

ARTICLE

Special Feature: Dynamic Deserts

Seasonal carryover of water and effects on carbon dynamics in a dryland ecosystem

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Abstract

Net primary productivity in arid and semiarid regions is controlled by water availability for which rainfall has been a commonly used proxy at annual scales. However, the hydrological partitioning occurring through the water balance can also shape both seasonal and annual net ecosystem productivity. In this study, we used 10 years of water and carbon flux measurements in a mixed shrubland watershed of the Chihuahuan Desert to investigate the seasonal variability and controls on net ecosystem production. Over this period, the site exhibited a bimodal rainfall regime with an average of 211 and 67 mm for the wet (July–December) and dry (January–June) periods of the year, respectively. During the wet season, soil infiltration and channel transmission losses led to an average of 35.8 mm of water stored in the subsurface for subsequent dry periods. By contrast, dry seasons consumed 30.3 mm of stored subsurface water to fulfill the ecosystem water demand, particularly during the springtime. In response, gross primary productivity occurred in equal amounts for both seasons, while ecosystem respiration was substantially higher during the wet season. This resulted in the mixed shrubland acting as an annual net sink of carbon (average of $153.2 \text{ g C m}^{-2} \text{ year}^{-1}$) of which 65% occurred during the dry season. We determined that the wet season provided water in excess of vegetation demands in that season, a portion of which was stored in the watershed subsurface for subsequent use, leading to a legacy effect. Gross primary productivity during the dry season was dependent on carryover soil moisture accessed by deep-rooted shrubs. Our coordinated observations of water–carbon dynamics revealed that water availability during the wet season can sustain the annual ecosystem productivity by impacting the subsequent dry season carbon uptake.

KEYWORDS

Chihuahuan Desert, dryland ecohydrology, ecosystem productivity, eddy covariance, environmental sensor network, shrubland, Special Feature: Dynamic Deserts, watershed hydrology

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INTRODUCTION

In arid and semiarid landscapes, primary productivity is controlled by soil water availability (e.g., Noy-Meir, 1973; Reynolds et al., 2000, 2004; Scott et al., 2006). Annual rainfall has been commonly used as a proxy of water availability to determine productivity (Biederman et al., 2016; Flanagan & Flanagan, 2018; Hsu et al., 2012; Huxman et al., 2004; Maurer et al., 2020; Ogle & Reynolds, 2004; Sala et al., 1988; Sala et al., 2012; Scott et al., 2015; Thomey et al., 2011). Nevertheless, several studies have found weak relations between annual rainfall and annual productivity (Biederman et al., 2018; Jia et al., 2016; Ukkola et al., 2021) and have suggested that seasonal water balance variations may shape the productivity of arid and semiarid ecosystems (Baldocchi et al., 2018; Jia et al., 2016; Liu et al., 2020; Méndez-Barroso et al., 2009). Recent observational and modeling efforts have also suggested that soil moisture carryover from rainy periods to subsequent dry periods can play an important role in vegetation water use (e.g., Brooks et al., 2015; McCormick et al., 2021; Miguez-Macho & Fan, 2021; Mu et al., 2022). A useful approach to explore this soil moisture carryover or legacy effect is by inspecting relationships between seasonal patterns of water availability and ecosystem productivity.

It is well known that biogeochemical processes in arid and semiarid ecosystems are tied to the hydrological cycle (e.g., Huxman et al., 2004; Lohse et al., 2009; Scott et al., 2006; Williams et al., 2006; Yahdjian et al., 2006; Yahdjian et al., 2011). While rainfall is a useful proxy for this coupling, the water balance (or hydrological partitioning) constrains the availability and use of water by vegetation over seasonal to interannual time periods (e.g., Biederman et al., 2016; Jia et al., 2016; Scott et al., 2015). For instance, evapotranspiration (ET) and shallow soil moisture within a season have been shown to be improved indicators of ecosystem water use relative to seasonal precipitation (e.g., Biederman et al., 2016, 2017; Kurc & Small, 2004, 2007; Scott & Biederman, 2017; Vivoni et al., 2008; Yépez et al., 2007). An open question remains as to whether the hydrological partitioning during the wet season can influence biogeochemical processes and ecosystem productivity in a subsequent dry season. For instance, Reichmann et al. (2013) found no seasonal soil moisture carryover effect on annual plant productivity in an arid ecosystem with flat slopes. Much less attention has been placed on the role of soil moisture carryover on arid and semiarid ecosystem productivity where complex terrain is present.

Soil moisture carryover or legacy effects can be studied in North American deserts since water input occurs during both the winter and summer seasons (Sponseller et al., 2012). This bimodal regime is characterized by convective storms during the summer and widespread frontal

storms during the winter (Scott et al., 2009; Scott & Biederman, 2019). The seasonal variability of water input and atmospheric conditions generates differences in hydrological partitioning and can lead to divergent patterns of ecosystem water use and productivity. Specifically, during the North American monsoon (NAM; Adams & Comrie, 1997), larger rainfall events combined with higher radiation and atmospheric water demand typically lead to higher water losses through ET and from runoff occurring through channels (e.g., McKenna & Sala, 2018; Méndez-Barroso et al., 2009; Pérez-Ruiz et al., 2021; Pierini et al., 2014; Templeton et al., 2014; Vivoni et al., 2010). By contrast, the lower intensity precipitation during the winter, when radiation and atmospheric water demands are much lower, typically favors the downward percolation of water through deeper soil layers, with minimal ET and runoff production, but may still support ecosystem productivity and water use within that season (e.g., Anderson-Teixeira et al., 2011; Scott & Biederman, 2019; Wilcox et al., 2006).

