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ARTICLE

Vegetation Ecology

Radiation use and understory aboveground net primary production in a temperate dryland

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Abstract

We investigated the spatial and temporal variability of herbaceous radiation use efficiency (RUE$_h$) and herbaceous aboveground net primary production (ANPP$_h$) of big sagebrush ecosystems in Wyoming's Upper Green River Basin. Using a combination of field data, Sentinel-2 satellite imagery, and global radiation datasets, we inverted the Monteith model to estimate RUE$_h$ across 80 field plots. We examined the influence of environmental factors such as temperature, precipitation, soil texture, and grazing intensity on RUE$_h$ and ANPP$_h$. Our findings revealed significant variability in RUE$_h$, with a mean of 0.56 g/Mj, and ANPP$_h$, averaging 32 g/m^2/year. RUE$_h$ was significantly influenced by growing season evapotranspiration, while ANPP$_h$ was primarily driven by annual precipitation and soil clay content. Additionally, we explored the regional and interannual variation in ANPP$_h$ over 1075 sites using 5-day averages over 5 years. ANPP$_h$ peaked in late June to early July, closely following the peak of photosynthetically active radiation (fAPAR$_h$), while maximum temperatures peaked later in summer. Precipitation emerged as a major factor explaining 54% of the spatial variability in ANPP$_h$ across the study region.

KEYWORDS

herbaceous productivity, production controls, sagebrush, Sentinel-2, spatial variability

INTRODUCTION

Drylands occur on a large fraction of the world's surface, and temperate drylands contain roughly 38 percent of the global human population (Prăvălie, 2016; Reynolds et al., 2007). Land use in these regions is primarily livestock grazing, as water is too scarce for crops and large-scale agriculture. This reliance on livestock requires careful decisions about stocking rates and grazing allotments. Drylands are sensitive to overgrazing, with many examples of desertification occurring as a result (Reynolds et al., 2007). Drylands also face threats from disrupted disturbance cycles due to invasive species (Monaco et al., 2017), woody plant encroachment (Schreiner-McGraw et al., 2020), and extreme weather-driven plant mortality (Renne, Schlaepfer, et al., 2019). For residents of these parts of the world, it is imperative that land managers and livestock owners have an understanding of the production capabilities and limitations of the land that they graze.

Big sagebrush ecosystems comprise a large part of remaining drylands in the United States and support most of the cattle raised in the western United States (Davies et al., 2011; DelCurto et al., 2023). They are largely under the jurisdiction of the Bureau of Land Management (BLM); a key task of this federal agency is to determine the proper stocking rate for the lands they manage (Kleinhesselink et al., 2023). Aboveground net primary production (ANPP) is difficult to estimate in many ecosystems, including drylands, and field estimates are commonly based on harvesting a single year's growth in a small area. Those measurements are used to estimate forage production at the scale of grazing allotments (Lauenroth et al., 1986). Field measurements have significant limitations in that they are time-consuming and can miss important spatial heterogeneity (Byrne et al., 2011). There are several methods for estimating ANPP remotely; the most common is the Monteith model, which uses a combination of measurements of photosynthetically active radiation (PARi), the fraction of PARi intersecting leaves (fAPAR), and radiation use efficiency (RUE) to estimate annual production (Equation 1, Table 1) (Monteith et al., 1977; Piñeiro et al., 2006). RUE (in grams per megajoule) is a measure of how much incoming PARi is absorbed by a plant (megajoules of radiation) and used for growth (grams of biomass) (Monteith, 1972). RUE was introduced as a key coefficient for estimating ANPP in the 1960s and has been used across many ecosystem types (Gu et al., 2002). The patterns of global RUE across space and time are relatively well understood, but much less so at the regional scale (Martínez et al., 2013). RUE can vary significantly across ecosystem types. While arid lands typically have values of slightly greater than zero to 1.2 g/Mj, some temperate grasslands and savannas have RUEs well above 2 g/Mj (Martínez et al., 2013). Poor estimates of RUE can cause ANPP estimates to vary from true conditions and lead to over or underestimation of forage availability.

TABLE 1 Acronyms.

