ECOHYDROLOGY
Ecohydrol. **7**, 1208–1215 (2014)
Published online 3 December 2013 in Wiley Online Library
(wileyonlinelibrary.com) DOI: 10.1002/eco.1452

Water use efficiency of annual-dominated and bunchgrass-dominated savanna intercanopy space

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ABSTRACT

In semi-arid savannas, dominance of intercanopy space by annual or perennial grasses may alter partitioning of ecosystem water and carbon fluxes and affect ecosystem water use efficiency (WUE_e), the ratio of net ecosystem carbon dioxide exchange (*NEE*) to evapotranspiration (*ET*). To establish if these contrasting growth habits changed controls to WUE_e, we tracked volumetric soil moisture (θ_{25cm}), *ET* and transpiration (*T*), *NEE* and its constituent ecosystem respiration (R_{eco}) and gross ecosystem photosynthesis (*GEP*) fluxes, and community water use efficiency ($WUE_c = GEP : T$) in annual-dominated and bunchgrass-dominated plots in a southern Arizona, United States, savanna. Annual and bunchgrass plots had similar θ_{25cm}, *ET*, and *T*, suggesting the similarity in *ET* was due to higher soil evaporation in annual plots. Seasonal *NEE* was delayed and lower in annual plots compared with that in bunchgrass plots, owing to higher R_{eco} in annual plots. Transpiration, *GEP*, and R_{eco} in both vegetation types increased following late-season rain, indicating similar late-season phenological constraint. WUE_e was lower in annual plots, but with similar WUE_c between plot types. These results suggest that differences in annual plant biomass allocation and plot-level leaf area distribution increased proportional soil evaporation and aboveground R_{eco} contributions, reducing plot-level WUE_e, not lowering plant *WUE* typical of arid-land annuals. Lower plot-level WUE_e suggests that any increase in annual plant dominance would increase interannual variation of productivity in savanna intercanopy spaces, which could enhance the negative effects of predicted higher temperatures, greater aridity, and larger and more widely spaced storms on arid-land watershed processes. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS evapotranspiration; net ecosystem carbon exchange; phenology; photosynthesis; respiration; transpiration

Received 21 February 2013; Revised 23 August 2013; Accepted 22 October 2013

INTRODUCTION

In shrub-dominated and tree-dominated semi-arid savanna systems, the intercanopy is where most hydrological dynamics occur, and shifts in intercanopy vegetation composition and structure have been associated with both positive and negative trajectories in hydrological function, watershed integrity, and ecosystem function (Cammeraat and Imerson, 1999; Huxman *et al*., 2005; Puigdefábregas, 2005). Intercanopy plant productivity also represents a significant proportion of total net annual primary productivity and is the primary resource for these economically important grazing systems (Walker *et al*., 1981; Scholes and Archer, 1997; Scott *et al*., 2009). Climate predictions for the Southwestern United States suggest a trend towards warmer temperatures and lower annual rainfall, but with an increase in larger, more widely spaced precipitation events (Diffenbaugh *et al*., 2005; Seager *et al*., 2007), which may alter savanna structure and function (Holmgren *et al*., 2006). Savanna intercanopy is typically dominated by perennial grasses, but following disturbance, opportunistic annual species may dominate (Scholes and Archer, 1997; Specht, 2000). In arid-land systems, warmer temperature and reduced and more variable precipitation can act as a disturbance (Moran *et al*., 2009; McAuliffe and Hamerlynck, 2010; Scott *et al*., 2010). Annual plants are ‘drought avoiders’ and are well adapted to capitalize on altered climate or disturbance regimes (Smith *et al*., 1997; Guo *et al*., 2002; Kimball *et al*., 2010). Thus, if climate change unfolds as predicted, widespread perennial grass mortality and reduced perennial grass cover observed in the current early 21st-century drought (Pennington and Collins, 2007; Moran *et al*., 2009; Scott *et al*., 2010) may lead to increasingly annual-plant-dominated intercanopy space, which would likely favour further woody plant expansion within Southwest US savannas (Scholes and Archer, 1997).