Some shrubland ecosystems follow a bimodal productivity regime that is controlled both by the winter and summer seasons. Studies have shown a high ecosystem carbon uptake in the winter season due to the presence of evergreen species or those shrubs with spring leaf-out characterized by a rooting structure that allows access to deep soil moisture (Biederman et al., 2018; Huxman et al., 2004; Kurc & Benton, 2010; Kurc & Small, 2004; Ogle & Reynolds, 2004; Reynolds et al., 2004; Wohlfahrt et al., 2008). Since water storage in deeper layers is influenced by the seasonality of water input and its partitioning, it is important to elucidate the mechanisms of primary productivity in those shrubland ecosystems where a bimodal rainfall regime might lead to soil moisture carryover effects between different seasons. Subsurface water storage accessed by deep shrub roots is a mechanism by which wet seasons can be linked to subsequent dry seasons (e.g., Duniway et al., 2007, 2010; Schreiner-McGraw & Vivoni, 2017, 2018; Schwinning, 2010). Thus, soil moisture carryover effects may be an important link between different seasons in bimodal regimes, particularly for ecosystems where complex terrain leads to a hydrological partitioning that promotes subsurface water storage during the wet season and where plants can access deep soil water during the subsequent dry season.

In this study, we investigated the seasonal dynamics of the water balance and its relation to seasonal primary productivity in a mixed shrubland of the Chihuahuan Desert using the eddy covariance (EC) method (Baldocchi, 2003) and a hydrological instrumentation network tailored to a site with complex terrain (Templeton et al., 2014). To conduct this, we analyzed the seasonal variability of water balance components and carbon fluxes, and their linkage, over a 10-year period. The bimodality of hydrological processes and ecosystem productivity in this dryland

ecosystem offered an opportunity to explore the soil moisture carryover effects between seasons and the role played by the elements of net ecosystem production (NEP; gross primary productivity [GPP] and ecosystem respiration [R_{eco}]) on the seasonal and annual carbon balance. Specifically, we addressed the following questions using the coordinated observations in the study watershed: (1) Do seasonal variations of water balance components indicate soil moisture carryover? (2) What is the seasonality in NEP and how is it explained by the carbon flux components? and (3) Is there a legacy of the wet season on NEP in the subsequent period? In addressing these questions, we considered how the complex terrain in the watershed affected its hydrological partitioning. In addition, we used the long-term observational record to discuss the interannual variations in the seasonal rainfall regime and its impact on the seasonal and annual carbon budget.

METHODS

Study site

The study site is a mixed shrubland in the Jornada Experimental Range (JER), ~20 km north of Las Cruces, NM, USA, within the northern portion of the Chihuahuan Desert (Figure 1). A small first-order watershed of approximately 4.7 ha was instrumented in 2010 to monitor water and carbon flux components (Anderson & Vivoni, 2016; Mascaro & Vivoni, 2016; Schreiner-McGraw et al., 2016; Templeton et al., 2014). Local climate is classified as a cold desert (Koppen zone BWk), with an annual average rainfall (R) of 277.9 mm and a mean annual temperature of 17.9°C during the study period of 2011–2020. A bimodal rainfall regime leads to ~65% of annual rainfall during the NAM in July through September (Adams & Comrie, 1997).