Acronym	Definition
ANPP	Aboveground net primary production
$ANPP_h$	Herbaceous aboveground net primary production
$ANPP_{hf}$	Herbaceous aboveground net primary production from field measurements
$ANPP_{hm}$	Herbaceous aboveground net primary production from modeling
RUE	Radiation use efficiency
RUE_h	Herbaceous radiation use efficiency
$fAPAR_h$	Fraction of available photosynthetically active radiation absorbed by the herbaceous layer
PARi	Incident photosynthetically active radiation
NDVI	Normalized difference vegetation index

Big sagebrush ecosystems have two layers of vegetation. The tallest and dominant plants are shrubs, usually big sagebrush (*Artemisia tridentata* spp.). The understory is composed of perennial forbs and grasses; however, introduced annuals have begun to dominate the understory of some big sagebrush ecosystems (Davies et al., 2011; Pennington et al., 2019). Because big sagebrush is poor forage for livestock, the understory is the key forage resource in these ecosystems (Jordan et al., 2022). Big sagebrush ecosystems are sensitive to over grazing, emphasizing the importance of keeping stocking rates at a sustainable level (Davies et al., 2011) based on reliable estimates of ANPP. Compounding the problem, temporal variability of ANPP is high in big sagebrush ecosystems, with variability often driven by the current year's precipitation and the previous year's precipitation (Bates et al., 2024; Copeland et al., 2022; Sneva, 1982). This makes understanding the properties of the understory important for ANPP and forage production modeling. However, because these ecosystems are dominated by big sagebrush and other shrubs, methods to estimate RUE must filter out the signal of woody plants. Several authors have used vegetation spectral indices (specifically the normalized difference vegetation index, NDVI) to estimate the relative proportion of herbaceous and woody components (DeFries et al. 2000; Lu et al., 2003; Roderick et al. 1999; Scanlon et al., 2002). The seasonal trend decomposition (STL) procedure (Cleveland et al., 1990), which identifies the trend and seasonal and residual components of a time series, has been used to decompose NDVI time series into woody and herbaceous components. Blanco et al. (2016) applied this approach to estimate the herbaceous ANPP from NDVI data in the semiarid shrublands in South America.

Our research sought to answer three questions: (1) What is the range and distribution of the RUE of the herbaceous component (RUE_h) of a big sagebrush ecosystem, and which environmental variables best explain its variability? (2) What is the range and distribution of herbaceous ANPP ($ANPP_h$) in a big sagebrush ecosystem, and which environmental variables best explain its variability? (3) What are the seasonal and annual distributions of temperature, $ANPP_h$, the fraction of the PARi intercepted by the herbaceous layer ($fAPAR_h$), and incident solar radiation (PARi) over 1075 plots in the Upper Green River Basin of Wyoming, USA?

To answer the first question, we estimated RUE_h using data from three sources: (1) peak biomass of 80 plots sampled in the field to estimate $ANPP_{hf}$; (2) $fAPAR_h$ derived from NDVI Sentinel-2 satellite data; and (3) a global radiation dataset (ERA5) to calculate PARi at each plot.

METHODS

Study region

We conducted field work in the Upper Green River Basin of Wyoming in the United States (109° 9′ to 110° 27′ W, 42° 7′ to 43° 3′ N). The basin spans more than one million acres. The vegetation in the basin is dominated by big sagebrush (*Artemisia tridentata* Nutt.), needle and thread grass (*Hesperostipa comata*), Indian ricegrass (*Achnatherum hymenoides*), and bottlebrush squirreltail (*Elymus elymoides*). The basin is confined by mountain ranges to the north, east, and west. Mean annual precipitation is approximately 265 mm, remaining mostly constant throughout the year, with a slight peak in late spring (Thornton et al., 2022). Average monthly temperatures range from approximately 32°C in July to −10°C in January (Thornton et al., 2022), with a mean annual temperature of approximately 3°C. Elevation ranges from 1850 to 2300 m. The basin is primarily owned by the US BLM and is managed for cattle grazing.

Plots and sampling areas

We sampled 80 randomly selected plots from BLM lands dominated by big sagebrush in the Upper Green River Basin (Figure 1). The average stocking rate for BLM lands in Wyoming is 3.56-ha animal unit^{-1} month^{-1} (one animal unit, AU, is equivalent to the amount of forage required for a mature cow with calf for the specified time period) (Duffus et al., 1992). Each sampling plot covered an area of 0.01 ha, equivalent to the size of a Sentinel-2 pixel. We conducted sampling in June–August 2023. Soil texture varied across the plots; percent sand ranged from 18% to 88% and percent clay ranged from 5% to 39% (Soil Survey Staff, NRCS, USDA, 2023). Vegetation composition varied, with differences in percent cover of shrubs, annual forbs/grasses, and perennial forbs/grasses.

Estimation of RUE_h

We used a combination of field data, Sentinel-2 NDVI, and modeled incoming solar radiation to estimate herbaceous radiation use efficiency (RUE_h) at each plot using the Monteith model (Monteith et al., 1977):

$$\mathrm{RUE}_h = \frac{\mathrm{ANPP}_h(t)}{\Sigma[\mathrm{PARi}(t)\times \mathrm{fAPAR}_h(t)]}. \tag{1}$$

$\mathrm{fAPAR}_h(t)$ represents the fraction of PARi absorbed by herbaceous plants over time interval "*t*." $\mathrm{PARi}(t)$ is the total incoming PARi at each plot over the same time interval "*t*." The time interval we used represents the start of the growing season until peak biomass when sampling was conducted. $\mathrm{ANPP}_h(t)$ is the aboveground net primary production of the herbaceous layer for the time interval "*t*."

