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Ecosystem hydrologic and metabolic flashiness are shaped by plant community traits and precipitation

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ABSTRACT

Understanding the hydrologic and carbon cycling consequences of precipitation variability in dryland ecosystems requires improved appreciation and accounting of how above- and belowground biophysical processes differ in their response to rainfall. Our objective was to contrast the sensitivity of dryland ecosystem evapotranspiration (ET), gross ecosystem productivity (GEP), and ecosystem respiration (R_e) in response to inter- and intra-annual precipitation variability in a nearby grassland, savanna, and shrubland ecosystems in southeastern Arizona. To do this, we modified the Richards-Baker index, which quantifies the flashiness of a stream's hydrograph, to calculate analogous indices of ecosystem hydrologic and metabolic flashiness. In this way, ecosystem flashiness describes the frequency and rapidity of short-term fluctuations in H_2O and CO_2 exchange in response to precipitation while preserving the sequence of day-to-day variation in fluxes using tower-based time-series of daily averaged ET, GEP and R_e. We calculated annual hydrologic, GEP, and R_e flashiness (f_{ET}, f_{GEP} and f_{Re} respectively) using 6 years of daily-averaged fluxes estimated from eddy covariance. In contrast to our prediction, annual f_{GEP} was consistently greater than annual f_{Re}. Furthermore, we predicted that increasing rooting depth would correlate with a decline in annual f_{ET} and f_{GEP}. In fact, annual f_{GEP} was similar between the grassland, savanna, and shrubland. Whereas the response of annual f_{ET} and f_{GEP} to annual precipitation was plant community dependent and generally declined with increasing rainfall, annual f_{Re} did not vary in response to precipitation. The effect of late summer storms on f_{GEP} was plant community dependent such that shrubland f_{GEP} and f_{Re} strongly declined in response to rainfall whereas grassland and savanna f_{GEP} was relatively unresponsive. Conceptually similar to hydrologic flashiness, ecosystem flashiness may provide an additional lens through which to observe the influence of resource availability, shifts in community composition, and disturbance on ecosystem hydrologic and carbon cycling.

1. Introduction

In drylands, water limitation controls the pace of biological activity, and persistent water limitation is a defining characteristic of these ecosystems (Noy-Meir, 1973; Feldman et al., 2018). As in other terrestrial ecosystems, soils act as a capacitor for precipitation and thereby influence the biological availability of water from precipitation (Weltzin et al., 2003). Aboveground, plant-soil interactions and feedbacks influence plant physiognomy, leaf area index, and phenology to influence the spatial and temporal availability of soil moisture, which, in turn, constrains biophysical processes (Reynolds et al., 2004; Potts et al., 2010). Belowground, biophysical activity is influenced by plant-soil interactions, which control functional rooting depth, patterns of hydraulic redistribution, and rhizosphere dynamics (van der Putten et al., 2009; Barron-Gafford et al., 2017; Jackson et al., 2017).

These above- and belowground biophysical processes shape temporal variation in dryland evapotranspiration (ET) - the movement of water from the land surface to the atmosphere (Villegas et al., 2015). For example, plant community structure and composition shapes dryland ET through influencing soil evaporation and leaf transpiration, as well as the depth of soil water uptake by roots (Jenerette et al., 2012). Similarly, precipitation regimes (e.g., mainly winter versus summer rainfall) profoundly influence seasonal patterns of ET in drylands (Villarreal et al., 2016). ET is a major component of dryland hydrologic cycling (Biederman et al., 2017) and so how dryland ecosystems translate precipitation inputs into ET has profound implications for water yield, forage production, wildfire, and forest mortality.

Similar to ET, net ecosystem CO_2 exchange (NEE) is an important

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ecosystem function, which is affected by above- and belowground biophysical processes (Baldocchi et al., 2001). NEE is expressed as the difference between two, complementary metabolic processes, ecosystem CO_2 uptake by photosynthesis (gross ecosystem productivity; GEP) and the efflux of CO_2 by the respiration of plants and soil microbes (ecosystem respiration; R_e). Predicting the sensitivity and responses of these competing metabolic processes to environmental variability is a long-sought goal of ecologists (Huxman et al., 2004). In dryland ecosystems, NEE varies in characteristic ways over a wide range of time scales, from days to seasons to years with potentially significant impacts on global carbon cycling (Poulter et al., 2014; Ahlström et al., 2015). In addition to temporal variability in soil moisture associated with precipitation variability, NEE is shaped by the plant community composition and structure (Potts et al., 2006b). Understanding the carbon cycling consequences of precipitation variability in dryland ecosystems requires improved appreciation and accounting of how plant-mediated GEP and plant- and soil microbial respiration differ in their response to rapid changes in soil moisture availability (Sponseller, 2007).