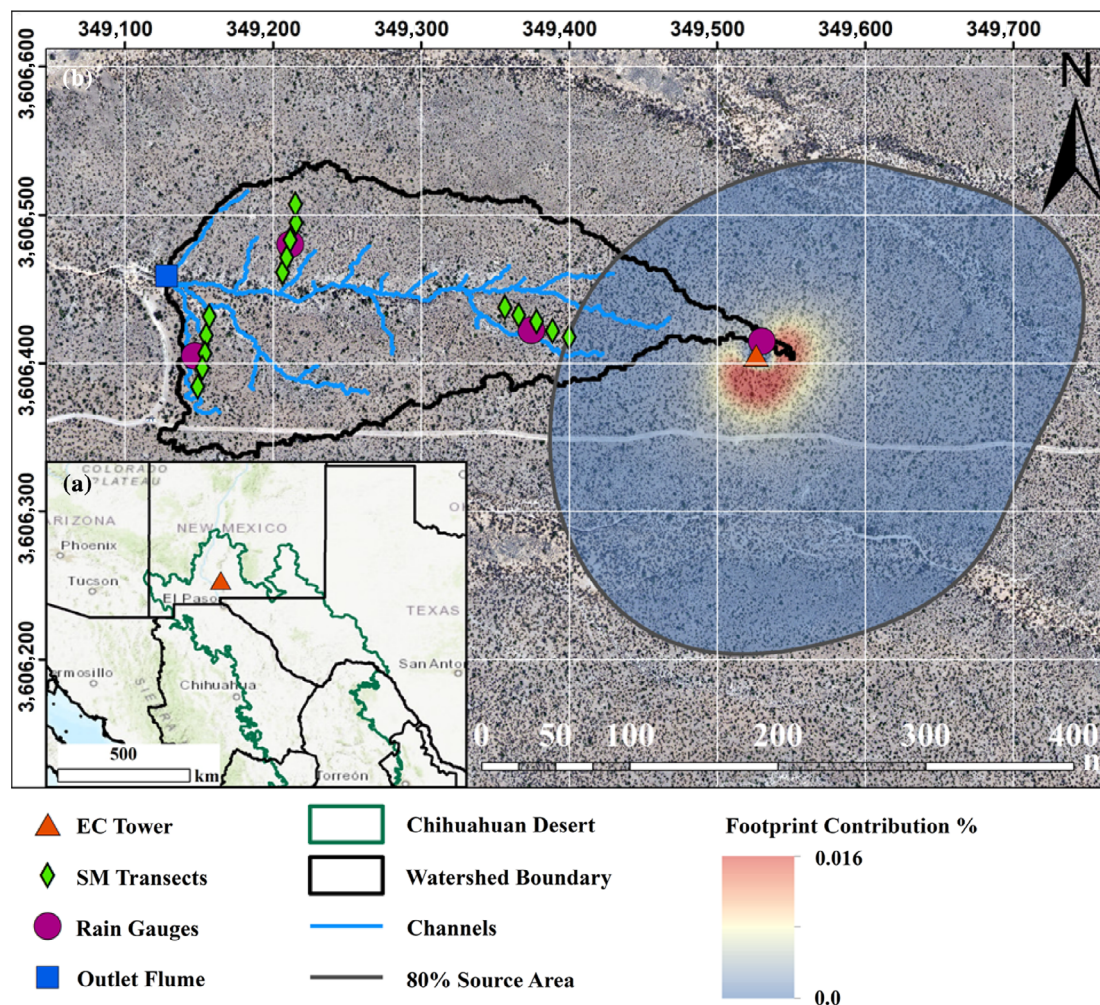


FIGURE 1 (a) Location of the study site in relation to the southwestern United States and the Chihuahuan Desert. (b) Instrumented first-order watershed showing the location of the eddy covariance (EC) tower, soil moisture (SM) transects, rain gauges, and outlet flume, as well as the 80% source area of fluxes and the percentage of contribution to the EC footprint.

The process of woody plant encroachment in the last 150 years (Gibbens et al., 2005) has led to a mixed shrubland consisting of creosote bush (*Larrea tridentata*), honey mesquite (*Prosopis glandulosa* Torr.), mariola (*Parthenium incanum*), tarbush (*Flourensia cernua*), and snakeweed (*Gutierrezia sarothrae*), as well as the lower presence of several grass species, including bush muhly (*Muhlenbergia porteri*), tobosa grass (*Pleuraphis mutica*), and sand dropseed (*Sporobolus cryptandrus*). A high-resolution terrain and vegetation product (Templeton et al., 2014) indicated that the watershed consists of ~4% grasses, ~30% shrubs, and ~66% bare soil. The study site has sandy-loam soil textures with a high gravel content, and a CaCO₃ layer at a depth of ~40 cm (Anderson & Vivoni, 2016). The watershed has north-, south-, and west-facing hillslopes with modest slopes (0–6°), except along the channel banks where higher slopes are found (15–25°). The main channel of ~0.5 m in width has a sandy bottom that allows percolation of runoff (Schreiner-McGraw & Vivoni, 2017). More limited vertical infiltration occurs on the hillslopes themselves due to the CaCO₃ layer. As a result, the complex arrangement of hillslopes and channels within the watershed allows for overland and channel runoff to occur in response to winter and summer storm events.

Water balance and carbon fluxes measurements

High-frequency measurements of water, energy, and carbon fluxes were obtained using the EC method at a location whose footprint represented well the watershed area (Anderson & Vivoni, 2016). Fluxes included NEP, latent heat flux (λET), and sensible heat flux (H). The EC system consisted of an infrared gas analyzer (IRGA) to measure H₂O and CO₂ concentrations and a sonic anemometer to measure wind components. The IRGA used was a LI-7500 (Li-COR Biosciences, Lincoln, NE, USA), while the sonic anemometer was a CSAT-3 (Campbell Scientific, Logan, UT, USA). The EC system was installed at 7.1 m above the ground, at an elevation of 1469 m, and the ecosystem had an average canopy height of 1 m (Templeton et al., 2014). Fluxes were calculated at 30-min intervals with EddyPro 7.0.6. Data quality control and flux processing followed the standards of the EC community as described in Pérez-Ruiz et al. (2021). As a result, the EC site is registered as part of the AmeriFlux network as “Jornada Experimental Range Mixed Shrubland” (code US-Jo2; <https://ameriflux.lbl.gov/sites/siteinfo/US-Jo2>), and the datasets presented here are published at the AmeriFlux repository (Vivoni & Pérez-Ruiz, 2022).

Processed 30-min-averaged fluxes were filtered to exclude periods with rainfall ($R > 0.2 \text{ mm } 30 \text{ min}^{-1}$), for data when winds were $\pm 10^\circ$ from the opposite direction of the

instruments (206–226°), and for data beyond plausible values ($NEP \pm 6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, λET from -50 to 450 W m^{-2} , and H from -200 to 600 W m^{-2}), following the procedures of Schmid et al. (2000). We filtered the dataset using a friction velocity criterion of $u^* < 0.16 \text{ m s}^{-1}$ estimated using the moving point test (Papale et al., 2006). Gap filling of missing data was applied using Reichstein et al. (2005) through REddyProc (Wutzler et al., 2018). During the study period, about 36.0%, 35.4%, and 6.8% of data were missing for NEP, λET , and H , respectively, in line with data availability in other EC studies (e.g., Wutzler et al., 2018). The average footprint of the 80% source area was obtained using the approach of Kljun et al. (2015), as shown in Figure 1b.

We estimated the components of NEP, R_{eco} , and GPP, using the flux partitioning tool in REddyProc. Since $NEP = GPP - R_{\text{eco}}$, positive values of NEP represent carbon uptake, while negative values indicate carbon release. The partitioning procedure was based on the night-time sensitivity of NEP with the ratio of the measured air temperature to the soil temperature obtained from site sensors and based on the exponential regression model of Lloyd and Taylor (1994). As part of the quality control, we inspected the energy balance closure using two methods: (1) the ratio between the sum of scalar fluxes and available energy ($\epsilon = \sum[H + \lambda ET] / \sum[R_n - G]$), and (2) a simple linear regression ($H + \lambda ET = m[R_n - G] + b$), where R_n is the net radiation and G is the ground heat flux measured at the EC site (Templeton et al., 2014). The energy balance closure was determined for periods of simultaneous fluxes, finding that results ($\epsilon = 0.82$, $m = 0.61$, $b = 20.6$, and $R^2 = 0.83$) are within the range of other EC studies across different ecosystems (Wilson et al., 2002).

