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Seasonal Precipitation Legacy Effects Determine the Carbon Balance of a Semiarid Grassland.

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Key Points:

- We tested hypothesis of lagged effects of precipitation as this factor does not fully explain interannual variability of carbon flux in semiarid grasslands.
- Dry season precipitation highly determines the annual C balance of the humid growing season with larger effects on gross ecosystem productivity than ecosystem respiration.

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- Semiarid grasslands of central Mexico are likely to be carbon sources in the face of drier winters predicted at the end of this century.

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Abstract

Semiarid grasslands are water-limited ecosystems where precipitation (PPT) controls the onset and duration of the growing season; however, this variable does not fully explain interannual variability of productivity at temporal scales. We examined the relationship between PPT and C fluxes in a semiarid grassland at both seasonal and interannual scales, as well as the role of lagged effects of PPT and asymmetric sensitivities of net ecosystem carbon exchange (NEE) to PPT and its components (gross ecosystem exchange, GEE, and ecosystem respiration, ER). Six years of continuous NEE data measured with the eddy covariance technique (EC) and GEE estimated with 15 years of enhanced vegetation index (EVI) and the gross primary productivity (GPP) of MODIS were used. The semiarid grassland was a C source and a C sink among contrasting PPT years (114 to $-107 \text{ g C m}^{-2} \text{ y}^{-1}$). At seasonal scale, PPT relationship with the 15-years of GEE derived from EVI and GPP was sigmoidal. Moreover, PPT legacies of the previous dry-season determined the C balance of the grassland by affecting the C uptake and ecosystem respiration of the following growing season, but productivity was more sensitive to PPT changes than respiration. Models of climate change for semiarid grasslands in North America predict up to 30% reduction of winter-spring precipitation and slight summer PPT decrease. Thus, our results suggest that future changes in PPT may have a strong impact on the C uptake capacity of this ecosystem due to weakened legacy effects in summer C uptake.

Keywords: Blue grama, ecosystem respiration, eddy covariance, Enhanced Vegetation Index, gross ecosystem exchange, net ecosystem exchange, short-grass steppe.

Plain language summary

Precipitation is the main driver of productivity in semiarid ecosystems; however, annual precipitation does not fully explain interannual variability of productivity. Semiarid grasslands influenced by monsoonal precipitation regimes exhibit 6 to 8 months of drought with less than 20% of annual precipitation. This small amount of rain when vegetation is dormant would seem to be unimportant in terms of imposing control on productivity or carbon (C) fluxes. Using ecosystem flux data, we tested whether this small precipitation amount in the dry season had a role in controlling C fluxes and productivity and how much this affects the annual C uptake. We demonstrated for a semiarid grassland with summer prevailing rains that the small dry season precipitation highly determines the carbon balance of both the humid growing season as well as the annual C balance. Also, we found that dry seasons with large amounts of precipitation enhanced productivity more than ecosystem respiration in summer. Our study highlights the importance of the dry season precipitation on the productivity of semiarid grasslands where it is forecasted a greater proportion of precipitation reduction for winter than for summer at the end of this century. In this sense, our study highlights possible impacts of climate change on the vulnerability of semiarid ecosystems.

1. Introduction

Productivity in semiarid ecosystems is strongly controlled by water availability, and it is subject to the variability in seasonal and annual precipitation (Lal, 2004; Sala & Lauenroth, 1982). These conditions impose strong seasonal patterns for plant and microorganism activity, restricting growth to the season with the largest amount of precipitation (e.g., summer in semiarid tropical grasslands with monsoon influence). Even though these ecosystems have low rates of productivity, they are hotspots of climate variability (Vargas et al., 2016). Moreover, semiarid ecosystems cover 17.7% of the terrestrial surface (Lal, 2004) and show a global trend for increased productivity in the past few years (Ahlström et al., 2015). Thus, a better understanding of the precipitation control on productivity will improve the forecasting accuracy of global climate change models and the specific role of semiarid ecosystems in the regional and global carbon (C) cycle.

Strong correlation between precipitation (PPT) and aboveground net primary productivity (ANPP) has been shown to occur spatially (i.e. among sites), but not temporally in semiarid grasslands (Hsu & Adler 2014). These results suggest other processes like precipitation legacy effects of previous precipitation periods (seasons/years) affect net productivity rates of current years (Shen et al., 2016; Arredondo et al., 2016). Sala et al. (2012) for instance, showed that a

previous-dry year did lead to a decrease in annual productivity rates in the following year, while a previous wet year amplified productivity rates at the following growing season in grassland ecosystems. On the other hand, Arredondo et al. (2016) showed lagged effects of the dry season precipitation affecting productivity of the growing season in summer. The responses in net productivity to legacies from either previous dry or wet periods are likely caused by: 1) structural changes of plant communities due to either plant mortality following severe droughts, or increased tiller production during wet years (Reichmann, Sala & Peters 2013a), and 2) biogeochemical processes that increase nutrient availability due to larger litter inputs from previous wet years (Sala et al., 2012), or 3) some combination of both mechanisms. It is likely that PPT legacy effects may also explain annual net ecosystem C exchange rates (NEE) in semiarid grasslands. Following this logic, the capacity for ecosystem C uptake may be enhanced by a previous wet year or season, or on the contrary, reduced by a previous dry year/seasons.

On the other hand, some studies have shown “asymmetries” in the relationship between C fluxes and precipitation which alter our understanding of the PPT control on ecosystem C exchange rates. Different types of asymmetries can be identified; one asymmetry is related to differential responses (sensitivities) of productivity and respiration to PPT (Shi et al., 2014), and a second one is related to non-linear responses between C fluxes and PPT (Knapp, Ciais & Smith 2016). Here, we define nonlinearity as non-proportional changes of productivity with the increase or decrease of precipitation, i.e. another relationship than a straight line (Hsu and Adler, 2014). For instance, 1) changes of PPT affect more to gross ecosystem exchange rates (C uptake; GEE) than

to ecosystem respiration (C release; ER; where $-NEE = GEE + ER$; Loescher et al. 2006; Shi et al., 2014, and references there in). This is derived from the fact that at short-term scales, rates of autotrophic respiration (R_a) decreases rapidly following the decline in labile C substrate pools coming from photosynthates (Bahn et al., 2008). In contrast, heterotrophic respiration (R_h ; where $ER = R_h + R_a$) uses the long-term recalcitrant C sources by which R_h changes very slowly. This prevents annual ER rates to change except after a multi-year drought (Shi et al., 2014). Therefore, the overall response of ecosystem respiration to PPT change would be less affected by interannual changes in PPT and will likely result in small responses to the previous year's PPT (i.e. no PPT legacy effects on ER). On the other hand, 2) the gross ecosystem exchange may exhibit asymptotic responses to extreme PPT years because one of the main plant adaptations to dry environments includes an inherent low relative growth rate as well as low productivity rates (Grime, 1977). Thus, more PPT than a maximum threshold will not result in additional productivity.