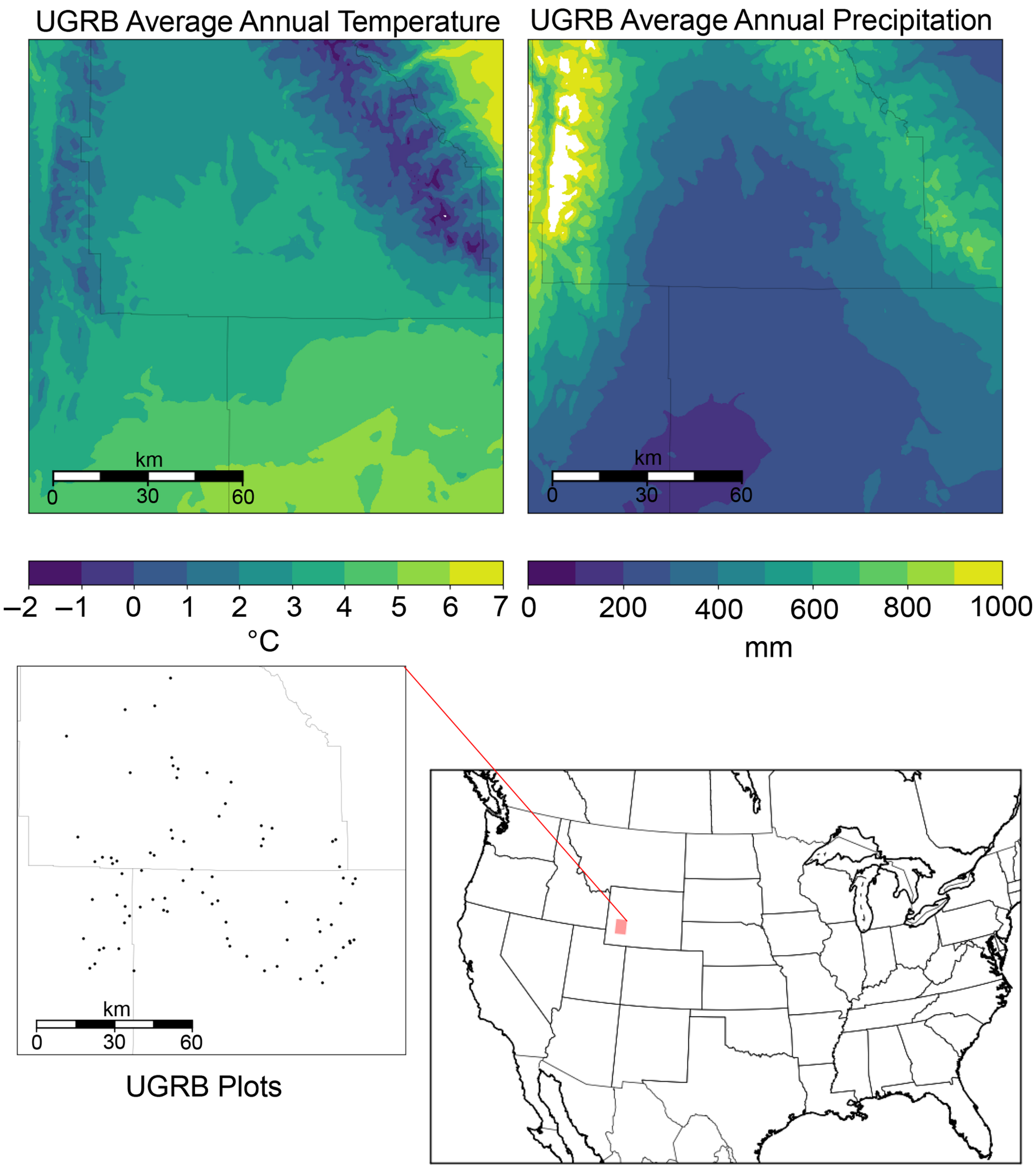
To estimate ANPP_{hf}, we harvested vegetation, when peak biomass had been reached for the region (late June through early August, 2023). We divided each 10 m × 10 m plot into 400 subplots of size 0.5 m × 0.2 m. From the 400 subplots, we randomly selected 20, representing 5% of the total area. At each subplot, we harvested the herbaceous biomass with shears at ground level, excluding any perennial storage organs. We placed the samples into paper bags and air-dried them until we transported to the lab. In the lab, we dried samples in an oven at 70°C until the mass of the samples remained constant. We separated samples into two groups: current year's growth and previous years' growth. We then weighed the samples and calculated the total mass of the current year's growth (Lauenroth et al., 1986).