Previous research has sought to describe and compare the sensitivity of dryland ecosystem water and carbon cycling to precipitation. Rainfall manipulation studies have revealed the contribution of rainfall variability, antecedent soil moisture conditions, nutrient availability, drought severity, fire disturbance, and presence of nonnative grasses in shaping water and carbon fluxes in response to rainfall in a range of dryland ecosystems (Potts et al., 2006a; Harpole et al., 2007; Potts et al., 2012; Barron-Gafford et al., 2014; Liu et al., 2017; Zhang et al., 2017). Observational studies using instrumented towers to measure high frequency measurements of ecosystem CO_2 exchange have revealed the carbon cycling consequences of intra-annual precipitation variability, multi-year drought, woody plant encroachment, and availability and accessibility of plant-available alluvial groundwater (Scott et al., 2009, 2014, 2015). Further, several approaches have been developed to partition tower-based measurements of net CO_2 exchange. For example, nighttime fluxes and air temperature relationships may be used to estimate concurrent rates of GEP and R_e, thereby providing even greater insight into the biotic and abiotic factors shaping the biological activity of plants and soil microbes (Reichstein et al., 2005).

Our objective was to contrast the biophysical sensitivity of several widespread dryland ecosystems in response to inter- and intra-annual precipitation variability. To address this objective, we adopted the concept of hydrologic flashiness from watershed hydrology (Poff et al., 1997). In watershed hydrology, flashiness describes the frequency and rapidity of short-term changes in streamflow associated with runoff events (Baker et al., 2004). Hydrologic flashiness reflects climate, topography, soil, vegetation, and land use and is an important descriptor of a stream's hydrologic regime (Baker et al., 2004). Hydrologic flashiness has been used to describe the impact of urbanization (Nagy et al., 2012) and wildfire (Saxe et al., 2018) on streamflow regimes and to assess the success of stream restoration efforts (Pennino et al., 2016). Here, we proposed the concept of hydrologic flashiness be analogously applied to describe the frequency and rapidity of fluctuations in ET, GEP, and R_e associated with precipitation to describe terrestrial ecosystems' hydrologic and metabolic responses.

We predicted that plant community traits and precipitation will interact to influence the flashiness of ecosystem water and CO_2 fluxes and that the flashiness concept will provide new insight into the relationship between dryland ecosystem structure and function. First, based on a widely-cited conceptual model of semi-arid ecosystem metabolism in response to rainfall pulses (Huxman et al., 2004), we predicted that the flashiness of ecosystem respiration would be greater than the flashiness of gross ecosystem productivity. Next, analogous to a decline in hydrologic flashiness associated with increasing annual discharge (Baker et al., 2004), we predicted that flashiness would decline with increasing annual ET, GEP, and R_e. Moreover, given that soil moisture modulates the effects of precipitation variability on plants in semi-arid ecosystems (Weltzin et al., 2003) and closely tracks seasonal and annual rainfall in southern Arizona (Potts et al., 2010), we predicted that increasing precipitation would be associated with a decline in the flashiness of ET and GEP and that increased functional root depth (grassland < shrubland < savanna) would also lead to a decline in ET and GEP flashiness.

Table 1
Site Descriptions (*modified from* Scott et al., 2015).

	Grassland	Savanna	Shrubland
Fluxnet/AmeriFlux Site ID	US-SRG	US-SRM	US-Whs
Latitude	31.789 °N	31.822 °N	31.749 °N
Longitude	110.828 °W	110.867 °W	110.052 °W
Elevation (m)	1291	1120	1370
Mean Annual Temp. (°C)	17	17.9	17.6
Mean Annual Precipitation (mm)	420	380	320
Soil Texture	Loamy sand	Loamy sand	Sandy loam
Canopy Height (m)	0.5	2.5	1
Woody Canopy Cover (%)	11	35	40
Herbaceous Canopy Cover (%)	44	15	3

2. Material and methods

2.1. Site description

Our three study sites are described in detail by Scott et al. (2015) and are representative of grasslands, savannas, and shrublands, which are widespread in southern Arizona. All three sites are at similar elevations and have broadly similar mean annual temperatures and average annual rainfall (Table 1). In this study, we used "hydrologic year" (November 1–October 31) to accommodate the hydroclimate of southern Arizona in which annual rainfall is divided between winter frontal storms and late summer convective storms associated with the North American Monsoon (Scott et al., 2015).

The grassland and savanna site are located near one another on the University of Arizona's Santa Rita Experimental Range and share common deep loamy sand soils (Table 1). The grassland's plant community is dominated by the nonnative warm-season bunchgrass *Eragrostis lehmaniana* and widely-scattered velvet mesquite shrubs (*Prosopis velutina*). The savanna site has a greater density and cover of velvet mesquite as well as an understory of *E. lehmaniana* and the native warm-season bunchgrass *Digitaria californica*. The third site is a shrubland located in the Walnut Gulch Experimental Watershed managed by the U.S. Department of Agriculture Agricultural Research Service, approximately 80 km east of the Santa Rita sites (Table 1). The shrubland's soil is a gravelly sandy loam, and the site hosts a diverse woody plant community and lacks an herbaceous understory where intercanopy spaces are instead characterized by exposed soil.

2.2. Measurements and data analysis

To address our research objectives, we obtained eddy covariance based measurements of CO_2 and H_2O fluxes as well as energy balance terms and micrometeorological variables at each of our sites from Ameriflux (http://ameriflux.lbl.gov) for the 2008–2014 hydrologic years. Similar data from Ameriflux's active and historic research sites have been used for decades to better understand the spatial and temporal dynamics of ecosystem carbon and water cycling in relationship to climate variability, disturbance, and human activities (Novick et al., 2018).