Direct continuous estimations of NEE rates have reported semiarid grasslands as small C sinks (Propastin & Kappas, 2009), net C sources (Mielnick et al., 2005), or C neutral (Petrie et al., 2016) ranging between -164 and $210 \text{ g C m}^{-2} \text{ y}^{-1}$ (where negative sign stands for C uptake). Therefore, it is likely that semiarid grasslands at the interannual and decadal time scales must be near C neutral or minor C sinks (Sierra et al., 2009), such that, in favorable growth years grasslands are small C sinks, whereas in unfavorable environmental conditions grasslands are small C sources. However, precipitation amount of previous year/season and asymmetries in the

PPT-C fluxes relationship may influence the current years' C balance. Overall, changes in synoptic scale climate patterns will differentially affect each of these processes and may result in different grassland responses to C capture.

By the end of the 21st century, global circulation models forecast a reduction of mean annual PPT between 10 - 15% in summer, and between 10 - 30% in winter-spring for the arid and semiarid regions of Mexico and Southwest of USA (Christensen et al., 2007). An overall decrease of PPT will affect net ecosystem productivity and will modify the carbon and water cycles. This implies that expected scenarios with a larger decrease in winter-spring PPT could threaten the overall stability of the C cycle of these ecosystems.

The overall aim of this study was to identify PPT legacy effects on NEE and on its component processes (GEE and ER), and to identify asymmetries in relationships between C fluxes and PPT. For this, we hypothesized that previous year/season PPT will affect the annual C balance of the semiarid grassland. We expect that a severe previous drought year/season will reduce the net C gain of the current year/season (H1), whereas a transition from a previous wet year/season the grassland will increase its net C uptake rate (H2). Moreover, by partitioning NEE components, we expect that GEE – current PPT relationship will be non-linear (H3); GEE will be more sensitive than ER to current or previous PPT (H4); and finally, we expect no legacy effect of previous PPT on ER (H5).

2. Materials and Methods

2.1. Site description

The study site is located on a semiarid grassland, within the Llanos de Ojuelos geographic subprovince, NE of Jalisco state, Mexico (Fig 1). The grassland biome in Mexico extends from the North American Midwest along a strip that follows the *Sierra Madre Occidental* and the *Chihuahuan* Desert into the subprovince *Llanos de Ojuelos*. Vegetation is dominated by grasses, with *Bouteloua gracilis* H.B.K. Lag ex Steud (blue grama) as the key grass species, forming nearly mono-specific stands under well-preserved conditions. The region has a semiarid climate with mean annual precipitation of $424 \text{ mm} \pm 11 \text{ mm}$ (mean ± 1 SE, last 30 years; INIFAP, Rancho experimental Vaquerías. SMN) mainly distributed between June and September and exhibiting 6 to 9 months of low precipitation (<20% of annual precipitation). Mean annual air temperature is 17.5 ± 0.5 °C. The topography is characterized by valleys and gentle rolling hills with soils classified as haplic xerosols (associated with lithosols and eutric planosols), and haplic phaeozems (associated with lithosols) (Aguado-Santacruz, 1993). Soils are shallow with an average depth of 0.3-0.4 m containing a calcic cemented layer at ~ 0.5 m in depth, with textures dominated by silty clay and sandy loam soils (COTECOCA, 1979).

This eddy covariance site, “Ojuelos”, is part of MexFlux (Vargas et al., 2013), the Mexican consortium of carbon and energy flux measurement sites. This site is a fenced area of ~ 64 ha of semiarid grassland under grazing and fire management. A 6 m high tower was placed at the center of the area of interest. That location allowed for an ever-changing and integrated measurement footprint of 320 m, 410 m, 580 m, and 260 m from the tower according to the N, E, S, and W orientations, respectively. The footprint model (Kormann & Meixner, 2001) indicated

>80% of cumulative fluxes came from this ecosystem. For this study, we used data collected from 2011 to 2016.

2.2. Meteorological and soil measurements

Meteorological data were collected continuously at a rate of 1 s and averaged at 30 min intervals using a datalogger (CR3000, Campbell Scientific Inc., Logan, Utah). Measured variables included air temperature (T_a) and relative humidity (Rh) (1000 Ω PRT, HMP45C, Vaisala, Helsinki, Finland) housed into a radiation shield (R.M. Young Company Inc., Traverse City, MI), and solar net radiation (NR01, Hukseflux, Netherlands). Soil variables were measured at a 5 min frequency and averaged at 30 min intervals. These included four self-calibrating soil heat flux plates buried at 8 cm deep (HFP01SC, Hukseflux, Netherlands). Four volumetric soil water content (SWC) probes (CS616, Campbell Scientific Inc.) were positioned horizontally at 2.5 cm and 15 cm deep. Average soil temperature was measured with two sensors positioned on the top 8 cm of the soil profile, and two other soil temperature probes at 5 cm deep (T108, Campbell Scientific Inc., Logan, Utah). Precipitation was measured with a bucket rain gauge (FTS Inc., Victoria, British Columbia, Canada). When T_a , Rh, or solar radiation variables were not available, they were estimated from another set of meteorological instruments mounted on the same tower (FTS Inc.).

2.3. Net ecosystem CO₂ exchange measurements

An open path eddy covariance (EC) system was used to measure NEE over the semiarid grassland. The system consisted of a three-dimensional sonic anemometer (CSAT-3D, Campbell

Scientific Inc.), and an open-path infrared gas analyzer (IRGA, Li-7500, LI-COR Inc., Lincoln, NE). Instruments were mounted in a tower at 3 m above ground level oriented towards the prevailing winds. The IRGA was mounted such that the optic path and the sonic volume were at the same height and tilted 45° to reduce dust and water accumulation in the IRGA optical path. Digital signal of both sensors was acquired at a sampling rate of 10 Hz by a datalogger (CR3000, Campbell Scientific Inc.).

2.4. Data processing

Raw eddy covariance data were processed in EdiRe (v1.5.0.10, The University of Edinburgh) following standard procedures (Aubinet *et al.*, 2012). Wind velocities, sonic temperature, [CO₂], and [H₂O] signals were despiked considering outliers those values greater than ±8 SD. A 2-D coordinate rotation was applied to sonic anemometer wind velocities. Lags between the vertical wind velocity and scalars were removed with a cross-correlation procedure. Carbon and water vapor fluxes were estimated as molar fluxes (mol m⁻² s⁻¹) using a 30 min block average, and then they were corrected for air density fluctuations (WPL correction, Webb, Pearman, & Leuning, 1980). To account for frequency loss on NEE, the frequency response correction was done (Baldocchi & Meyers, 1989). We did not estimate a storage flux because of the low vegetation stature, and we assumed it would be 0 over a 24-h period (Loescher *et al.*, 2006).

Fluxes were subjected to quality control procedures: i) stationarity (<50 %, Foken & Wichura, 1996), ii) integral turbulence characteristics (<50%), iii) flags of IRGA and sonic anemometer (AGC value < 75, Max CSAT diagnostic flag = 63) which are strongly related with rain events,

iv) range tests ($\pm 20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Taylor & Loescher, 2013), and v) a threshold of $u^* = 0.1 \text{ m s}^{-1}$, which was defined through the 99% threshold criterion after Reichstein et al. (2005).