Water balance components were estimated following Schreiner-McGraw and Vivoni (2017). Rainfall (R) was measured using up to four tipping-bucket rain gauges (TE525MM; Texas Electronics, Dallas, TX, USA; Vivoni et al., 2022a) to construct a 30-min average using Thiessen polygons. Streamflow (Q) at 30-min intervals was measured at the outlet using a Santa Rita supercritical flume (Smith et al., 1981), a pressure transducer (CS450; Campbell Scientific, Logan, UT, USA), and a local calibration (Turnbull et al., 2013). ET was calculated at 30-min resolution with the EC method. Watershed average volumetric soil moisture (s) was obtained at three depths (sensors placed at 5, 15, and 30 cm) using soil dielectric probes (Hydra Probe; Stevens Water, Portland, OR, USA; Vivoni et al., 2022b) along three hillslope profiles in the watershed and then depth-averaged following Schreiner-McGraw and Vivoni (2017). Percolation (P) was estimated as the residual of the watershed water balance:

$$Z_r \frac{\Delta s}{\Delta t} = R - ET - Q - P, \quad (1)$$

where Δs is the change in volumetric soil moisture over the time interval Δt (1 month) and Z_r is the soil depth. Positive P values indicate percolation from the shallow soil surface into the deeper subsurface below Z_r , particularly due to channel transmission losses resulting from overland flow to the channel network by infiltration-excess runoff, while negative P values suggest an upward movement of water from beneath Z_r (Schreiner-McGraw & Vivoni, 2017). As the CaCO_3 horizon is considered a semi-impermeable boundary, Z_r was estimated as 40 cm in Equation (1). Monthly estimates of Δs and P from the watershed network provide insights into the shallow and deep subsurface water storage changes and their carryover across seasons, respectively.

Data analysis

We divided each year in two seasons that represent dry (January–June) and wet (July–December) periods, each with 6 months. The dry season included the six driest months, while the wet season consisted of the six wettest months within a year. Daily values of water balance components (R , ET , Q , s , and P) and carbon fluxes (GPP, R_{eco} , and NEP) were aggregated to monthly, seasonal, and annual scales (see Appendix S1: Figure S1 for daily variations). We compared water balance components and carbon fluxes for the dry and wet seasons in each year using the Wilcoxon signed-rank test (Wilcoxon, 1945) and for seasonal differences when averaged across all years using a paired t test. To assess the relationship between water and carbon fluxes, Pearson correlation coefficients were obtained between annual, dry season, and wet season sums and seasonal proportions of annual values. Correlation analyses between water and carbon fluxes at seasonal and annual scales are suitable for our purposes as follows: (1) aggregated data conform to normal distributions; (2) negligible autocorrelation is present at these time scales; and (3) fluxes are based on different trace gas measurements. Annual series linear trend analyses were also performed and assessed through the coefficient of determination (R^2). Statistics were tested with significance determined by $p < 0.05$ and $p < 0.10$ using IBM SPSS Statistics 26.

RESULTS

Annual and seasonal variations of water balance components

During the study period, annual R at the shrubland was $277.9 \pm 53.3 \text{ mm year}^{-1}$ (Appendix S1: Table S1), consistent with long-term records (Peters et al., 2021). Annual ET

($264.8 \pm 50.9 \text{ mm year}^{-1}$) was 95.3% of annual rainfall (ET/R near 100% implies ET was the largest water loss) and had similar interannual variability to R . The remainder of annual R went to streamflow (2.7% of annual R or $7.6 \pm 6.7 \text{ mm year}^{-1}$), percolation (1.8% of annual R or $5.0 \pm 38.4 \text{ mm year}^{-1}$), and the change in volumetric soil moisture ($0.5 \pm 23.5 \text{ mm year}^{-1}$), with a large interannual variability in all components (Appendix S1: Table S1). Importantly, P was generally positive during wet years and negative during dry years, with an interannual average near zero (Appendix S1: Table S1), indicating that water input to the subsurface storage increased or decreased depending on the annual R .

The shrubland had a bimodal distribution of monthly R with higher values in the wet season of $211 \pm 62.4 \text{ mm}$ or 75.6% of annual R (Figure 2a; Appendix S1: Table S2). By contrast, the dry season received $67 \pm 44 \text{ mm}$ of R , representing a 24.4% of annual R (statistically significant difference between wet and dry season R at $p < 0.05$). ET during the seasons was also significantly different ($p < 0.05$; Appendix S1: Table S2). The wet season had ET/R of 79.4% (ET of $167.6 \pm 38.2 \text{ mm}$), lower than the annual ET/R . In response, the wet season had a larger proportion of streamflow losses, $Q/R = 3.6\%$ (Q of $7.6 \pm 6.7 \text{ mm}$), and percolation, $P/R = 10.4\%$ (P of $21.8 \pm 32.3 \text{ mm}$; Figure 2b), as well as a greater soil water storage, $\Delta s/R = 6.6\%$ (Δs of $14.0 \pm 14.6 \text{ mm}$; Figure 2c). During the wet season, high s was more evenly distributed in the measured soil depth, with seasonal averages of $6.9 \pm 1.5\%$, $8.2 \pm 1.6\%$, and $7.6 \pm 1.3\%$ at 5, 15, and 30 cm depths, respectively. Positive wet season values of P suggest that water was lost to deeper soil layers. Thus, the wet season preferentially led to soil water increases in the hillslopes and channels of the watershed. By contrast, the dry season had ET of $97.2 \pm 49 \text{ mm}$, representing 145.3% of R and reductions were noted in s throughout the soil depths while dry season P was negative. Both of these changes indicated that water from shallow and deep soil layers was consumed as ET (Schreiner-McGraw & Vivoni, 2017). Of the additional water used for ET during the dry season, $13.4 \pm 12.6 \text{ mm}$ corresponded to Δs and $16.8 \pm 13.8 \text{ mm}$ to P , suggesting that carryover soil moisture from the prior wet season supported ET .