For all our analyses, we used daily average values calculated from gap-filled, 30-min average data. GEP and R_e were derived using the nighttime partitioning method (Reichstein et al., 2005) and we calculated daily average ET (g H_2O m^{-2}) from latent heat flux (Q_E; Wm^{-2}) and air temperature (T_a; °C) according to Shi et al. (2008):

$$ET = \frac{Q_E}{2501 - 2.366(T_a)} \quad (1)$$

From the resulting ET time-series, as well as daily average GEP and R_e time-series for each site, we calculated the Richard-Baker flashiness index (*f*) for each hydrologic year for the period 2008–2014 according to Baker et al. (2004):

$$f = \frac{\sum_{i=1}^{n} |q_i - q_{i-1}|}{\sum_{i=1}^{n} q_i} \quad (2)$$

Where q is daily average ET (g H_2O m^{-2} d^{-1}), GEP (g C m^{-2} d^{-1}), or R_e (g C m^{-2} d^{-1}) for a given time period of interest. Expressed in this way, f is dimensionless, independent of the units chosen to represent flux, and incorporates oscillations in flux relative to total flux. As such, f quantifies terrestrial ecosystems' rapidity and persistence of biophysical activity in response to precipitation.

As a means to express variability, the coefficient of variation of daily average flux (CV_d) is similar to f in that it is calculated using the same daily average flux data and is similarly dimensionless. However, Baker et al. (2004) noted that f incorporates the daily sequence of fluxes where CV_d considers fluxes without regard to their sequence in time. By incorporating the sequence of day-to-day variability, f may provide a more ecologically-relevant perspective on the variability of ecosystem water and carbon fluxes across space and time in response to antecedent moisture than has previously been described in the literature (Fig. 1). In this theoretical example, the left figure panel illustrates a period of high fluxes followed by a period of low fluxes while the right figure panel presents the same data in a reorganized sequence in which high and low fluxes alternate through time. In this example, reliance on comparisons of total, mean, and the CV of fluxes might cause researchers to overlook ecologically significant differences that would be otherwise quantified using flashiness.

We used multiple regression to examine the correlation between CV_d and f as well as the interaction between CV_d and site against annual f_{ET}, f_{GEP}, and f_{Re}. We used similar multiple regression models to examine the interaction between summed annual flux and site on f_{ET}, f_{GEP}, and f_{Re}, as well as the interaction between annual precipitation and site on f_{ET}, f_{GEP}, and f_{Re}.

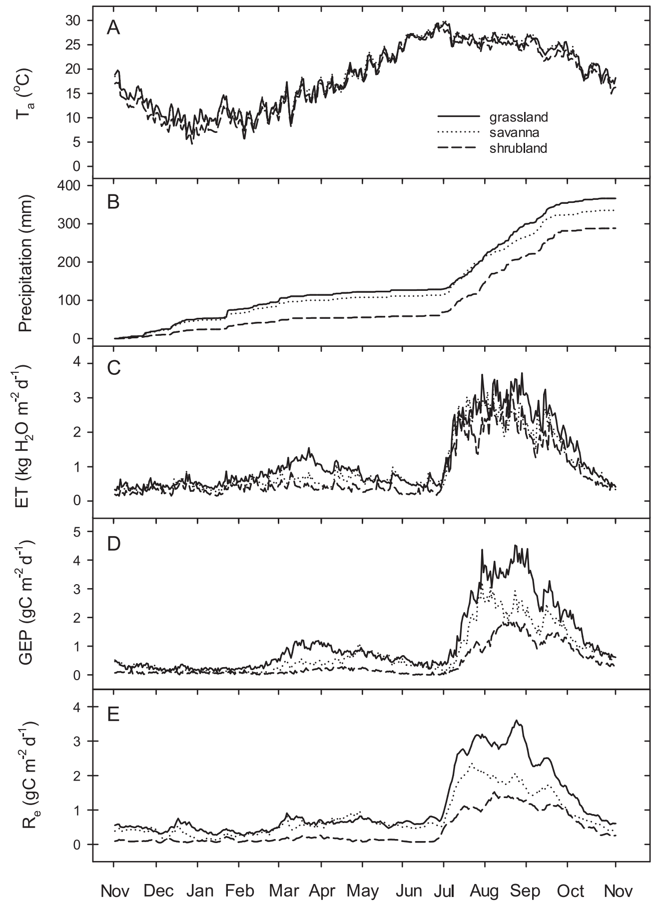

Fig. 2. (A) Daily average air temperature (T_a; °C); (B) cumulative precipitation (mm); (C) daily average evapotranspiration (ET; kg H_2O m^{-2} d^{-1}); (B) daily average gross ecosystem productivity (GEP; g C m^{-2} d^{-1}); (C) daily average ecosystem respiration (R_e; g C m^{-2} d^{-1}) in a grassland, a savanna, and a shrubland ecosystem in southeastern Arizona, USA for the 2008–2014 hydrologic years. The solid line indicates the grassland; the dotted line indicates the savanna; the dashed line indicates the shrubland.

