carbon uptake and the water balance of plants in semiarid ecosystems (Aguirre-Gutiérrez et al., 2019; Liu et al., 2020). Thus, these small but consistent moisture inputs may

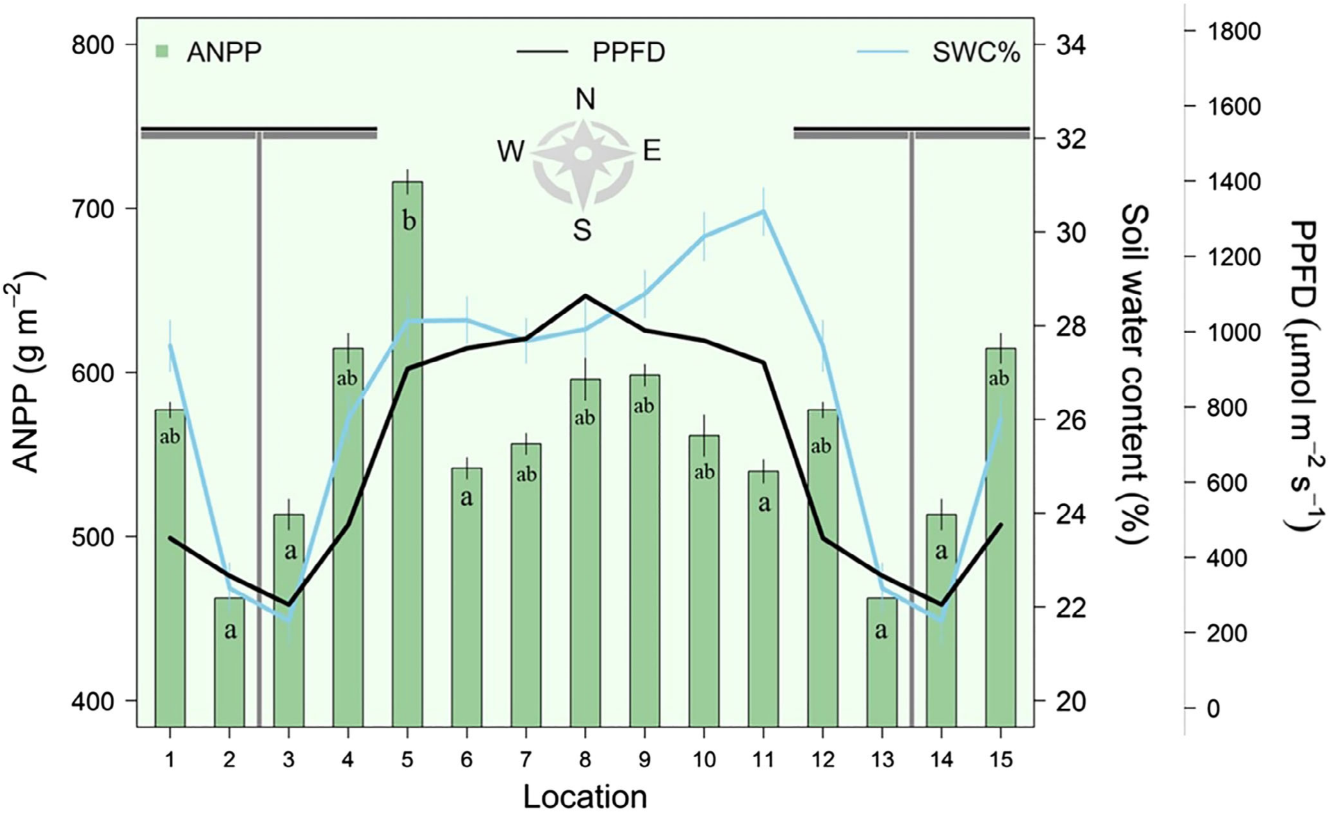

FIGURE 5 Spatial patterns of mean (±SE) aboveground net primary production (ANPP; green bars) along a transect perpendicular to rows of PV panels. The blue line represents the mean (±SE) growing season soil water content (SWC) at each location. The black line represents the mean daily photosynthetic photon flux density (PPFD) at each location, presented to demonstrate light patterns simultaneously with soil moisture percentage and ANPP. Letters a, ab, and b denote levels of significant differences in measurements of ANPP. Bars that share letters are not significantly different from each other.

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 versus PV shading. At this location with PV arrays, direct sunlight is received in the morning hours when T_{air} and vapor pressure deficit (VPD) are both relatively low throughout the growing season (Appendix S1: Figures S4 and S5), likely enhancing A_{sat} and water-use efficiency in the dominant C_3 grass. In the afternoon, when T_{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 (Ding et al., 2018; Konings & Gentine, 2017; Novick et al., 2016). 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 AV systems. As such, future measurements throughout a diel period could assess how these concomitant spatiotemporal drivers of photosynthesis determine the diel pattern of A_{sat} and daily cumulative CO_2 assimilation.