Annual and seasonal variations of carbon fluxes

During the study period, the shrubland acted as a net carbon sink in all years, with an annual NEP of $153.2 \pm 42.6 \text{ g C m}^{-2} \text{ year}^{-1}$, resulting from annual GPP of $393.6 \pm 57.2 \text{ g C m}^{-2} \text{ year}^{-1}$ and annual R_{eco} of $240.4 \pm 38.6 \text{ g C m}^{-2} \text{ year}^{-1}$. An amplified interannual

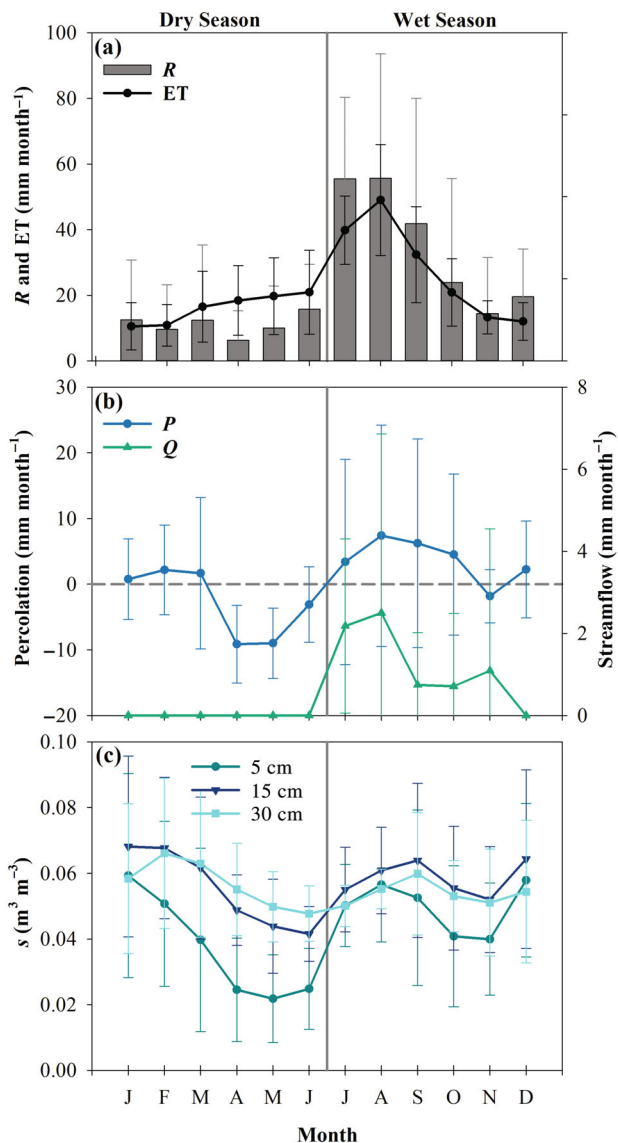


FIGURE 2 Monthly averages of water balance components from 2011 to 2020. (a) Rainfall (R) and evapotranspiration (ET). (b) Streamflow (Q) and percolation (P). (c) Volumetric soil moisture (s) at 5, 15, and 30 cm depths. Bars represent ± 1 monthly SDs. Vertical lines divide the dry and wet seasons.

variability was noted for NEP as compared to both GPP and R_{eco} (Appendix S1: Table S3). Seasonal differences in GPP and R_{eco} led to an uneven distribution of NEP among the seasons (Figure 3). The dry season had a higher contribution to NEP during all years at $99.6 \pm 26.7 \text{ g C m}^{-2}$, or 65% of the annual NEP, with the remainder during the wet season (significant differences in seasonal NEP at $p < 0.05$; Appendix S1: Table S3). The higher NEP during the dry season coincided with a relatively low R_{eco} (40.1% of annual R_{eco} or 96.3 g C m^{-2}) due to limitations in surface soil water availability and temperature (not shown). By contrast, GPP