In southern Arizona, the early spring growing season is characterized by dry and increasingly warm conditions during which biological activity is facilitated by residual soil moisture from previous winter storms. In contrast, the later mid-summer growing season is characterized by warm and humid conditions during which biological activity is linked to convective summer storms associated with the North American Monsoon. We examined the influence of intraseasonal precipitation variability and site on ecosystem flashiness by comparing f_{ET}, f_{GEP}, and f_{Re} during the early growing season (March–June) and late growing season (July–October) using repeated measures ANOVA to

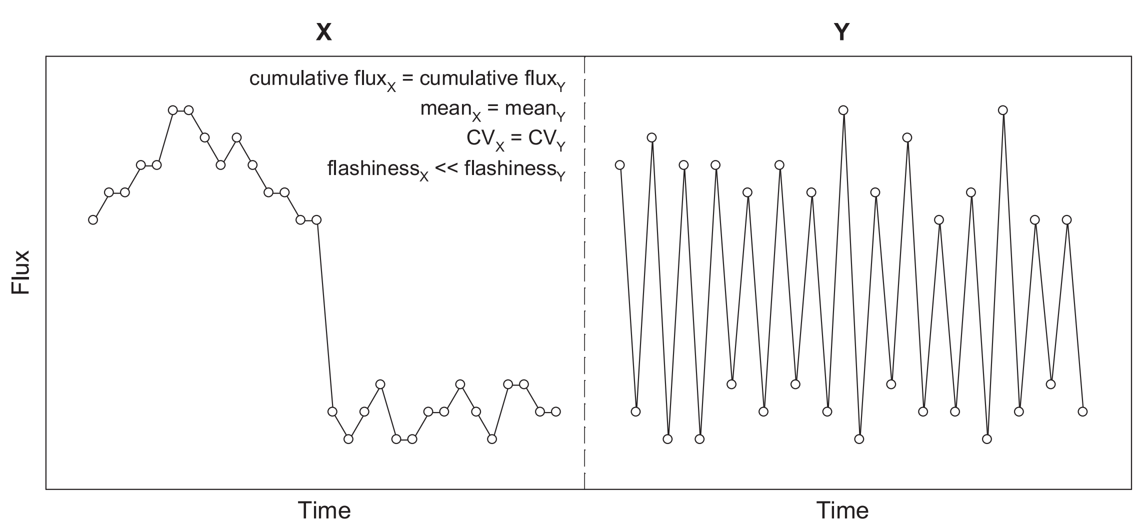

Fig. 1. Two theoretical time series of ecosystem CO_2 flux illustrate the difference between several widely-applied metrics and flashiness (figure modified from Reyer et al., 2013). In this example, flashiness reveals an ecologically significant contrast that is missed by other metrics.

examine the interactive effects of site and season on f_{ET}, f_{GEP}, and f_{Re}.

3. Results

In southeastern Arizona, the period December–February is characterized by cool conditions with occasional rainfall. Increasingly warm and dry conditions are typical for the early growing season (March–June), which is followed by a warm late growing season (July–October) punctuated by convective storms associated with the North American monsoon (Fig. 2A & B). In turn, the seasonal dynamics of evapotranspiration (ET) track seasonal patterns of precipitation and were broadly similar across the grassland, savanna, and shrubland sites (Fig. 2C). Warm and dry conditions during the early growing season (March–June) were associated with declining daily average ET. Later, storms in early July drive an increase in ET, which peaks in mid- to late August before gradually declining through the remainder of the hydrologic year.

Unlike ET, where the seasonal dynamics of the grassland, savanna, and shrubland closely overlap, community types were more distinct in terms of their seasonal patterns of gross ecosystem productivity (GEP) and ecosystem respiration (R_e) during the late growing season. Winter fluxes were close to zero, consistent with low temperature constraints on metabolic activity at all three sites, while an increase in both above- and belowground metabolic activity associated with GEP and R_e at the beginning of March, marked the start of the growing season (Fig. 2D & E). Late growing season GEP and R_e reveals clearer differences between the grassland, savanna, and shrubland, such that the grassland had greater and more variable GEP than either the savanna or shrubland sites. Likewise, the grassland maintained greater rates of R_e than either the savanna or shrubland during the late growing season.

Because CV_d is likely to be more familiar to ecologists than *f*, we used linear correlation to compare annual values of H_2O and CO_2 flux CV_d against their corresponding annual values of *f* (Fig. 3A–C). In each case, CV_d was weakly correlated with *f*, a pattern that was consistent across fluxes and sites.

We compared annual ET and the flashiness of ET (f_{ET}) across sites to better understand how plant community functional traits may alter the relationship between these two elements of the hydrologic cycle (Fig. 4A). Annual ET broadly overlapped across all three sites for the period 2008–2014, and increasing annual ET correlated with a decline in f_{ET} (multiple regression, $F_{1,17} = 40.4$, $P < 0.0001$). Moreover, this decline in flashiness was mediated by community type such that shrubland f_{ET} declined at a greater rate in responses to increases in ET than either the savanna or grassland ($F_{3,17} = 7.74$, $P = 0.007$).

A comparison of annual GEP and GEP flashiness (f_{GEP}) shows a similar, albeit marginally significant pattern of community-specific responses (Fig. 4B; multiple regression, $F_{3,17} = 3.31$, $P = 0.07$). Like patterns of ET, an increase in annual GEP was associated with a decline in f_{GEP} ($F_{1,17} = 39.1$, $P < 0.0006$). Interestingly, in this 6-year comparison, the largest values of GEP at the shrubland overlapped with years of intermediate GEP at the savanna and the year of lowest GEP at the grassland. A qualitative comparison of the sites within this narrow range of overlapping GEP suggests differences among the sites in terms of f_{GEP}. Also interesting to note in this contrast is the fact that despite a nearly three-fold increase in annual GEP between the most productive years in the shrubland and grassland communities, both sites had very similar, low values of f_{GEP}. In contrast to ET and GEP, the flashiness of ecosystem respiration (f_{Re}) was very low and was uncorrelated with variation in annual ecosystem respiration (R_e) across all three community types (Fig. 4C).