Community composition is an important determinant of ecosystem-level water use efficiency (WUE_e), the ratio of net ecosystem carbon dioxide exchange to evapotranspiration rate (*NEE* : *ET*). WUE_e integrates biotic and abiotic features

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that couple ecosystem water and carbon cycling, making WUE_e an important metric of ecosystem functional resilience to environmental variability (Emmerich, 2007; Hu *et al.*, 2008; Monson *et al.*, 2010). Better understanding the linkages that establish WUE_e is important, in that the processes shaping intercanopy WUE_e and productivity influence watershed processes such as runoff and erosion (Cammeraat and Imerson, 1999; Puigdefábregas, 2005; Polyakov *et al.*, 2010). However, it is not clear how different WUE_e actually is between annual and perennial plant-dominated intercanopy space.

Compared with perennial grasses, annuals typically have higher leaf-level transpiration and lower stomatal resistance to water vapour loss, supporting high photosynthetic and respiration rates, and resulting in low leaf-level *WUE* (Smith *et al.*, 1997). In addition, annual grasses allocate more to aboveground biomass than perennial species (Holmes and Rice, 1996; Smith *et al.*, 1997; Monaco *et al.*, 2003). This could affect partitioning of *ET* between transpiration (*T*) and soil evaporation (*E*), as well as *NEE* and its constituent fluxes, ecosystem respiration (R_{eco}), and gross ecosystem photosynthesis ($GEP = NEE - R_{eco}$). These studies suggest *T* should proportionally contribute more to *ET* in annual-dominated plots over plant active periods. Indeed, intercanopy space dominated by annuals can have a higher leaf area index (*LAI*) and transpiration (*T*) (Specht, 2000), leading to depleted root zone soil volumetric water content (Holmes and Rice, 1996; Specht, 2000). However, other studies showing greater proportional *T* in annual-dominated areas also had lower *ET* and *LAI* (Prater *et al.*, 2006). More aboveground allocation could result in *GEP* contributing more to *NEE* in annual-plant-dominated intercanopy. However, lower plant cover could increase soil contributions to R_{eco} (Flanagan and Johnson, 2005; Sponseller, 2007). In addition, arid-land annuals also have distinct environmental phenological triggers to seasonal activity, and their rapid life cycle may limit responses to rainfall following germination and establishment (Angert *et al.*, 2007; Kimball *et al.*, 2010; Barron-Gafford *et al.*, 2013), imposing stronger phenological constraints to ecosystem function compared with perennial bunchgrasses. Overall, these findings suggest annual and perennial grasses may distinctly affect intercanopy site water and carbon balance dynamics and WUE_e.

Here, we present a field study of gas exchange dynamics of intercanopy plots dominated by annual and perennial grasses in a Southern Arizona, United States, savanna. We specifically expected annual-dominated plots to have the following:

1. Greater proportional contributions of *T* to *ET* (Specht, 2000; Prater and DeLucia, 2006)
2. An *NEE* that is more sensitive to *GEP* than R_{eco}, as annuals allocate more to aboveground biomass and photosynthetic capacity than perennial grasses (Enloe *et al.*, 2004)
3. Lower WUE_e than that in bunchgrass plots because of lower community water use efficiency ($WUE_c = GEP : T$), consistent with lower leaf-level *WUE* (Smith *et al.*, 1997)

MATERIALS AND METHODS

Field work was conducted at the US Department of Agriculture Agricultural Research Service Southwest Watershed Research Center Santa Rita mesquite savanna site (31·821°N, 110·866°W, elevation: 1120 m above sea level) on the Santa Rita Experimental Range, 45 km south of Tucson, AZ, United States (Scott *et al.*, 2009). Mean precipitation is 377 mm (1937–2007), with most of the growing season coinciding with the North American monsoon starting late June to early July and continuing through September, with sporadic, but often intense, rainfall through October often associated with tropical disturbances (Adams and Comrie, 1997). The site is representative of semidesert grassland conversion to savanna following ~100 years of velvet mesquite expansion (McClaran, 2003). Vegetation consists of a mesquite overstory of ~35% cover and a ground layer of native C_4 grasses and the introduced Lehmann lovegrass (*Eragrostis lehmanniana*), with scattered subshrubs and cacti. Soils are Combate series, well-drained coarse-loamy, mixed, nonacid Ustic Torrifluvents, with poor soil horizon development (Breckenfeld and Robinett, 2003). The site has been protected from grazing since 2007.