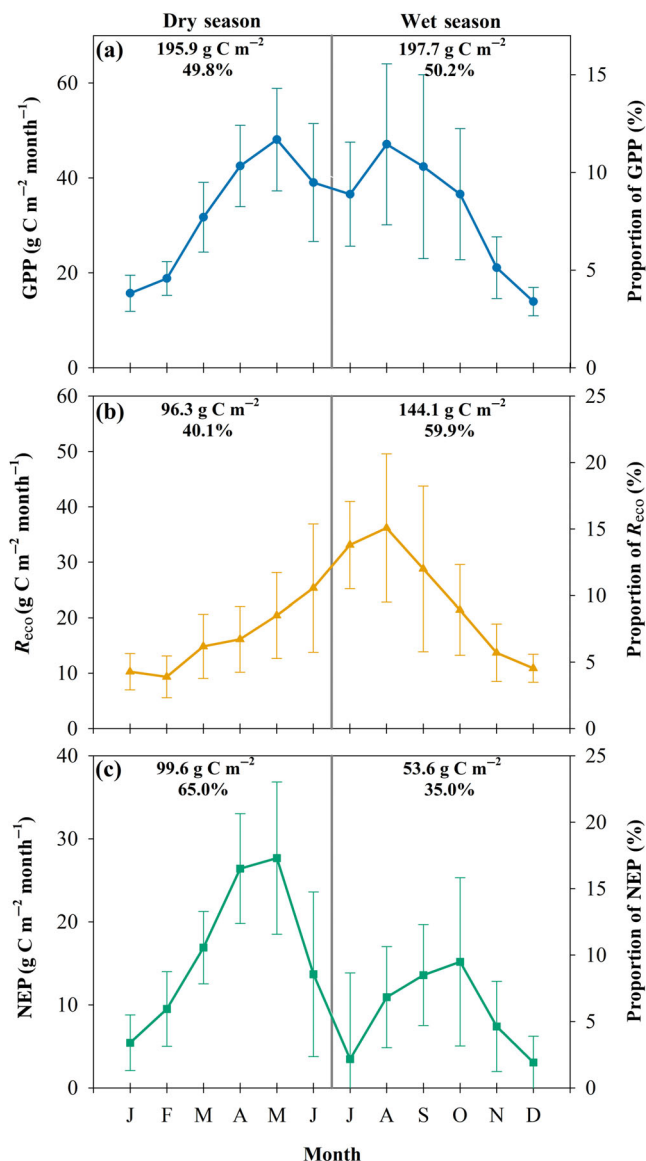


FIGURE 3 Monthly averages (left) and proportions (right) of carbon balance components from 2011 to 2020. (a) Gross primary productivity (GPP). (b) Ecosystem respiration (R_{eco}). (c) Net ecosystem production (NEP). Bars represent ± 1 monthly SDs. Vertical lines divide the dry and wet seasons.

showed two evenly distributed peaks in the dry and wet seasons, contributing to 49.8% and 50.2% of the annual GPP (no statistically significant seasonal difference at $p < 0.05$, Appendix S1: Table S3). Dry season GPP is supported by ET that exceeds R during April through June, as noted previously. A correlation analysis between annual and seasonal NEP with respective annual and seasonal GPP and R_{eco} resulted in significant correlations for: (1) annual GPP and NEP (0.737 , $p < 0.05$), (2) wet season GPP and NEP (0.825 , $p < 0.05$), and (3) dry season GPP and NEP (0.564 , $p < 0.01$). No significant correlations between NEP and R_{eco} were obtained.

TABLE 1 Pearson correlation coefficients between carbon fluxes (total values of gross primary productivity [GPP], ecosystem respiration [R_{eco}], and net ecosystem production [NEP] in grams of C per square meter) and water balance components (total values of rainfall [R], evapotranspiration [ET], streamflow [Q], and percolation [P] in millimeters) for annual and seasonal periods.

Water balance component	Annual			Dry season			Wet season		
	GPP	R_{eco}	NEP	GPP	R_{eco}	NEP	GPP	R_{eco}	NEP
R	0.614	0.883	0.023	0.261	0.799	-0.544	0.788	0.782	0.552
ET	0.503	0.879	-0.121	0.524	0.849	-0.258	0.788	0.893	0.414
Q	0.749	0.656	0.410	0.640	0.613	0.477
P	0.159	0.096	0.125	-0.713	0.228	-0.675	0.553	0.459	0.502

Note: Values in boldface represent statistically significant correlations at $p < 0.05$.

Linkages between water and carbon dynamics at annual and seasonal scales

Table 1 shows the Pearson correlation coefficients between water balance components (R , ET, Q , and P) and carbon fluxes (GPP, R_{eco} , and NEP) for annual and seasonal periods. GPP generally showed positive correlations with water balance components, but these were only significant for the wet season. A significant negative correlation between GPP and P in the dry season can be attributed to the upward movement (negative P) of deeper soil water (Figure 2b). R_{eco} showed a statistically significant correlation with both R and ET over the annual scale and for each season, suggesting that water availability was critical for carbon releases. As a result of the different correlations for GPP and R_{eco} , NEP generally showed nonsignificant relations with the water balance components, particularly at the annual scale and for the wet season. A negative correlation between NEP and P during the dry season further supported that higher carbon uptake was linked to the uptake of subsurface water made available from the prior wet season.

Figure 4 shows how the wet season rainfall was linked to the seasonal and annual NEP in the shrubland ecosystem. For this analysis, annual NEP was calculated from July of a particular year until the following June to capture the potential carryover or legacy effect from a wet season to the subsequent dry season, thus spanning two calendar years. All years from 2011 to 2019 had wet season rainfall amounts that accounted for greater than 64% of the annual R . By contrast, the wet season proportion of NEP remained below 45% of the annual NEP, indicating the dry season dominated the annual ecosystem productivity. Table 2 presents Pearson correlation coefficients between seasonal and annual NEP with different rainfall metrics, showing a stronger correlation when wet season R values are considered. In particular, the wet season proportion of R (%) has a significant correlation with annual (July–June) NEP ($p < 0.05$) and dry season NEP ($p < 0.10$). Correlations

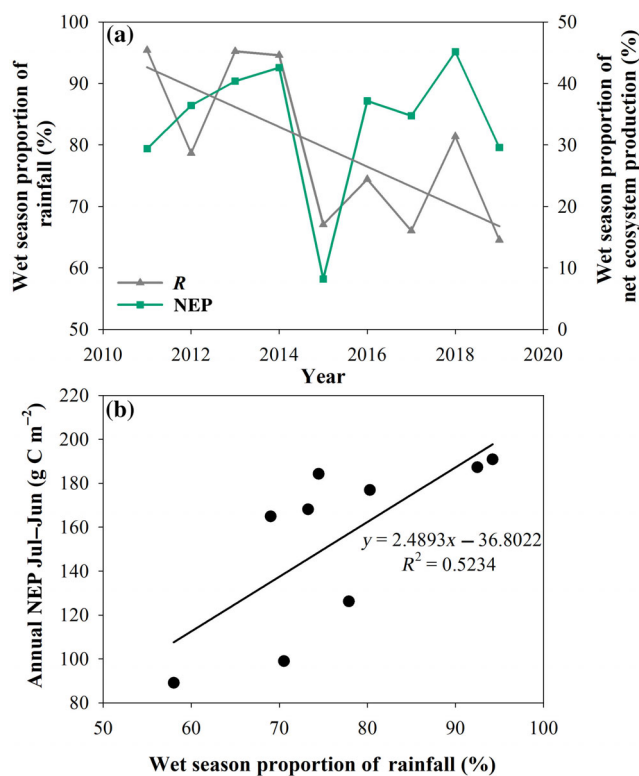


FIGURE 4 (a) Wet season proportions (%) of rainfall (R) and net ecosystem production (NEP) from 2011 to 2019. (b) Relation between wet season proportion of R and annual NEP obtained over the period July to June. Calendar year 2020 is excluded from this analysis. Lines represent statistically significant correlations.