Increasing annual precipitation was associated with a decline in the flashiness of evapotranspiration (f_{ET}; Fig. 5A; multiple regression, $F_{1,17} = 16.75$, $P = 0.001$), as well as the flashiness of GEP (f_{GEP}; Fig. 5B; multiple regression, $F_{1,17} = 14.99$, $P = 0.002$). In the case of both f_{ET} and f_{GEP}, site specific regressions did not explain significant additional variance, suggesting that these sites share a common functional response to rainfall. The observation that f_{ET} and f_{GEP} decline in response to increasing precipitation indicates that as precipitation increases, day-to-day variation in ET and GEP declines relative to annual ET and GEP (Eq. (2)). In contrast to the responses of f_{ET} and f_{GEP} to rainfall variability, the flashiness of ecosystem respiration (f_{Re}) did not vary in response to increasing precipitation (Fig. 5C). Such f_{Re} consistency indicates that across a wide range of annual precipitation totals, day-to-day variation in ecosystem respiration remains proportional to total annual ecosystem respiration (Eq. (2)).

To better understand how community specific responses of ecosystem hydrologic flashiness are shaped by seasonal variation in precipitation, we contrasted f_{ET} during the early (March–June) and late (July–October) portions of the growing season (Fig. 6A). Warm and dry conditions characterized the early portion of the growing season and were associated with greater f_{ET} in the shrubland than in the grassland or savanna. The onset of summer monsoonal rains during the late growing season resulted a sharp decline in shrubland f_{ET} and a modest increase in grassland and savanna f_{ET} which resulted in the in three sites converging on a common, intermediate value of f_{ET} (repeated measures ANOVA, $F_{2,15} = 5.53$, $P = 0.015$).

The flashiness of GEP (f_{GEP}) varied by season and community type (Fig. 6B; repeated measures ANOVA, $F_{2,15} = 13.37$, $P = 0.0005$). Grassland f_{GEP} was very low during the warm and dry early growing season compared to the shrubland and savanna and remained at a similar low level with the onset of late summer monsoonal storms. In the shrubland and savanna, f_{GEP} declined from the early growing season to

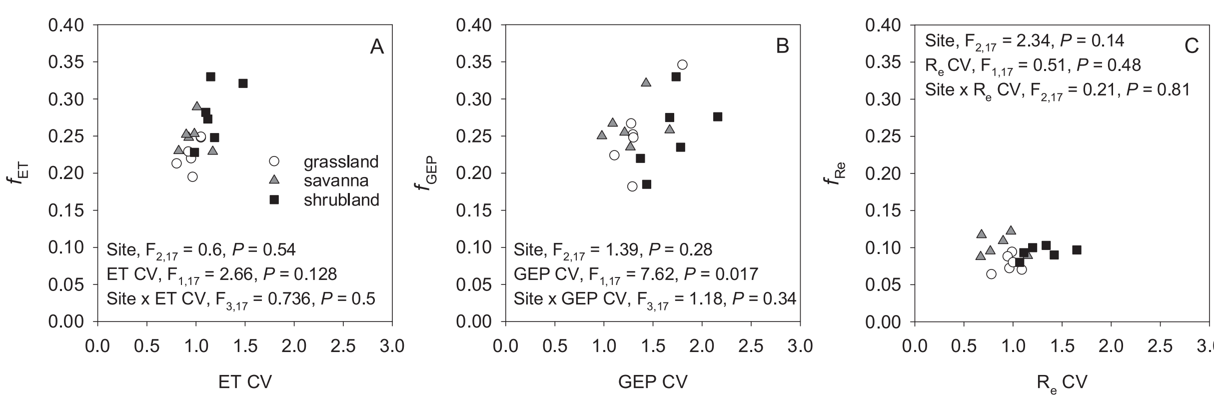

Fig. 3. (A) Annual coefficient of variation of daily evapotranspiration (ET CV) versus annual ET flashiness (f_{ET}); (B) Annual coefficient of variation of daily GEP (CV GEP) versus annual GEP flashiness (f_{GEP}); (C) Annual coefficient of variation of daily ecosystem respiration (CV R_e) versus ecosystem respiration flashiness (f_{Re}) in a grassland, a savanna, and a shrubland ecosystem in southeastern Arizona, USA for the period 2008–2014. Circles represent the grassland, triangles represent the savanna, and squares represent the shrubland.