We estimated fAPAR_h using Sentinel-2 NDVI, which has a five-day return interval. For each site, we extracted NDVI from the last 5 years (2019–2013). We applied a STL procedure based on LOESS using R version 4.3.1 (Cleveland et al., 1990; RStudio Team, 2020). This method divides time series data into three parts: trend, seasonal, and residual. We separated NDVI into its herbaceous and woody components using the output of this decomposition and a procedure laid out by Blanco et al. (2016). This procedure assumes that the herbaceous component of NDVI is close to the seasonal component but makes corrections based on soil background contribution and annual variability (Lu et al., 2003). We used the herbaceous component of NDVI in a linear regression model to compute fAPAR_h using an existing regression model (Blanco et al., 2016). The Blanco et al. (2016) model was developed in a controlled field experiment with a C_3 bunchgrass similar to those found in our study. The strong predictive power of the model in previous studies supported its use in our study ($r^2 = 0.74$).

We estimated PARi using an equation published by Tsubo and Walker (2004) as 0.48 times accumulated incoming radiation for the between imagery dates. Incoming radiation was based on the ERA5 global radiation dataset (Munoz Sabater, 2019). We used a single point in the center of the study area for radiation data, since variation is often very low over a limited study area (Baeza & Paruelo, 2020).

Explanatory variables

We used temperature and precipitation data from a gridded daily dataset, Daymet (Thornton et al., 2022), with 30-year


UGRB Average Annual Temperature

UGRB Average Annual Precipitation

UGRB Plots

FIGURE 1 Average annual temperature of the Upper Green River Basin (UGRB), average annual precipitation of the UGRB, and locations of plots in the UGRB in southwestern Wyoming.

averages (1990–2020). We estimated elevation and aspect from a 10-m resolution national digital elevation model (United State Geological Survey, 2020), and grazing intensity data from the BLM, using three levels of grazing—no grazing, low-moderate grazing, and moderate-heavy grazing. Low-moderate grazing was defined as annual aboveground biomass removal of less than 35% of expected annual production, and moderate-heavy grazing was defined as greater than 35% of expected annual production (Milchunas & Lauenroth, 1993). We obtained soil texture data and gravel content from the USDA SSURGO dataset (Soil Survey Staff, NRCS, USDA, 2023). We used a daily gridded climate dataset (Thornton et al., 2022) combined with SOILWAT2, a process-based dryland ecosystem simulation model (Lauenroth & Bradford, 2006; Parton, 1978), to estimate evapotranspiration (ET) at a daily scale from 1993 to 2023. We then calculated the cumulative ET for each site, starting on January 1 and ending on the sample date. The cumulative ET for the sampling year (2023) was then divided by the 30-year average cumulative ET at each site to give a measure of annual relative ET at each site that allowed us to address the relative drought conditions at each site at the time of sampling.

We used ordinary least squares regression with RUE_h as our dependent variable and the variables laid out above as our independent variables to test for linear relationships. We applied analysis of variance to test for differences in RUE_h among grazing levels. In addition, we performed piece-wise multiple regression to understand the maximum variability explained by each potential explanatory variable. All statistics and time series analyses were conducted in RStudio (RStudio Team, 2020).

Regional extrapolation

To investigate the annual and interannual variability of ANPP_{hm} and fAPAR_h, we selected 1075 points within our study area (the Upper Green River Basin) in a grid pattern to capture data across the basin and through 5 years. To estimate these variables, we used the Monteith model to estimate ANPP across the entire region (Monteith, 1972):

$$\text{ANPP}_{hm} = \text{fAPAR}_h \times \text{PARi} \times RUE_h. \tag{2}$$

We were interested in annual and interannual variability, so we used data from 5 years (2019–2023). For fAPAR_h and PARi, we used the methods laid out above, with fAPAR_h calculated from the herbaceous component of NDVI from Sentinel-2 imagery and PARi calculated from the ERA5 Land dataset (Munoz Sabater, 2019). To account for the spatial heterogeneity of RUE_h, we used an inverse distance-weighted algorithm to assign RUE_h to each gridded point, based on the values of the closest field points (Mueller et al., 2004).