with wet season R are stronger than those obtained between annual (July–June) NEP and other water balance components (Table 2), with correlations of 0.415 (P), 0.139 (ET), and 0.075 (Δs), respectively. This implies that the carryover or legacy effect is best represented by the prior wet season rainfall, followed by the wet season percolation. Despite a significant short-term decrease in wet season R during the study period ($R^2 = 0.61$, $p < 0.05$; Figure 4a), no significant trend was noted in wet season proportion of NEP during the study period ($R^2 = 0.02$), suggesting a lack

TABLE 2 Pearson correlation coefficients between carbon fluxes (seasonal and annual values of net ecosystem production [NEP] in grams of C per square meter) and water balance components (seasonal and annual values of rainfall [R] in millimeters and % of annual; seasonal and annual values of evapotranspiration [ET], percolation [P], and change in volumetric soil moisture [Δs] in millimeters).

Water balance metric	Annual Jul–Jun NEP	Dry season NEP	Wet season NEP
Annual R (mm)	−0.045	−0.126	0.078
Wet season R (mm)	0.432	0.275	0.422
Wet season proportion of R (%)	0.724	<i>0.616</i>	0.515
Annual ET (mm)	−0.191	−0.124	−0.183
Wet season ET (mm)	0.139	0.018	0.223
Wet season proportion of ET (%)	0.491	0.269	0.533
Annual P (mm)	0.232	−0.027	0.444
Wet season P (mm)	0.415	0.250	0.424
Annual Δs (mm)	0.097	0.176	−0.048
Wet season Δs (mm)	0.075	0.315	−0.259

Note: Values in boldface and italics represent statistically significant correlations at $p < 0.05$ and $p < 0.10$, respectively.

of sensitivity of wet season NEP to rainfall in that season. Nevertheless, the annual NEP was significantly controlled by wet season R , such that carryover soil moisture influenced both the dry season and annual productivity in the mixed shrubland. As a result, a short-term decrease was noted in dry season NEP ($R^2 = 0.51$, $p < 0.05$).

DISCUSSION

Seasonality of hydrological partitioning

In arid and semiarid regions, ET is the principal means by which water is lost from an ecosystem, and the ratio ET/ R tends to be close to 100% on annual to interannual scales (e.g., Kurc & Small, 2004; Scott, 2010; Tarín et al., 2020; Vivoni et al., 2021; Yépez et al., 2007). However, the seasonality of internal water storages, typically in the subsurface, can lead to seasons or longer periods when ET/ $R > 100%$ (e.g., Flerchinger et al., 2020; Knowles et al., 2020; Pérez-Ruiz et al., 2021; Scott et al., 2008). As a result, in seasonal ecosystems, ET is often drawn from deep water sources during dry periods (e.g., Antunes et al., 2018; Barbeta & Peñuelas, 2017; Miguez-Macho & Fan, 2021; Pérez-Ruiz et al., 2021). Consistent with this, we found that the Chihuahuan Desert shrubland relied on carryover soil moisture to support ecosystem productivity and ET during the dry season. High rainfall during the wet season provided sufficient water to meet the ET demand (wet season ET/ $R = 79%$), despite the small losses to runoff ($Q/R = 4%$), while also supporting large increases in shallow and deep soil water, $(\Delta s + P)/R = 17%$. As described by Schreiner-McGraw and Vivoni (2017), summer storms led to soil infiltration and hillslope runoff that contributed to percolation in the downstream channel, both

serving as sources for carryover water to the subsequent dry season. Percolated water can remain stored in deeper layers of the channel sediments or in the CaCO_3 horizon (Duniway et al., 2007, 2010). As shown in the long-term average seasonal cycles (Figure 2), shallow soil water from the wet season was consumed rapidly in the fall season, while deep percolation persisted to at least the following spring.

During the dry season, ET exceeded the seasonal water input (ET/ $R = 145%$), implying that 30.3 mm on average of dry season ET was drawn from the soil moisture carryover, of which about half of the amount (13.4 mm) was stored in the soil profile above Z_r . Below Z_r , the presence of CaCO_3 horizons provided the opportunity to store subsurface water, which is available for plants to extract over periods from several months to a year (Duniway et al., 2007, 2010). The deep rooting systems of creosote bush, honey mesquite, and tarbush are known to extend into and below CaCO_3 horizons as well as into the subsurface sediments underneath channels (e.g., Gibbens & Lenz, 2001; Gile et al., 1998; Schwinning, 2010). Of these shrub species, evergreen creosote bush and winter deciduous honey mesquite have phenological activity during the dry season, which could be linked to the uptake of deep soil water (e.g., Kurc & Benton, 2010; Muldavin et al., 2008; Schreiner-McGraw & Vivoni, 2018). Evidence from large negative values of P in the dry season ($P/R = -30%$) indicated an upward movement of water that is simultaneous with the springtime ET.