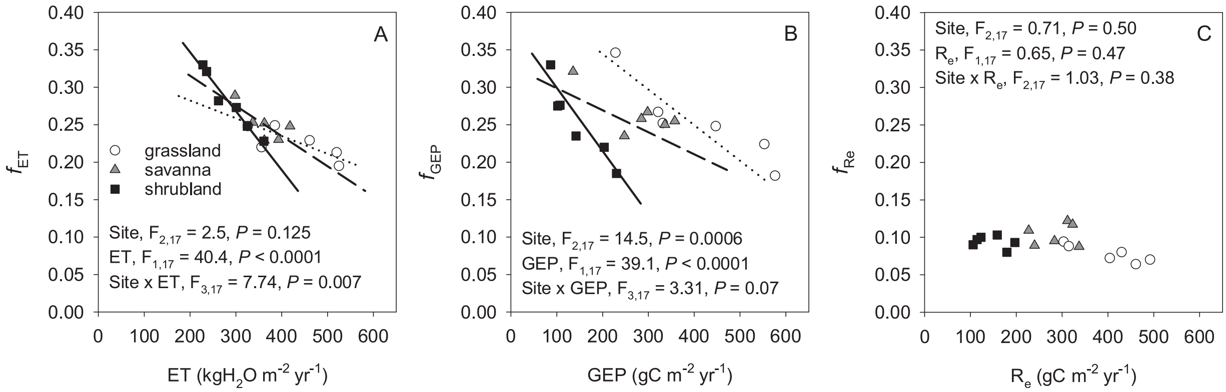

Fig. 4. (A) Total annual ET (kg H_2O m^{-2} yr^{-1}) versus ET flashiness (f_{ET}); (B) Total annual GEP (g C m^{-2} yr^{-1}) versus GEP flashiness (f_{GEP}); (C) Total annual R_e (g C m^{-2} yr^{-1}) versus R_e flashiness (f_{Re}) in a grassland, a savanna, and a shrubland ecosystem in southeastern Arizona, USA for the period 2008–2014. Symbols follow Fig. 3.

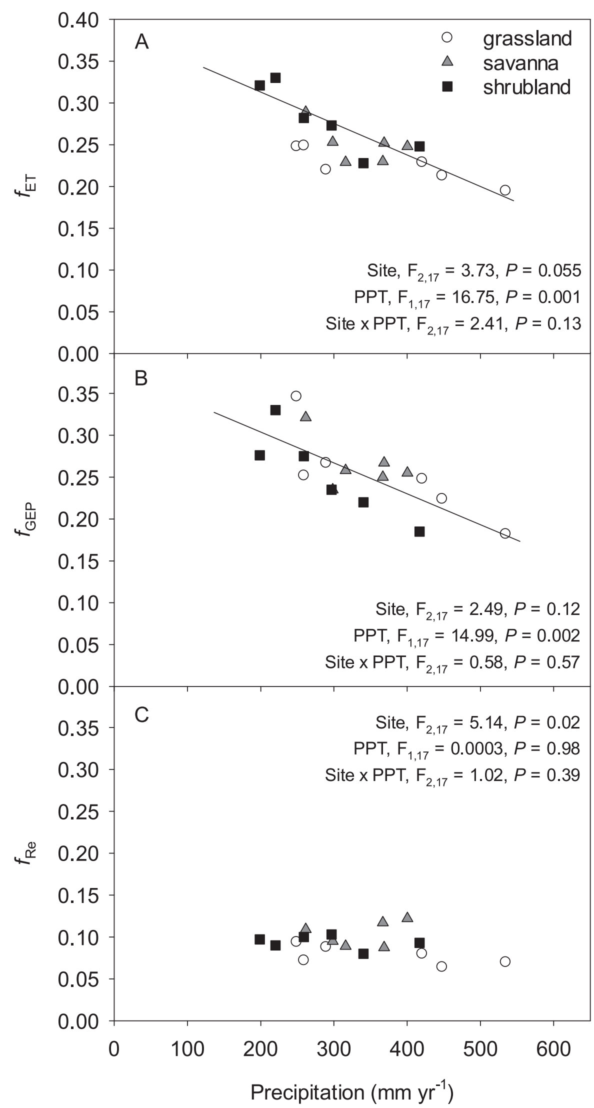

Fig. 5. Annual precipitation (mm yr^{-1}) versus (A) evapotranspiration flashiness (f_{ET}); (B) gross ecosystem productivity flashiness (f_{GEP}); (C) ecosystem respiration flashiness (f_{Re}) in a grassland, a savanna, and a shrubland ecosystem in southeastern Arizona, USA for the period 2008–2014. Symbols follow Fig. 3.