RESULTS

Herbaceous aboveground net primary production

Field estimates of annual herbaceous above ground net primary production (ANPP_{hf}) were variable across plots with a mean of 320 kg/ha (32 g/m^2) (Figure 2). Mean annual precipitation and percent clay of the top ten centimeters of soil had the largest impact on variability of ANPP_{hf} ($p < 0.05$), and in a multiple linear regression, they explained 16% of the variability of ANPP_{hf}. In a single variable regression, percent clay of the top ten centimeters explained 13% and precipitation explained 5% of variability in ANPP_{hf}. All other variables (percent of average growing season evapotranspiration, sand content, gravel content, shrub cover, and elevation) had nonsignificant relationships with ANPP_{hf} ($p > 0.05$), and no significant difference was detected between grazing levels. In addition, the precipitation for the sampling year was above normal. Precipitation during our sampling season (summer 2023) consistently exceeded the 75th percentile of historical values (1990–2020) across the 80 plots we sampled (Figure 3).

Radiation use efficiency

RUE_h calculated using field and remotely sensed data at our 80 plots was variable with a mean of 0.56 g/Mj (Figure 2). The distribution of RUE_h was slightly skewed right, with the mean higher than the median. The minimum value was ~0.1 g/Mj, while the maximum was 1.5 g/Mj. Multiple linear regression analysis of RUE_h resulted in a model containing the same two significant variables from the single variable models, percent gravel and percent of average growing season evapotranspiration ($p = 0.007$, $r^2 = 0.12$, $n = 80$). Soil texture, annual precipitation, relative shrub cover, and elevation did not have a significant effect on the spatial variability of RUE_h. An analysis of variance for RUE_h on our three grazing levels showed no significant differences.

Regional patterns

ANPP_{hm}, fAPAR_h, and temperature showed a unimodal distribution annually with clear highs in summers and lows in winters, and with high interannual variability (Figure 4). However, peaks of each variable occurred during different parts of summer: fAPAR_h consistently peaked in mid to late June for all 5 years across the sites and ANPP_{hm} followed a similar pattern just slightly delayed, with peaks occurring in late June and early July for four of the five years studied. Maximum temperatures consistently peaked in late July and early August, typically 30–45 days after maximum herbaceous biomass was achieved for the year. The average minimum fAPAR_h and average minimum ANPP_{hm} were close to 0.

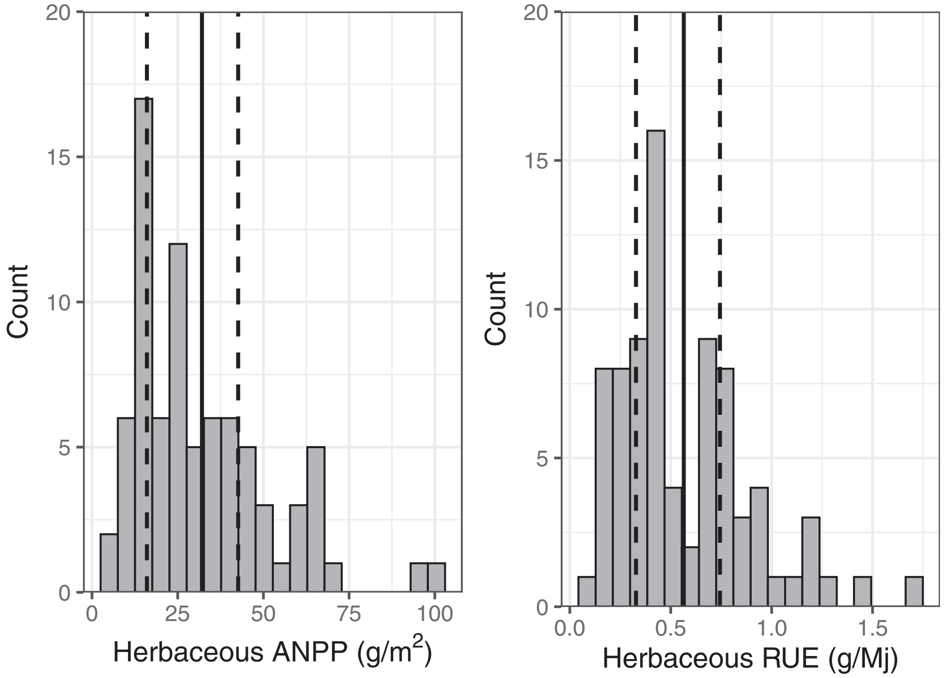


FIGURE 2 Herbaceous aboveground net primary production (ANPP) and radiation use efficiency (RUE). The solid black line represents the mean, with dashed lines representing the lower and upper bounds of the interquartile range. The ANPP data were taken from 80 field plots in the Upper Green River Basin and the RUE data were modeled for those same 80 plots using the Monteith model.