Closure of energy balance was $> 70\%$ for all years, except for the period before October 2011, when storage and soil heat flux terms were not included in the balance because soil heat flux sensors were not installed at that time.

On average, 40% of half-hour data periods per year were lost after quality filtering. Data gaps shorter than two hours were linearly interpolated. Gaps larger than two hours in flux data were filled with the Marginal Distribution Sampling algorithm (MDS) (Reichstein et al., 2005). The online MPI Jena tool, www.bgc-jena.mpg.de/REddyProc/ brew/REddyProc.rhtml, based on the ReddyProc R package (The R project, 2014) was used for this gap-filling procedure and for the flux partitioning of NEE.

2.5. Long-term gross primary productivity from MODIS' GPP product and EVI

For covering more environmental conditions, and for comparison purposes of the eddy covariance GEE with an independent productivity measurement, we use 15 years of the MODIS GPP (gross primary productivity) product from 2000 to 2016 (hereafter GPPM; Running et al., 2015) of 500 m spatial resolution and 8-day time resolution. The GPPM was integrated (summed) by year and by season for testing the same hypothesis as that for measured eddy covariance GEE. Here we use GPP and GEE as equivalent C fluxes; however, GEE does not consider recycling of C within the leaf or within the canopy volume (Stoy et al., 2006). Due to GPPM overestimated GEE at low productive years/seasons, whereas underestimated GEE at

high productive years/seasons (Fig. S2), we also estimated GEE by a simple correlation with the enhanced vegetation index (EVI) at 250 m and 16 days of spatial and time resolution, respectively (hereafter GEE_{EVI} ; Didan, 2015). The Savitsky-Golay (Savitsky & Golay, 1964) filter was used to eliminate outliers of GPP and EVI derived from adverse atmospheric conditions. Years with PPT data loss or prescribed fire in the site were not used.

2.6 Precipitation legacies

Precipitation legacies are the effects of droughts or uncommon wet periods (years/season) after it has occurred (Sala et al., 2012), and are defined as the difference between observed C flux ($F_{C_{observed}}$) and the expected ($F_{C_{expected}}$), which is calculated from the C flux – current precipitation relationship.

$$F_{C_{legacy}} = F_{C_{observed}} - F_{C_{expected}} \quad (1)$$

Where F_c is the C flux (i.e. NEE, GEE, ER, GPPM, or GEE_{EVI}).

Then, it was tested if $F_{C_{legacy}}$ was a function of previous season/year precipitation. Additionally, we used the previous season soil water content (SWC), and the SWC at the beginning of the current season for testing soil moisture carry-overs as the mechanism of the PPT legacy effect.

2.7. Asymmetries

We distinguished between two types of asymmetries: 1) whether GEE and ER have different sensitivity to PPT change (i.e. homogeneity of slopes of linear regressions), and 2) whether there

is nonlinear relationship than a straight line between C flux (NEE, GEE or ER) and precipitation (current or previous).

Relationships between GPPM or GEE_{EVI} and PPT were fitted with a linear (i.e. a straight line) and a sigmoidal function:

$$F_c = y_0 + A / (1 + \exp(-(PPT - x_0)/d)) \quad (2)$$

where F_c is the carbon flux (i.e. GPPM or GEE_{EVI}), y_0 is the initial background F_c value, A is the amplitude of the curve at the y -axis ($\max(y) - \min(y)$), PPT is the precipitation (mm), x_0 is the midpoint of the curve at the x -axis, and d is related to the slope of the curve. The rate of change in the curvature of F_c function was used to identify the lower and upper PPT threshold for C uptake (Zhang et al., 2003).

2.8. Hydroecological years

We use the concept of hydroecological year (HEY, Thomas et al., 2009) to evaluate the interannual variability of C fluxes. At the study site, the first frost in the year generally occurs in November, concomitantly with a significant decrease in PPT. Thus, we considered this month as the end of the growing season and the start of HEY in December.

Two seasons were derived by dividing the HEY as the dry season comprising from December to May, and the humid season comprising from June to November. Hereafter, these periods will be referred as dry and wet seasons. Carbon fluxes and environmental variables at each season were separately considered for legacy effects analyses.

2.9. Statistical analyses

For testing linear relationships between: 1) C flux and PTT, 2) $F_{C_{\text{legacy}}}$ and PPT_{t-1} , and 3) $F_{C_{\text{legacy}}}$ and SWC, non-parametric Kendall correlation tests with the Fisher z-transformation (Bonett and Wright; 2000) were performed. If the correlation was significant, the non-parametric Theil-Sen method (Sen, 1968) was used to estimate the slope and intercept of the regression lines. For testing type 1 asymmetry, a rank-based ANCOVA (Kloke and McKean, 2015) was used to compare slopes between ER and GEE legacies. In contrast, for testing type 2 asymmetries in the GPPM/ GEE_{EVI} – PPT relationship, we compare the Akaike's (AIC) Information Criterion between the linear and the sigmoidal model (the smallest, the best). We used the PROC CORR procedure of SAS 9.04 with the Kendall macro (Looney, 2015) for correlation tests, and the “mblm”, “Rfit” and “npsm” packages of R (The R-CRAN project, 2018) for the Theil-Sen slope estimations and rank-based analysis. All analyses were performed at a level of significance of $\alpha = 0.05$.

3. Results

3.1. Environmental variables

We observed a range in annual PPT including the lowest record in 2011 to almost the wettest years in modern records (2014 and 2015, Fig. 2a). In addition, we also observed distinctive annual PPT patterns with three years of low cumulative PPT during the dry season (2011, 2013,

and 2016), and three others with high cumulative PPT during the dry season (2012, 2014, and 2015). In examining the HEY division by season, an average of 21% of precipitation occurred during the dry season hydroecological year (107.8 ± 69.43 mm, mean \pm 1 SD).

Volumetric soil water content (SWC) at both 2.5 and 15 cm depth changed with PPT. Maximum SWC (0.3, Fig. 2b) was reached for short time periods within summer and at the end of winter season in 2012. More variation in SWC was observed at shallow depths (2.5-5.0 cm), where soil dried and wetted faster than at 15 cm (Figure 2b).

3.2. Annual CO₂ balance

Although the driest year coincided with the largest C emission, we found that wetter years varied as sources and sinks, and increased rainfall did not necessarily lead to increased carbon uptake. For instance, a very wet year (2013, 523.4 mm) showed a net C release of $28.86 \text{ g C m}^{-2} \text{ y}^{-1}$, even though the site received 70 mm above MAP, and 120 mm more than 2012, whereas a wetter than the MAP year (2014, 610.4 mm) coincided with the largest annual C uptake of $-107.65 \text{ g C m}^{-2} \text{ y}^{-1}$ (Fig. 3). Even though 2015 was the wettest year, the net C uptake of $-96.87 \text{ g C m}^{-2} \text{ y}^{-1}$ was lower than in 2014.