Seasonality of NEP

Shrublands in the North American deserts are net carbon sinks at the annual scale (e.g., Biederman et al., 2017; Hinojo-Hinojo et al., 2019; Petrie et al., 2015; Verduzco

et al., 2018), and it has been argued that the winter season plays an important role through a reduced amount of ecosystem respiration (Biederman et al., 2018). At the mixed shrubland site, we found that the ecosystem carbon balance was strongly affected by the seasonality of both GPP and R_{eco} . Indeed, a lower R_{eco} is not a sufficient condition to result in the high NEP during the dry season as springtime GPP is also required. We found that GPP showed a bimodal pattern during the year that cannot be explained solely by winter rainfall since ET/R largely exceeds 100%. By contrast, prior work often attributes the dominant contribution of the spring season to annual NEP to winter rainfall (e.g., Biederman et al., 2018; Huenneke et al., 2002; Huxman et al., 2004; Muldavin et al., 2008; Petrie et al., 2015; Wohlfahrt et al., 2008). Here, we identified that the high values of GPP and ET occurring when R was low in the dry season were an indication of the effect of carry-over subsurface water from the prior wet season. Furthermore, the water use efficiency ($WUE = GPP/ET$) during the dry season ($WUE = 2.02 \text{ g C mm H}_2\text{O}^{-1}$) was substantially larger than during the wet season ($WUE = 1.18 \text{ g C mm H}_2\text{O}^{-1}$). We attribute this to the consumption of carryover water from deep layers in the dry season by shrub transpiration and the lower evaporation rates from dry surface soils (e.g., Scott & Biederman, 2017; Wang et al., 2010; Yépez et al., 2007). These effects led to a bimodality in NEP during the year that is asymmetric, with higher values in the dry season than in the wet season, leading to 65% of the annual carbon uptake occurring in the dry season. High R_{eco} in the wet season counteracted the nearly equal seasonal amounts of GPP and led to the asymmetric bimodality in NEP. Bimodality in GPP and NEP were consistent across all years but exhibited interannual variations in relative size depending on the seasonal water availability (Appendix S1: Tables S1–S3).

Legacies of the wet season on the seasonal and annual ecosystem productivity

The interannual variability of water and carbon dynamics revealed that net ecosystem productivity during the wet season was unaffected by its proportion of annual rainfall. Note that the wet season contributed about 75% of annual R on average, such that it is the main source of water to the ecosystem. This was attributed to the inability of the shrubland to fully utilize available soil water within the wet season, and to the hydrological processes leading to runoff production and channel transmission losses (Schreiner-McGraw & Vivoni, 2017). As further evidence, we noted that despite a decreasing trend in the wet season proportion of annual rainfall, no trend was observed in the wet season proportion of NEP. Though the sensitivity of

NEP to rainfall is low within the wet season, we found a statistically significant relation between the wet season proportion of R and the subsequent annual NEP, and a weaker effect of wet season percolation. This evidence indicated the importance of the wet season in defining the magnitude of the annual carbon sink in the mixed shrubland ecosystem. Higher proportional rainfall during the wet season benefits the hydrological partitioning of water into subsurface storage, which then serves to increase dry season NEP. The soil moisture carryover is considered as a legacy effect mediated by landscape properties in the watershed (e.g., CaCO_3 horizons in hillslope soils and subsurface porous media under channels). This mechanism allowed for water to be reserved for ecosystem use during the dry season, when GPP can be sustained at higher levels than R_{eco} , thus enhancing annual NEP and the strength of the mixed shrubland carbon sink.

The study period was characterized by average rainfall conditions at the JER as compared to the long-term record, as noted by Peters et al. (2021) who analyzed multi-year sequences of above-, below-, and average precipitation each lasting about 5–6 years. As a result, the effects of the carry-over subsurface water on the annual carbon budget are robust features during average hydrological conditions of the study site. Based on the findings of Peters et al. (2021), we would expect that multi-year wet or dry periods would lead to longer-term legacy effects that are superimposed on the seasonal soil moisture carryover occurring in areas of complex terrain. Furthermore, comparisons to the work of Reichmann et al. (2013) at a nearby flat location are illustrative of the importance of the landscape properties in the watershed on the seasonal soil moisture carryover effect. As opposed to flat areas, the connected system of hillslopes and channels in the shrubland watershed provided hydrologic pathways for subsurface water storage that could be used in the subsequent dry season. We further hypothesize that landscape properties, such as bare soil cover and its connectivity, and terrain conditions, such as the hillslope and channel arrangement, will determine the degree of a soil moisture carryover or legacy effect. Thus, enhancements in subsurface water storage, for instance through higher shrub cover or higher slopes (Schreiner-McGraw et al., 2020; Schreiner-McGraw & Vivoni, 2018), could promote a higher legacy effect and larger fraction of productivity during the dry season.

CONCLUDING REMARKS

In this study, we found that the seasonal dynamics of hydrological partitioning has an amplified role on ecosystem productivity in a mixed shrubland of the Chihuahuan Desert that exhibits topographic and subsurface complexity. Fed by soil infiltration and channel transmission losses,

the subsurface environment can serve as a temporary storage of water that is accessed by deep-rooted shrubs over longer time scales. As a result, water recharged during periods of high rainfall such as the summer season in the study region can support ecosystem water use in dry periods, including the subsequent dry spring. In addition, this carryover effect allows ET and GPP to occur when shrub processes are more favorable since ecosystem respiration and soil evaporation are more limited under dry shallow soils and lower temperatures. For larger proportions of water during the summer season, this ecohydrological mechanism is favored to a greater extent, allowing for a stronger net carbon sink. While previous studies have highlighted the important role of winter periods for North American shrubland carbon dynamics, we documented how hydrological and ecological processes interact to favor the establishment of deep-rooted shrubs in complex watersheds that can store and carryover water in the subsurface across multiple seasons.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Vivoni et al., 2022a, 2022b; Vivoni & Pérez-Ruiz, 2022) are available from Ameriflux (<http://ameriflux.lbl.gov/sites/siteinfo/US-Jo2>) and the Environmental Data Initiative (<http://doi.org/10.6073/pasta/759f2f1bc29df9bd15a9a9bfd6a15470> and <http://doi.org/10.6073/pasta/470a77c31c5f27b54edd1acd544e3c3b>).

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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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