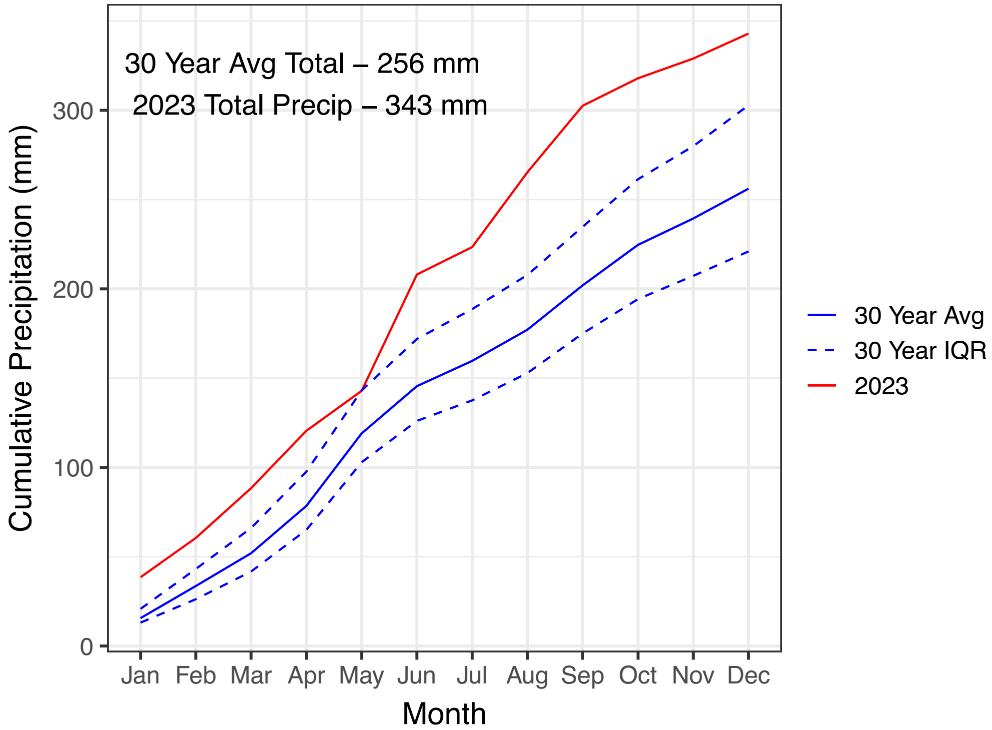


FIGURE 3 Cumulative precipitation by month (Thornton et al., 2022). The solid blue line represents the median of the 30 year (1990–2020) average monthly precipitation of the 80 field plots in the Upper Green River Basin. The upper and lower dotted blue lines represent the upper and lower bounds of the interquantile range (IQR), respectively, of the 30 year average monthly precipitation for the field plots. The solid red line represents the median monthly precipitation for the year 2023 across the 80 field plots.