3.3. Temporal C balances – current PPT relationship

The EC-measured annual C balance (NEE) was not linearly correlated with annual PPT ($\tau = 0.6$, $P > 0.05$) (Fig. 4a). In contrast, GEE and ER increased at a rate of 1.54 and 1.12 $\text{g C m}^{-2} \text{ y}^{-1}$ per each millimeter of annual PPT ($P < 0.05$, Fig. 4b). The statistical analysis did not reveal a

significant difference between ER and GEE slopes ($P > 0.05$, Fig. 3b). Similarly, the GPP of MODIS (GPPM) was linearly correlated with current PPT (Fig. S2) On the other hand, at seasonal scales, NEE, GEE and ER were also linearly correlated with current PPT ($P < 0.05$, Fig. 5a, b). The C uptake and C release rates were of 1.22 and $0.93 \text{ g C m}^{-2} \text{ y}^{-1}$ per mm of seasonal PPT, for GEE and ER, respectively. This resulted in a net ecosystem C uptake rate of $0.33 \text{ g C m}^{-2} \text{ y}^{-1}$ per mm of seasonal PPT.). In agreement with annual scales, GEE and ER slopes were not significantly different ($P > 0.05$).

In contrast with measured GEE, the relationship between PPT and the fifteen years of GPPM and GEE_{EVI} at season scale were better fitted with a sigmoidal than with a straight-line model (AIC = 327.44 for the linear model, and AIC = 291.66 for the sigmoidal model. Fig. 6a and S3a). The GPPM increase started at 141 mm of PPT, and the largest GPPM change occurred between 200 and 470 mm, achieving an asymptote at 417 mm of PPT (173 and 387 mm for the beginning and asymptote of GEE_{EVI} ; Fig S3a).

3.4. Precipitation legacy effects

Legacies of annual GEE, GPPM, or ER fluxes were not correlated with previous year PPT (Eq. 1; Fig. 4c and S2b). In contrast, all wet-season $\text{NEE}_{\text{legacy}}$, $\text{ER}_{\text{legacy}}$, and $\text{GEE}_{\text{legacy}}$ were correlated with the previous dry season PPT ($P < 0.05$, Fig. 5c and 5d), i.e. there was a linear-positive PPT legacy effect of the dry over the wet-season. Larger dry-season PPT than ~ 160 mm enhanced C uptake of the wet season, whereas lower than that PPT reduced the C uptake. For instance, a

large PPT during the dry season enhanced C uptake (negative NEE) of 2012, 2014, and 2015 growing seasons, whereas a dry winter-spring season reduced C uptake in 2011 and 2013. This occurred even though summer 2013 was among the wettest of the six study years (466.3 mm). In contrast, neither dry-season NEE, nor ER, nor GEE legacies were correlated with PPT of the previous wet season ($P > 0.05$, Fig. 5c, d). The effect of dry-season PPT was larger over GEE_{legacy} than ER_{legacy} (a rate of 1.08 and 0.47 $\text{g C m}^{-2} \text{ season}^{-1}$ per mm of dry season PPT, for GEE_{legacy} and ER_{legacy} , respectively; $p < 0.05$; Fig. 5d). Even though the GPPM and GEE_{EVI} – PPT relationships were sigmoidal, the dry season PPT legacy effect on $GPPM_{\text{legacy}}$ and $GEE_{\text{EVI} \text{ legacy}}$ was linear and showed a lower slope than the estimated GEE_{legacy} using the measured GEE (0.35 and 0.88 for $GPPM_{\text{legacy}}$ and $GEE_{\text{EVI} \text{ legacy}}$, respectively; $P < 0.05$; Fig. 6b and S3b).

3.5. Asymmetries

We identified the two types of asymmetries, 1) a difference in PPT-sensitivity between GEE_{legacy} and ER_{legacy} , where GEE_{legacy} was as twice sensitive to previous seasonal PPT than ER_{legacy} (1.08 and 0.47 for GEE_{legacy} and ER_{legacy} , respectively; Fig. 5d). Moreover, all dry season $F_{\text{c}} \text{ legacies}$ were not sensitive to previous wet season PPT (Fig. 5c, d, and 6b); and 2) a non-linearity of the long-term GPPM and GEE_{EVI} that were better fitted by a sigmoidal function than a straight line (AIC = 327.44 for the linear model, and AIC = 291.66 for the sigmoidal model. Fig. 6a). The asymmetric response of GPPM and GEE_{EVI} will depend on the variability of the PPT pattern (i.e. if PPT is deviated towards the left or to the right of the curve center). For instance, a similar

increase of the dry and wet-season PPT will enhance more C uptake of the dry than the wet season. In contrast, the wet-season C uptake will be more affected by a low wet-season PPT than the dry-season C uptake by low dry-season PPT (Fig. 6a).

3.6. The soil water content and C legacies.

Both wet season NEE_{legacy} and GEE_{legacy} were correlated with the previous dry season mean soil SWC at 2.5 cm depth (Fig. S4). In contrast, notwithstanding wet season ER_{legacy} showed the same pattern than GEE_{legacy} , it was not correlated with previous dry season SWC. Similarly, the shallow depth SWC at the beginning of the wet season, i.e. mean SWC in May and June, was not correlated with NEE_{legacy} , GEE_{legacy} nor ER_{legacy} ($p > 0.05$; Fig. S5).

4. Discussion

Precipitation during this study ranged from the worst drought in the past 70 years (2011) to the wettest records in this site (2014 and 2015), allowing us to describe a full response of the semiarid grassland C fluxes to PPT. Our results determined the contribution of winter-spring PPT to summer-fall net ecosystem C exchange. Using the approach of Sala et al. (2012), we confirmed the PPT legacy hypothesis at a semiarid grassland site but occurring at seasonal scales.

4.1. Precipitation legacy effects

Dry season precipitation in this predominantly summer-rain ecosystem had more effect on productivity than previously thought, based on its observed average 22% contribution to the total annual precipitation along the study period (16% for the 30 years of PPT data). We expected previous season PPT would affect the C balance (NEE) of the semiarid grassland through two response types: 1) we expected a positive effect on C uptake of previous wet seasons (H1), and results showed “wet” dry-seasons (winter/spring) enhanced C uptake of the following wet season (summer-fall) at a rate of 0.54 g C per mm of PPT (Fig. 5c). On the other hand, 2) we expected dry seasons should reduce C uptake of grassland (H2); this was confirmed by observed “dry” dry-seasons reductions of C uptake of the wet-season at the same rate of 0.54 g C per mm of PPT (Fig. 5c). Both hypotheses also were confirmed for $GEE_{legacies}$ and $ER_{legacies}$ (Fig. 5d). Moreover, we could identify a PPT threshold of ~ 160 mm as a minimum dry-season PPT amount for having a positive effect on wet-season productivity. These responses coincide with the linear positive legacy hypothesis of Sala et al. (2012) that advocates equivalent responses to previous wet or dry years.