CONCLUSIONS

While AV systems have the potential to satisfy competing demands for land required for PV energy generation versus land currently used to produce forage in semiarid regions, understanding the ecological consequences of combining these land uses via AV systems should be a research priority (Barron-Gafford et al., 2019). Compared with 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 eightfold, SM by 30%, and aboveground plant productivity by approximately 40%. As a result, the

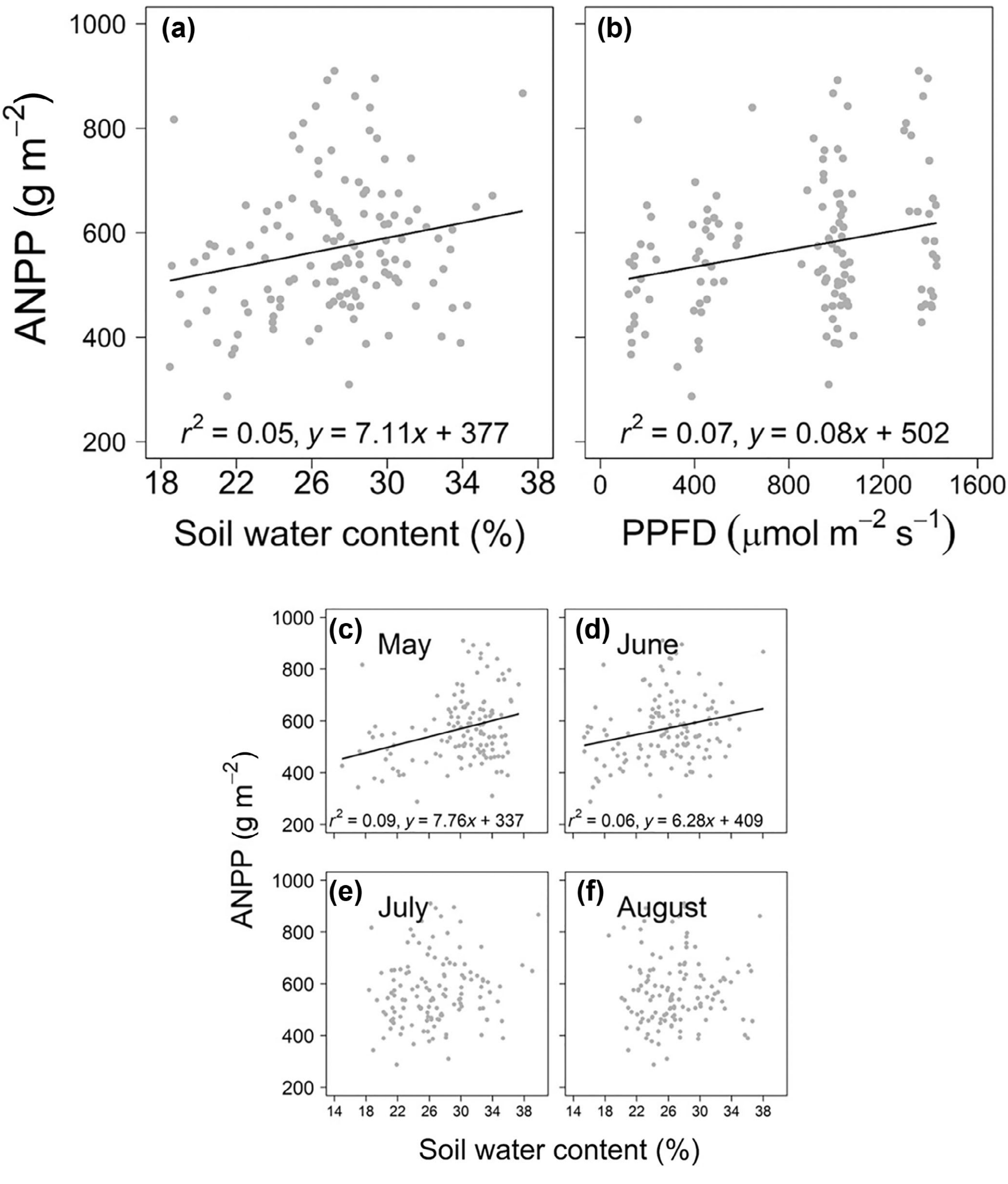

FIGURE 6 Plot-level relationships ($n = 128$) between aboveground net primary production (ANPP), mean growing season soil moisture (SM) (a), photosynthetic photon flux density (PPFD) (b), and monthly averages of SM% (c–f). Black solid lines signify a common relationship across transects. Slopes, intercepts, and r^2 values are displayed for all significant relationships.

expected primary determinant of forage production in this grassland, SM, was replaced by more complex interactions among SM, the time of day when light was available, and diurnal variation in air temperature and evaporative demand. Understanding how colocating PV panels in grasslands can alter key resources, ecological interactions and resulting ecosystem services should facilitate the design of new AV systems that can better balance renewable energy generation and agricultural productivity.

AUTHOR CONTRIBUTIONS

Alan K. Knapp and Matthew A. Sturchio conceived and designed the experiment. Matthew A. Sturchio, Greg A. Barron-Gafford, Cavin Alderfer, Anping Chen, Kathleen Condon, Olivia L. Hajek, Jordan E. Macknick, Benjamin Miller, Benjamin Pauletto, J. Alexander Siggers, Ingrid J. Slette, and Alan K. Knapp collected data. Matthew A. Sturchio and Alan K. Knapp led the data analysis with input from all authors. Matthew A. Sturchio and Alan K. Knapp wrote the manuscript with input from all authors.

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CONFLICT OF INTEREST

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Sturchio, 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.7032651.

ORCID

Matthew A. Sturchio https://orcid.org/0000-0001-5067-3770
Anping Chen https://orcid.org/0000-0003-2085-3863
Alan K. Knapp https://orcid.org/0000-0003-1695-4696

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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