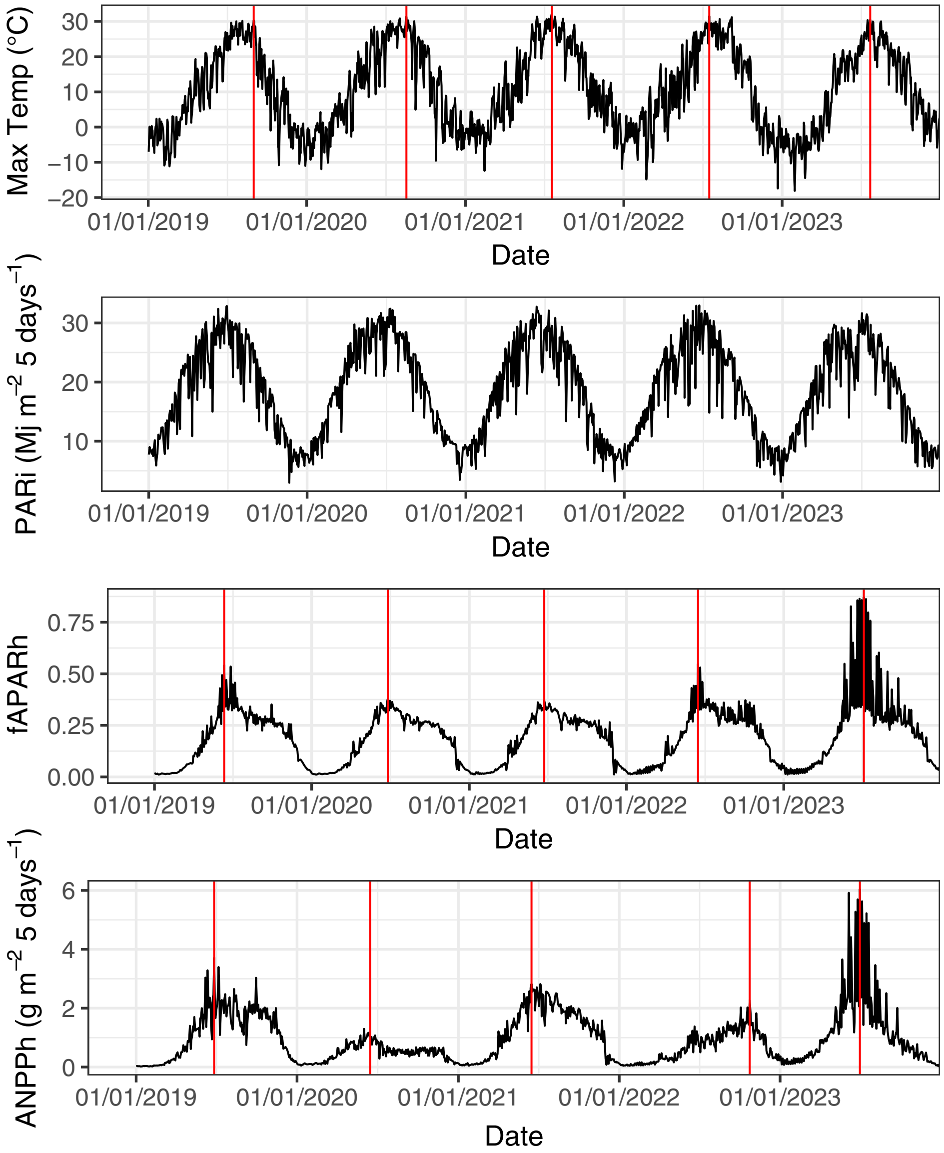


FIGURE 4 Maximum temperature (gridded dataset), incident photosynthetically active radiation (PARi, global radiation dataset), the fraction of available photosynthetically active radiation absorbed by the herbaceous layer (fAPAR), and herbaceous aboveground net primary production (ANPP_h), 2019–2023. The black line is the mean across 1075 sites in the Upper Green River Basin. The 1075 sites were selected in grid pattern across the basin to capture the variability of the entire study area. Vertical red lines represent the annual maximum of each graph.

Across the five years, peak herbaceous biomass showed the highest variability of all variables. The estimated mean peak of 5-day ANPP_{hm} for the gridded random points varied from ~2.5 to ~6 g/m^2. The mean peak fAPAR_h also had a high range of variability across years, but to a lesser degree. While the year of highest recorded ANPP_h was nearly double that of the other years, the other 3 years showed little variability. In contrast, ANPP_{hm} still had high variability outside of the extremely high year.

We found that predicted peak values of 5-day ANPP_{hm} ranged from 2 to 6 g/m^2 of herbaceous biomass across the 5 years studied. We found that mean annual precipitation explained 54% of the variability of the average ANPP_{hm} (2019–2022) (Figure 5). Also, ANPP_{hm} showed high correlation with temperature and elevation. However, both variables were correlated with precipitation, so we excluded them due to concerns about multicollinearity.

DISCUSSION

Our results showed substantial variability in RUE_h across the field plots, with soil gravel content in the upper soils

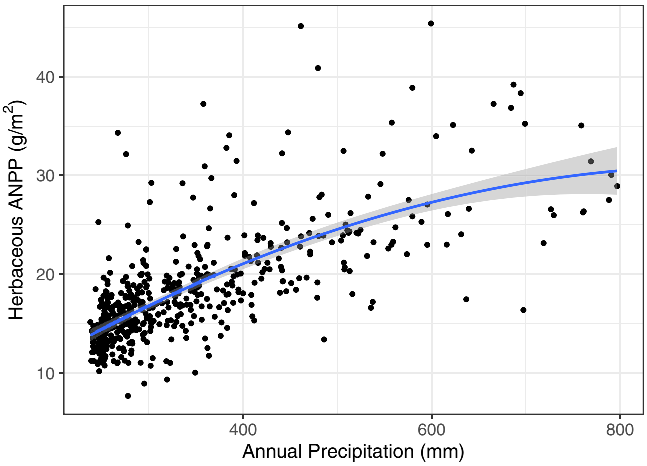


FIGURE 5 Mean annual herbaceous aboveground net primary production (ANPP$_h$) (2019–2023) by mean annual precipitation (1990–2020). The blue line represents the line of best fit ($R^2 = 0.57$, $p < 0.001$). Gray area represents the SE of the estimate. Each point represents one of 1075 points that were modeled in the Upper Green River Basin using the Monteith model. Data for the modeling came from global radiation data, field-based estimates of use efficiency, and remotely sensed values of normalized difference vegetation index (NDVI).