What are the mechanisms explaining the effects on productivity by a small proportion of rain that occurs when the vegetation is still dormant? The strong seasonal characteristics of semiarid regions have contributed to the evolution of mechanisms like translocation of carbohydrates from the shoots to crown and roots of grasses, as *B. gracilis*, the dominant species. When *B. gracilis* enters seasonal dormancy (in grasses a period of leaf senescence and metabolic reduction), it maintains physiological activity at the tiller base, therefore consumes carbohydrates and requires

water for maintaining medium water stress levels (e.g. above -2 MPa, Arredondo et al., 2016) in winter and spring (Sarath et al., 2014). The amount of carbohydrate reserves and its use depends on the length and amount of the previous growing season's PPT, but it also depends on soil and atmospheric humidity for the winter-spring period (Ares, 1976; White, 1973). Therefore, the maintenance of physiological and structural integrity of *B. gracilis* during the dry period greatly determines the amount of active tissues primed to capture carbon in the next growing season, i.e., reserves are used for winter/spring tissue maintenance and refoliation (Volaire & Norton, 2006). This interpretation agrees with Sala et al. (2012) and others (Reichmann et al., 2013b; Reichmann & Sala, 2014) that suggest the precipitation legacy effects are a consequence of plant structural changes like the number of tillers at the end of the growing season.

Temporal dynamics of soil water content may also control the observed differences of C balances among years and the legacy effects of PPT (Fig. S4). Our data (Fig. 2b) indicate that dry-season precipitation for 2012, 2014 and 2015 was large enough to recharge the soil profile to a depth where grasses have their largest root biomass (between 0 and 30 cm; Medina-Roldán, 2007; Delgado-Balbuena et al., 2013). This additional water (humidity) allows for the reactivation of photosynthesis when vegetation is usually dormant. However, the C flux legacies were not correlated with previous SWC at 30 cm depth, but at the shallow depth (2.5 cm; Fig S4) where more variability was observed. Moreover, the SWC at the beginning of the wet season (i.e. the SWC in May and June) was not correlated with $F_{C\text{legacy}}$ (Fig. S5), which indicated that soil moisture carry-over effect is not the mechanism of legacy effects, or it is not the only one.

Dynamics of root development of *B. gracilis* widely vary into the soil profile and along the seasons. This causes variability of sources of water from shallow to deeper soil profiles depending on water availability and phenology of grasses (Ares, 1976), and in addition, with short turn-over times of roots, this likely generates a better coupling of $F_{c\text{legacies}}$ with average SWC of the whole dry season (where several processes are combined) than with soil water at the beginning of the growing season.

4.2. Seasonal PPT legacy effects

Precipitation legacies at seasonal rather than at annual scales as observed in our study are supported by several studies. For instance, Craine et al. (2012) reported <4 months effects of drought on the productivity of a humid grassland with no clear effects on productivity at the end of the growing season. In addition, Jobbágy et al. (2002) showed two months PPT legacies delay in the above ground net primary productivity rates (ANPP) in a semiarid steppe. With respect to winter PPT legacies, Robertson et al. (2010) showed winter PPT control over grass cover density in a semiarid grassland, and, Li et al. (2015) showed a high dependence of growing season NDVI to previous year fall/winter PPT in the arid-semiarid desert. Previous studies at our site have shown a correlation of plant cover with winter PPT, but a null relationship with annual or summer PPT (Aguado-Santacruz, 1993). More recently, Arredondo et al. (2016) identified significant effects of winter PPT on annual aboveground net primary productivity.

Taken all together, there is a growing knowledge base that supports seasonal PPT legacy effects in grasslands. To reach a comprehensive understanding we still need to fill gaps about the (i) within plant carbohydrate ecophysiology, (ii) the direct mechanistic relationship between dry period water uptake from soils and plant maintenance, (iii) direct evidence of N cycling dynamics in these systems, and (iv) taken collectively, how these processes may change with future changes in PPT patterns and amounts as claimed by many, *e.g.*, Ciais et al. (2013).

4.3. Asymmetry of precipitation sensitivity and PPT legacies in NEE components

We postulated two types of asymmetries for GEE and ER in response to PPT as complementary ways for explaining the lack of their temporal relationship (Fig. S1). We expected that: 1) GEE would be non-linearly related with current PPT (H3, where nonlinear refers to the absence of a straight line relationship); 2) GEE would be more sensitive than ER to current PPT (H4, heterogeneity of slopes); and 3) ER_{legacy} would not be sensitive to previous PPT (H5). In agreement with our H3, the relationship between the fifteen years of GPPM and GEE_{EVI} and current PPT were not linear (Fig. 6a and S3b), although the relationship between measured 6 years-GEE and current PPT was linear. This was likely because more environmental conditions than PPT that also controls ecosystem productivity were not represented in six years of measurements (*e.g.* air and soil temperature, solar radiation, vapor pressure deficit, etc.; Baldocchi, 2008; Gilmanov et al., 2010), or because NDVI (the core of MODIS GPP) and EVI over-estimated productivity in dry seasons and saturate in high productive periods (Gu et al., 2013; Heinsch et al., 2006). With the sigmoidal model, around the midpoint of the GEE curve is

constrained by both extremely low and extremely high PPT ($141 > \text{PPT} > 417$ mm; Fig. 6a). However, because dry season GPPM is located on the left side of the sigmoidal curve (0 – 250 mm), and wet season GPPM at the right (221 – 700 mm, Fig 5a), the dry season GPPM is more enhanced by extreme wet dry-seasons, whereas wet-season GPPM is more affected by low wet-season PPT.

The sigmoidal model is more appropriate than the linear model for describing GEE dynamics in response to PPT variability. In water-limited ecosystems that enter in a latency period (as discussed above in PPT legacy effects causes), with lower PPT than the low threshold (~141 mm), plants do not photosynthesize or do it at minimum levels for maintaining medium water stress levels in dry conditions (Arredondo *et al.*, 2016), and any effect of extreme drought on plant mortality should be reflected in the next growing season, as a PPT legacy effect. In addition, limitation of C uptake at high PPT (asymptote) is caused by the inherent low growing rates of semiarid plant species (Grime, 1977) as well as the large fraction of runoff at ecosystem scale (Loik *et al.*, 2004) that reduce plant water availability.

We did find support to our hypothesis 3: both GEE and ER were equally sensitive to current PPT changes as indicated by their similar slopes (Fig. 3b and 4b). We interpret this result as: 1) compensatory controls of autotrophic and heterotrophic respiration (e.g. soil moisture), or 2) a fixed amount of respiratory tissues, *i.e.*, flat tax hypothesis (Wiesner *et al.* 2018).