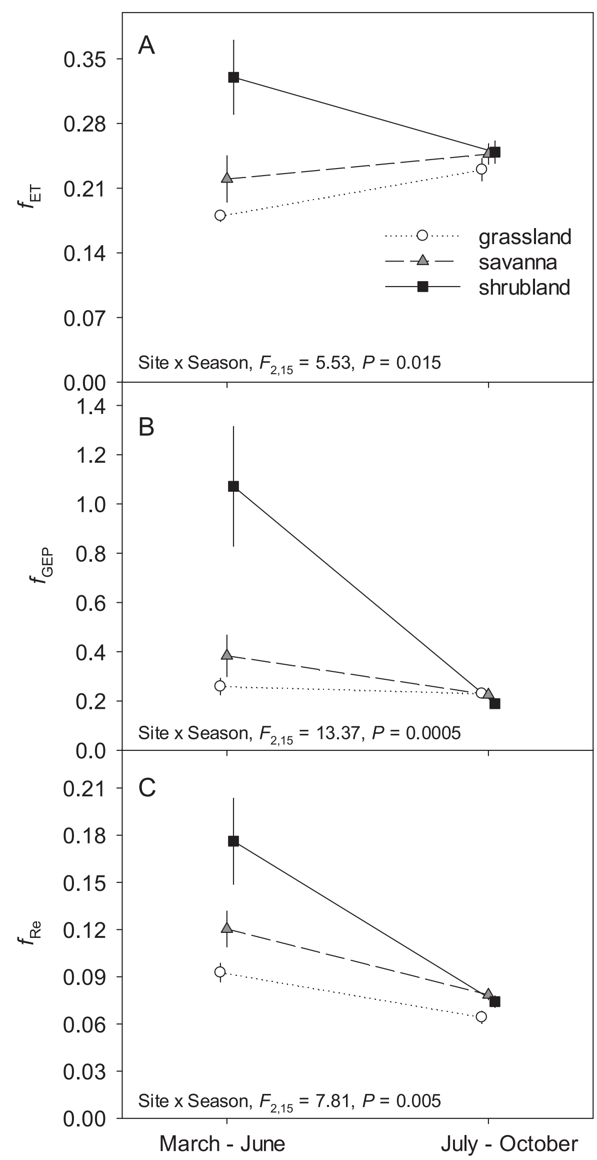

Fig. 6. Early growing season (March-June) to late growing season (July-October) shifts in (A) mean ± SE evapotranspiration flashiness (f_{ET}); (B) mean ± SE gross ecosystem productivity flashiness (f_{GEP}); (C) mean ± SE ecosystem respiration flashiness (f_{Re}) in a grassland, a savanna, and a shrubland ecosystem in southeastern Arizona, USA for the period 2008–2014. Please note y-axis scale differences among panels A–C. Symbols follow Fig. 3.

the late growing season. A decline in shrubland and savanna f_{GEP} during the late growing season may be explained as a decline in day-to-day variation in GEP relative to seasonal total GEP. In contrast, consistent f_{GEP} across the early and late growing season in the grassland suggest that the ratio of day-to-day variation in GEP to seasonal total GEP remained constant despite large increases in photosynthetic activity associated with late summer precipitation. Like f_{GEP}, the flashiness of ecosystem respiration (f_{Re}) varied by season and community type (Fig. 6C; repeated measures ANOVA, Site x Season, $F_{2,15} = 7.81$, $P = 0.005$) and, like growing season patterns of f_{ET} and f_{GEP}, revealed the three community types converging on a similarly low value of f_{Re} during the late growing season.

4. Discussion

Several alternative and potentially complementary descriptions of the sensitivity of semi-arid ecosystems to precipitation and antecedent moisture have been presented in the literature (Huxman et al., 2004; Potts et al., 2006b; Cable et al., 2008; Potts et al., 2014; Biederman et al., 2017). The present research extends that work by adopting and applying the concept of hydrologic flashiness to eddy-covariance measurements of ecosystem H_2O and CO_2 exchange. Analogous to the flashiness of streams and rivers and calculated in the same way (Poff et al., 1997; Baker et al., 2004), we describe temporal variability of above- and belowground biophysical activity as an ecosystem's hydrologic and metabolic flashiness. When applied to ecosystem H_2O and CO_2 exchange daily time-series, flashiness serves as a universally applicable metric quantifying the sensitivity of terrestrial ecosystems to rainfall. Documenting intra- and interannual variability in the flashiness of ET, GEP, R_e creates a conceptual, ecohydrological link between watershed hydrology and ecosystem ecology and provides novel insight into how plant community functional traits interact with precipitation to constrain the timing and magnitude of biophysical activity in drylands.

Unlike the CV_d of H_2O or CO_2 fluxes, which considers variation about the mean without regard to the order in which events occurred, flashiness preserves the sequence of day-to-day variation in fluxes and so presents a more ecologically informed description of temporal variability (Fig. 1). Thus, when these metrics were applied to actual H_2O and CO_2 flux time-series, we observed weak correlation between CV_d and f of H_2O and CO_2 fluxes (Fig. 3A–C). This is not to argue that the CV_d of H_2O and CO_2 fluxes are without utility or merit in ecology. Rather, given that antecedent conditions, ecological memory, and lag effects strongly influence ecological processes (Schwinning et al., 2004; Ogle et al., 2015; Peltier et al., 2017), we present these comparisons to argue that flashiness provides an alternative perspective in describing environmental and biophysical variability through time. For example, flashiness may prove to be particularly useful in quantifying ecohydrological responses to precipitation variability including shifts in the quantity, intensity, seasonality, and frequency of rainfall (Potts et al., 2019).

In southern Arizona, rapid wetting and drying of shallow soil leads to dramatic fluctuations in the rate of soil respiration (Cable et al., 2008; Roby et al., 2019). In contrast, GEP may lag several days behind precipitation but, due to infiltration by water to deeper soil layers, may continue after shallow soil moisture is depleted (Huxman et al., 2004; Potts et al., 2006a). Based on this, we predicted that across our sites, R_e would be flashier than GEP. In contrast to our prediction, not only was f_{Re} consistently lower than f_{GEP}, f_{Re} did not vary in response to 5-fold variation in annual R_e and a greater than 2-fold variation in annual precipitation (Figs. 4B–C & 5C). Baldocchi et al. (2018) presented a conceptual model describing the interacting environmental factors that shape ecosystem metabolic variability both above- and belowground to support their observation that across a broad range of terrestrial ecosystems interannual variability of R_e is less than that of GEP. Our comparisons of interannual f_{Re} and f_{GEP} are broadly consistent with this conceptual model and, furthermore, we suggest that metabolic flashiness may provide a means by which to quantify the complex, seasonally dynamic patterns of R_e and GEP described by Baldocchi et al. (2018).