(0–10 cm) and relative growing season evapotranspiration emerging as significant factors affecting RUE$_h$. Herbaceous aboveground net primary production (ANPP$_h$) also showed high variability, primarily influenced by the clay content in the upper soils (0–10 cm) and annual precipitation. In the expanded 1075 sites within the Upper Green River Basin, precipitation alone accounted for over half of the variability in ANPP$_h$ over 5 years.

The range of and variability in RUE$_h$ we found is consistent with other work in semiarid shrub dominated ecosystems elsewhere in the world (Blanco et al., 2022). The mean from our study was slightly higher than the mean RUE$_h$ found in other studies of similar areas. This is likely due to the above average precipitation that occurred in the year of sampling. Drought stress and water availability have been shown to strongly impact RUE$_h$ (Piñeiro et al., 2006) and having a year of above average precipitation likely led to higher-than-average estimates of RUE$_h$. We also acknowledge that the precipitation in the year of sampling may have contributed to the lack of patterns observed in our RUE data. RUE is thought to be maximized under ideal growing conditions, and since our system is water limited (Schlaepfer et al., 2012), it is possible that other influences on RUE$_h$ were masked by the high level of water availability during the growing season. For comparison, the strongest driver of variability in RUE$_h$ in the Chaco Shrublands of Argentina was grazing intensity (Blanco et al., 2022). Our analysis showed no significant difference with grazing intensity; however, we recorded higher values at the low-moderate and moderate-heavy grazing intensities than the ungrazed areas.

Our mean ANPP$_{hf}$ and its variability was consistent with other findings from big sagebrush ecosystems and other shrub dominated dryland ecosystems (Engda et al., 2016). Annual precipitation had a strong, positive correlation with ANPP$_{hf}$, a finding that is consistent with a wide body of research that has shown a similar relationship across drylands around the world (Lauenroth, 1979; McNaughton et al., 1989; Sala et al., 1988). The second most influential variable was clay content in the top ten centimeters of soil. Percent clay had a positive relationship with ANPP$_{hf}$, an apparent contradiction with the inverse texture effect, which states that coarser soils will have higher productivity in water limited systems due to elevated soil water availability (Noy-Meir, 1973). This relationship has strong support in big sagebrush ecosystems (Renne, Bradford, et al., 2019). Our findings suggest that if there is overall higher productivity on coarser soils in this region, it might be occurring in big sagebrush instead of the herbaceous understory. An in depth study that measured the annual production of sagebrush would be necessary to determine if this is the case.

Our results for the temporal variability of fAPAR$_h$, ANPP$_{hm}$, and maximum temperature showed that the three all peak at approximately the same time during summer. This can be attributed to the precipitation regime of the area, with the majority of precipitation occurring in late spring to early summer. In addition, the understory is dominated by C_3 grasses. In contrast to our study site, areas dominated by a mixture of C_3 and C_4 plants will achieve peak biomass at different times of the year, causing a bimodal distribution has been observed with a strong decoupling of the relationships that we observed (Baeza et al., 2010). We use a constant RUE$_h$ through the year, though research has shown that it can change slightly within and between years (Paruelo et al., 2010; Piñeiro et al., 2006).

We found a strong relationship between precipitation and ANPP$_{hm}$. This agrees with our findings for measured ANPP$_{hf}$, and the large literature pertaining to patterns of productivity in drylands. Our estimates from satellite data spanned a wide range (15–250 kg/ha) but were lower than in our measured ANPP$_{hf}$. Using a mean RUE$_h$ may account for this difference between the range of ANPP measured and modeled. Figure 2 highlights that the RUE$_h$ distribution was heavily right-skewed, and that using the mean significantly underestimates RUE$_h$ for many sites which would lead to lower estimates of ANPP. This would lead to an underestimate of ANPP$_{hm}$, for our predicted values. Improving both the description of the temporal and the spatial controls of RUE_h variability would improve ANPP estimates in sagebrush ecosystems. Underestimation of RUE_h can lead to underutilization of resources by land managers and does not allow for proper understanding of ecosystem functioning. Many factors may explain RUE_h variability. The largest are water stress and plant species composition. Species vary across the basin (Pennington et al., 2019) and it is possible that this is leading to the variability; however, an in depth study of the dominant herbaceous species would be required to address this.

Despite the relative homogeneity of big sagebrush ecosystems in the Upper Green River Basin, our study highlights the variability that exists within one basin dominated by the same plant species. While our regional estimates of ANPP_{hm} may underestimate field values in some locations, our methods provide a scalable framework for estimating ANPP across the big sagebrush ecosystem. We leveraged empirically derived estimates of RUE over a large area to generate a model to estimate a critical descriptor of ecosystem functioning. This work allows us to better understand the heterogeneity that exists in big sagebrush ecosystems and provides useful information for land managers in the region.

ACKNOWLEDGMENTS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Wilson, 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.15756026.

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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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