The flat tax hypothesis suggests that there is a fixed proportion of ecosystems gross carbon captured that goes toward respiration processes, i.e., a fractional based amount per unit mass of respiring plant materials (both living and dead along with microbial biomass). This should be the case even if the amount of respiring materials changes from year-to-year or from site-to-site; thus, if photosynthesis declines so will ER (Sierra et al. 2009). On the other hand, previous dry-season precipitation effects on GEE_{legacy} and ER_{legacy} were asymmetric (heterogeneity of slopes), with wet-season ER_{legacy} being less affected than GEE_{legacy} by previous dry-season PPT. The GEE_{legacy} was twice sensitive to changes in previous dry-season PPT than ER legacy (Fig. 5d). Therefore, we partially confirmed our H5 because it was hypothesized a null response of ER_{legacy} to previous precipitation. The lower response of ER can be a consequence of the dominant heterotrophic respiration that uses recalcitrant C substrates which require years to decades to change (Schmidt et al., 2011). For example, Shi et al. (2014) showed that ER is less sensitive to PPT decrease because the heterotrophic component of ER responds to long-term controls like quality and amount of soil organic matter. In our study site, a soil C reduction was observed only after decades of plant cover loss (Medina-Roldán et al., 2008). Thus, a significant R_h reduction could occur after a multi-year drought that reduces the recalcitrant soil carbon, and the effect of previous season PPT on RE would be the effect over R_a . Our finding about no effect of previous wet season over dry-season C flux legacies was also significant. Even though productivity of dry-season is relatively small and only serves as a counterbalance of respiration, large fluxes of ecosystem respiration after either dry or wet-season PPT are important

components of the C balance. The Birch effect (Jarvis et al., 2007), as has been named this C efflux phenomenon which is a short-duration process controlled by timing of precipitation, availability of labile nutrients in soil, and previous conditions of soil moisture and C flux before the event of PPT. We would expect some control of previous wet-season productivity on nutrient availability, and hence on the magnitude of the Birch effect and on productivity of the dry season; however, we could not detect any of these effects in this study.

5. Conclusions

Based on our results, the control of PPT on C fluxes in the semiarid grassland is a process that includes non-linear responses of vegetation to PPT variability as well as lagged effects of dry season PPT. Identification of non-linearities (asymmetries) of PPT-C fluxes relationship and quantification of PPT thresholds are sound results that will help to understand the C cycle in these water-limited ecosystems (Knapp, Ciais & Smith 2016). Climate change models for semiarid grasslands in Mexico predict up to 30% reduction of winter-spring precipitation in contrast to a slight decrease of summer PPT. According to our linear $F_{C_{\text{legacy}}}$ model, a 30% PPT reduction on the winter would reduce the C uptake by the semiarid grassland. Thus, our results suggest that future changes in winter-spring PPT will impact the C uptake capacity of this ecosystem due to weakened legacy effects in summer C uptake. In contrast, ecosystem respiration rates will likely remain less affected under this future scenario and will follow the

changes in respiratory biomass that support C uptake. Therefore, future precipitation scenarios threaten the stability of semiarid grasslands ecosystems likely leading them from being slight C sinks to net C sources.

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Figure Captions

Figure 1. Location of the site into the semiarid highlands in the Mexican Terrestrial Ecoregions classification (INEGI, 2007).

Figure 2. Seasonal and interannual variation of daily and cumulative precipitation (a), and volumetric soil water content at 2.5 cm and 15 cm of depth (gray and black lines, respectively, b). Vertical gray lines represent the HEY divisions, and shaded areas indicate the wet season of each HEY.

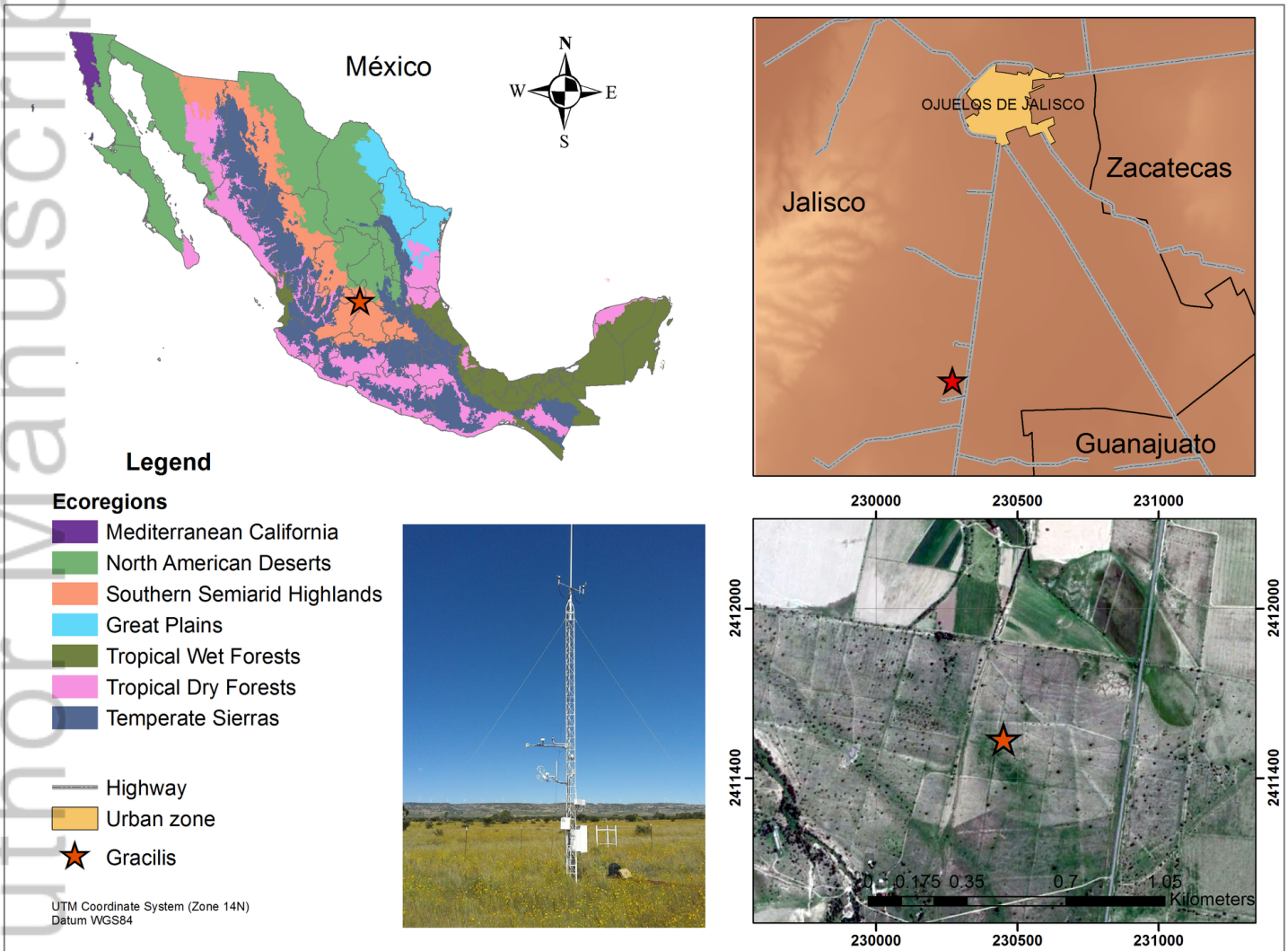
Figure 3. Seasonal and interannual variation of daily integrated NEE (black bars, $\text{g C m}^{-2} \text{d}^{-1}$) and cumulative NEE for each hydroecological year (HEY, dashed lines). Vertical gray lines represent the HEY divisions, and shaded areas indicate the wet season of each HEY.