Whereas f_{Re} was insensitive to interannual precipitation variability, intra-annual comparisons of growing season f_{Re} revealed the predicted pattern and showed that during the late growing season, a period of more abundant precipitation and greater rates of soil respiration, the flashiness of soil respiration declined (Fig. 6C). We compared patterns of early (March–June) and late (July–October) growing season metabolic flashiness as way to better understand how plant community functional traits interact with seasonal precipitation variability to constrain ecosystem sensitivity to rainfall and observed that the onset of late summer monsoonal precipitation was associated with site specific declines f_{GEP} and f_{Re} (Fig. 6B–C). This late growing season decline in ecosystem metabolic sensitivity to precipitation is consistent with observations from a grassland rainfall manipulation experiment located near our grassland and savanna sites on the Santa Rita Experimental Range (Potts et al., 2006a; Cable et al., 2008). An observed decline f_{Re} during the late-summer monsoon is also consistent with an analysis of rainfall-induced ecosystem respiration in relation to the time since previous precipitation using data from a network of eddy-covariance towers in southern Arizona (Jenerette et al., 2008). In addition, this intra-annual comparison of metabolic flashiness reveals seasonal ecosystem functional convergence and suggests that periods of relative resource abundance may mask trait-mediated differences in ecosystem function. Finally, while we sought to quantify the relationship between f_{Re} and seasonal precipitation it is important to note that seasonal shifts in labile carbon availability might also influence the flashiness of ecosystem respiration by constraining soil metabolic activity (Curiel-Yuste et al., 2007).

Consistent with our prediction, years of low annual ET tended to have greater annual f_{ET} and years of low annual GEP tended to have greater f_{GEP} (Fig. 4A–B), a relationship which is reinforced by the consistent inverse relationship between annual precipitation and f_{ET} and f_{GEP} (Fig. 5A–B). A decline in flashiness in response to increasing water availability is consistent with a recent analysis of 25 eddy-covariance sites located in the semi-arid southwestern United States and northwestern Mexico which found that coefficients of interannual variation of ET and GEP declined as mean annual ET increased to conclude that dryland ecosystem exchange exhibits a particularly high degree of interannual variability in comparison with more mesic ecosystems (Biederman et al., 2017). Across sites, a decline in f_{ET} with increasing annual precipitation might be attributed to precipitation-mediated increases in canopy leaf area and corresponding increases in the contribution of transpiration to ET (expressed as T/ET; Scott and Biederman, 2017). Establishing mechanistic links between f_{ET} and T/ET may improve our understanding of biotic and abiotic processes that influence intra- and interannual variation in T/ET and provide additional insight into the role of plant functional traits in shaping watershed hydrologic function. For example, shifts in f_{ET} caused by changes in canopy leaf area and functional rooting depth may influence the temporal flashiness of soil moisture (Potts et al., 2010) or help predict changes in streamflow flashiness associated with nonnative species invasions, disturbance, or human management activities.

In contrast to our prediction that annual f_{ET} and f_{GEP} would decline with increasing functional rooting depth, the three sites demonstrated broad overlap in annual f_{ET} and f_{GEP}. However, sites varied from one another in the relationship between annual ET and f_{ET} and annual GEP and f_{GEP} (Fig. 4A & B) suggesting a more nuanced role of plant community functional traits in shaping how an ecosystem translates precipitation in biophysical activity. For example, maximum annual GEP in the shrubland (230 gC m^{-2} yr^{-1}) overlapped with the grassland's minimum annual GEP (228 gC m^{-2} yr^{-1}; Fig. 4B). Despite very similar values of GEP in those years, the grassland was much flashier than the shrubland (Fig. 4B). This pattern is consistent with differences in the abundance of deeply-rooted woody plants at the two sites (40% and

11% woody plant canopy cover at the shrubland and grassland respectively; Table 1). In the shrubland, abundant woody plants extend their photosynthetic activity by accessing deeper pools of soil moisture and thereby reducing f_{GEP} relative to the grassland site where the photosynthetic activity of grasses is closely coupled to rapid fluctuations in shallow soil moisture and hence greater f_{GEP}.

4.1. Conclusions

We modified the Richards-Baker index of streamflow flashiness to better understand how three widely distributed aridland ecosystems vary in their ability to translate precipitation into H_2O and CO_2 fluxes between the land surface and the atmosphere. In addition to reinforcing the conceptual ecohydrological links between watershed hydrology and ecosystem ecology, this work describes how increasing annual precipitation is associated with a corresponding decline in hydrologic and photosynthetic, but not respiratory flashiness. How interannual hydrologic and metabolic flashiness of aridland ecosystems compares to that of other ecosystem types along regional and global gradients of productivity and precipitation should be the focus of additional investigations and may provide new insight into the differential sensitivity of ET, GEP, and R_e to increasing climate variability and land cover changes associated with anthropogenic global change.

Declaration of Competing Interest

None.

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