Figure 4. Linear relationships between current annual precipitation and a) measured annual NEE, and b) GEE and ER. c) Relationship between previous year PPT and GEE and ER legacies ($\text{GEE}_{\text{legacy}}$ and $\text{ER}_{\text{legacy}}$).

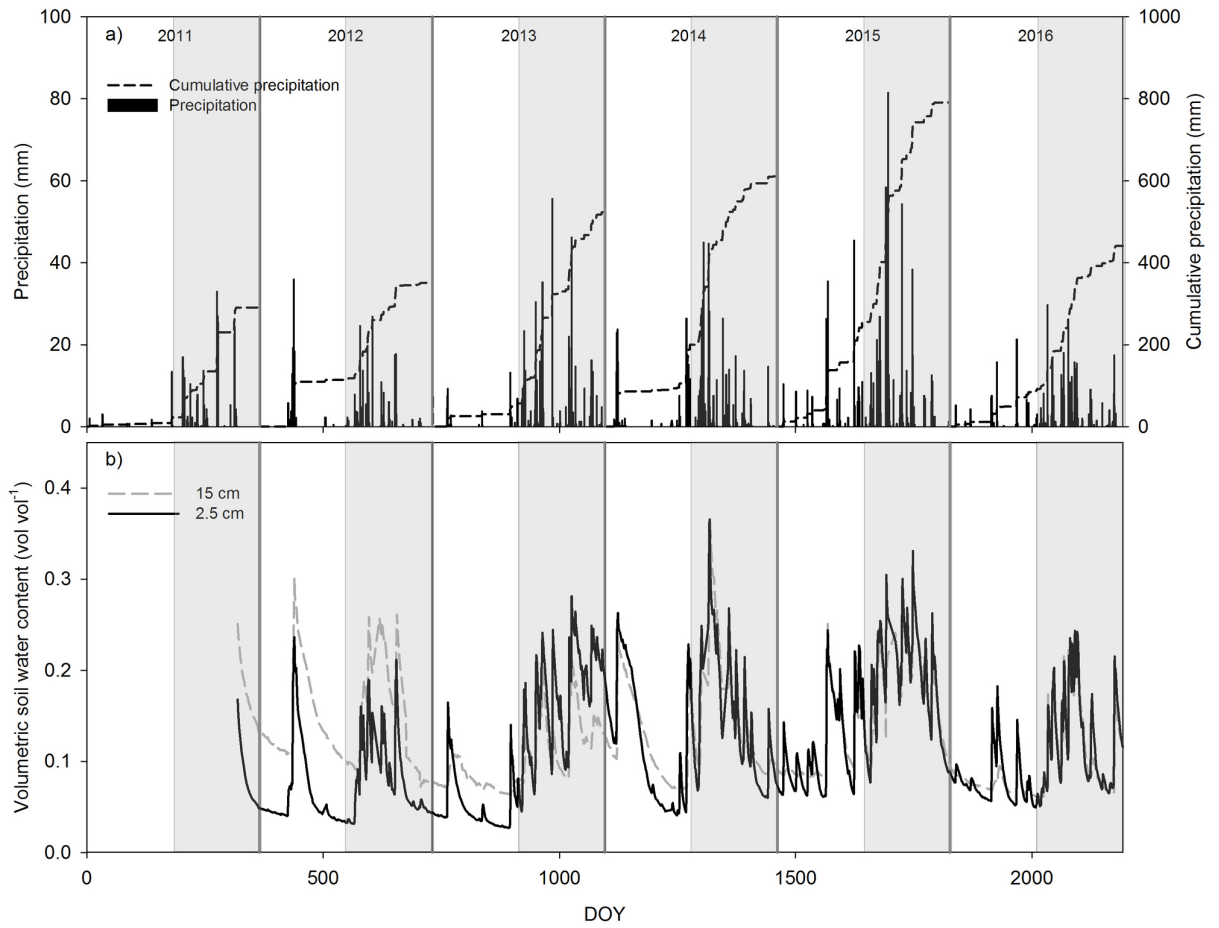
Figure 5. (a) The relationship between NEE and current seasonal PPT (open and closed symbols stand for dry and wet season C fluxes, respectively). (b) The relationship between ecosystem respiration (ER), gross ecosystem exchange (GEE) and current seasonal PPT. (c) The relationship between NEE legacies (Eq. 1) and previous seasonal PPT. (d) The relationships of previous seasonal PPT and C flux legacies ($\text{Fc}_{\text{legacy}}$) of both ER and GEE ($\text{GEE}_{\text{legacy}}$ and $\text{ER}_{\text{legacy}}$). The horizontal dotted line in c) and d) is a reference line indicating $\text{Fc}_{\text{legacy}} = 0$.

Figure 6. a) The relationship between the MODIS GPP (GPPM) and current seasonal PPT. Vertical gray lines stand for lower (141 mm) and upper (417 mm) seasonal PPT thresholds enhancing GEE. b) The relationships between previous season PPT legacies and $GPPM_{\text{legacy}}$. Open circles represent the December-May period (dry-season), whereas filled circles stand for June-November period (wet-season). The dotted line in b) is a reference line indicating $F_{c_{\text{legacy}}} = 0$.

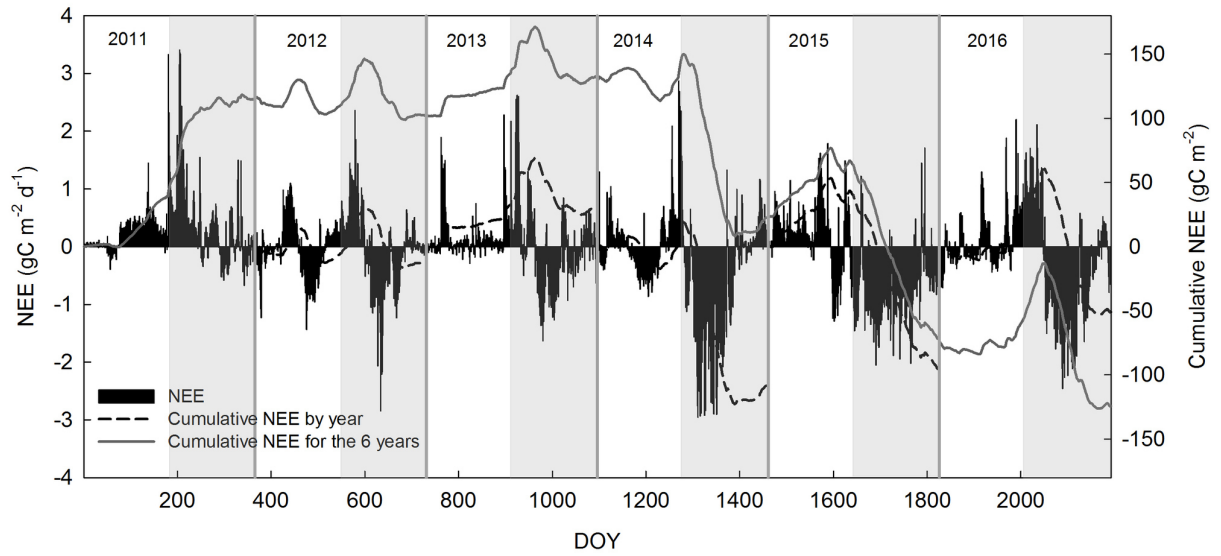
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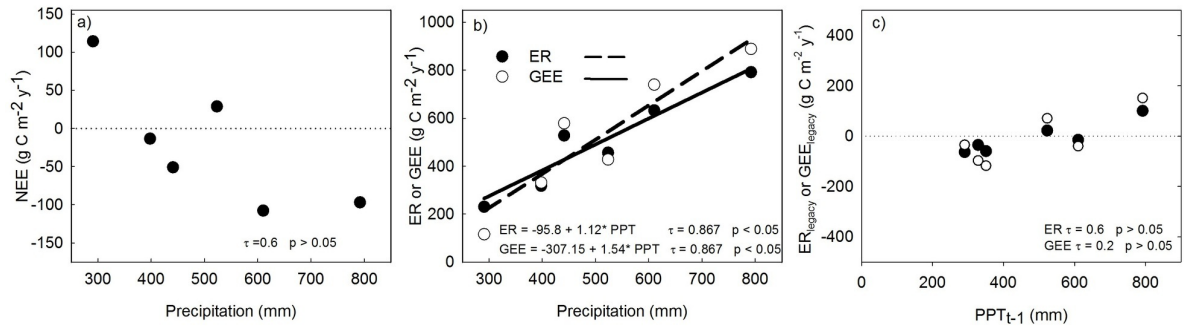
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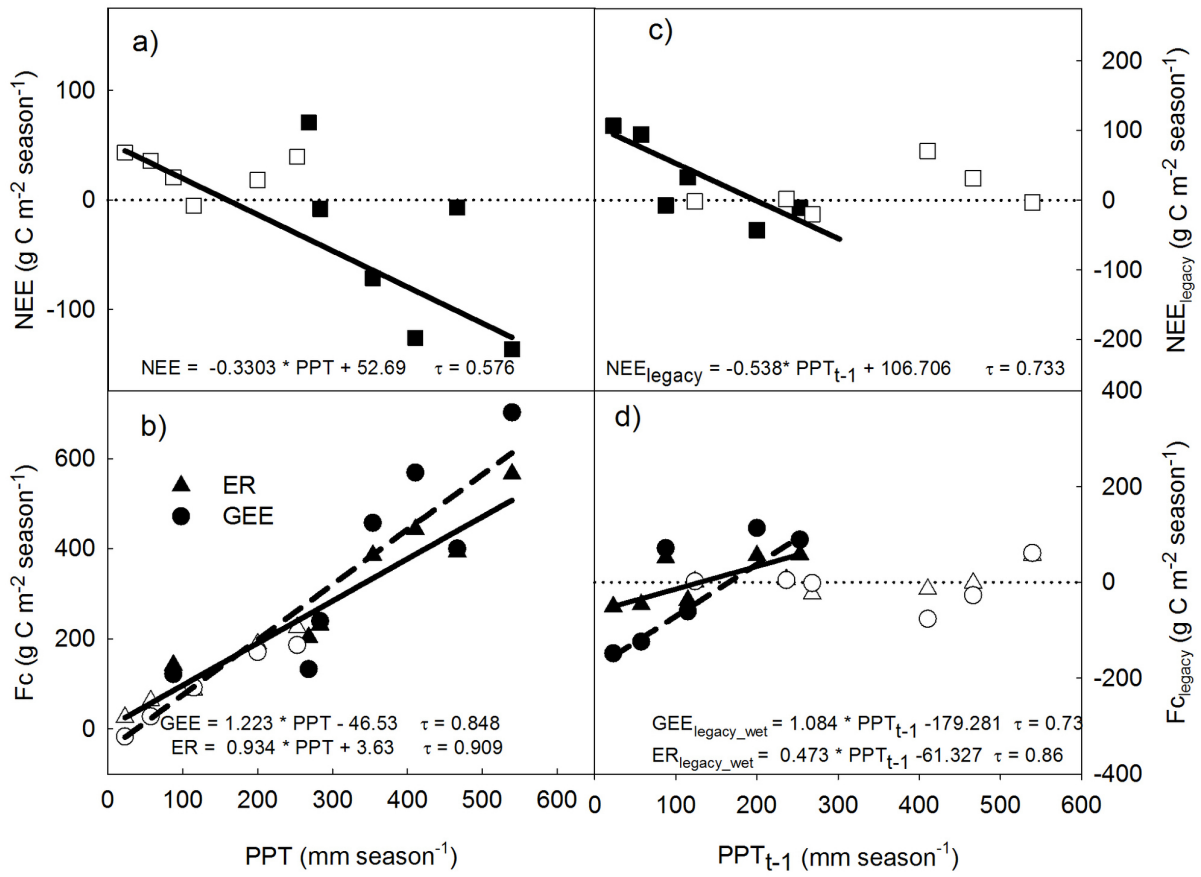
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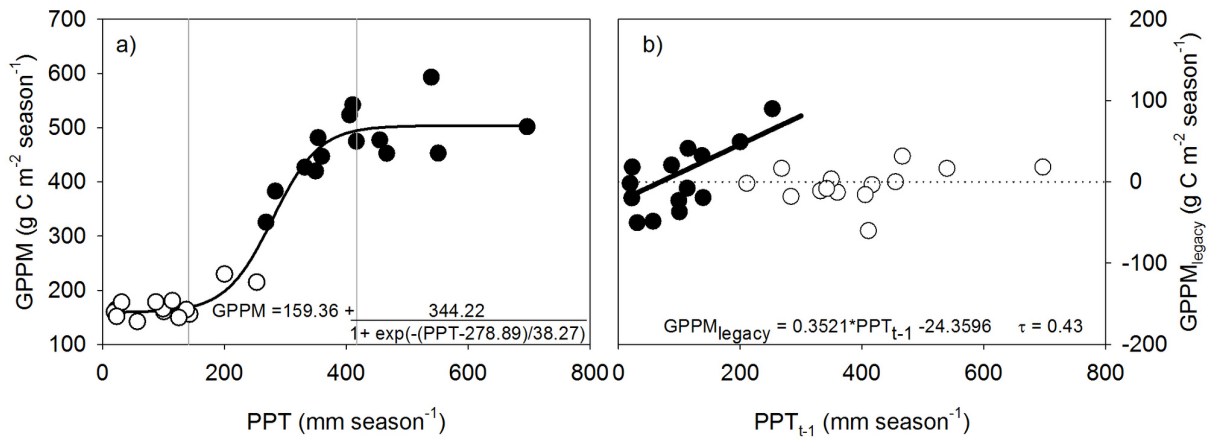
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