Rainfall was measured with a tipping-bucket rain gauge at an eddy-covariance tower located 40 m northwest of the study site. Volumetric soil moisture from 0 to 25 cm (θ_{25cm}) was measured using time domain reflectometry (TDR) probes (TDR-100, Campbell Scientific, Logan, UT). TDR waveguides (30-cm length) were deployed in perennial grass plots in May 2008 and in annual plant plots in April 2009 by inserting probes 60–70° from the horizon into the soil within four 0·75 × 0·75-m^2 annual and four bare soil plots and 12 bunchgrass plots, with probes placed underneath a single grass bunch in bunchgrass plots. Annual plots were dominated by six-weeks needle grama [*Bouteloua aristidoides* (Kunth) Griseb.], with infrequent Arizona poppy (*Kallstroemia grandiflora* Torr. Ex A. Gray), carpetweed (*Mollugo verticella* L.), chinchweed (*Pectis papposa* Harv. & A. Gray), and wooly tidestromia [*Tidestromia lanuginosa* (Nutt.) Standl.]. Perennial grass plots contained one or two individuals of either Lehmann lovegrass (*E. lehmanniana* Nees.), bush muhly (*Muhlenbergia porteri* Scribn. ex Beal), or Arizona cottontop [*Digitaria californica* (Benth.) Henr.]. Plots were selected from typical open intercanopy locations, and in bare soil plots in close proximity (around 1–1·5 m) to vegetated plots, whose dimensions matched the ecosystem gas exchange chamber (described later). Waveforms were generated every 30 min and converted to volumetric water content ($cm^3\,cm^{-3}$). Annual plants were removed regularly from bare soil and perennial grass plots to insure clear bare soil or perennial grass signals. To see if annual or perennial plant dominance affected soil water dynamics, e-folding times for θ_{25cm} were generated for dry-downs following each measureable precipitation event occurring when annual and perennial plants were active. Daily values of θ_{25cm} for each interstorm period were normalized by dividing the maximum daily value by that occurring the first day following the storm. Nonlinear regressions of exponential decay ($y = a\mathrm{e}^{-b^*X}$; SigmaPlot v10.0, SPSS, Chicago, IL) were generated for θ_{25cm} pooled for all four sampling plots for each storm. E-folding times were calculated as $1/b$ and show how many days it takes θ_{25cm} to reduce to 37% of maximum starting values.

Mid-morning (8:00–10:00 h Mountain Standard Time) whole-plant-and-soil (i.e. 'ecosystem') water vapour and carbon dioxide fluxes were measured every 2 weeks in bunchgrass plots from 2 August to 9 November and every week from 31 August to 22 October 2010 for annual plots. Prior to the 31 August sampling, there was no evident germination in the annual plots during the previous ongoing perennial grass monitoring (personal observation). Ecosystem fluxes were estimated by measuring changes in CO_2 and H_2O concentration with an open-path gas analyser (Li-7500, LiCOR, Lincoln, NE) following enclosure of the plot with a 0·75 × 0·75 × 0·75-m (0·422-m^3) chamber of tightly sewn polyethylene (Shelter Systems, Santa Cruz, CA) held taut within a tent frame of polyvinyl chloride pipe. The chamber material allowed 92% of photosynthetically active radiation to pass into the plots, while allowing infrared radiation to escape (Potts *et al*., 2006). A fan insured atmospheric mixing after enclosure and adequate sealing of the chamber base to the ground surface with a chain. Chamber air was mixed for 30 s prior to flux measurements, with concentrations logged every second for at least 90 s. The chamber was then removed, aerated for 0·5 min, re-placed over the plot, sealed, and shaded with a blanket to repeat measurements in the dark. All ambient-light measurements were made in saturating photosynthetic photon flux densities, measured with a LiCOR 190 quantum sensor (LiCOR) at an eddy covariance tower located ~100 m north-northwest of the study site. Ambient-light fluxes allowed estimation of net ecosystem carbon exchange (*NEE*) and evapotranspiration (*ET*), with negative *NEE* values indicating carbon dioxide uptake and positive values indicating carbon efflux. Dark measures gave ecosystem respiration (R_{eco}) and, by calculation, gross ecosystem photosynthesis [$GEP = -1 * (NEE + R_{eco})$]. Measurements on nearby bare soil plots were made to determine soil evaporation (E) to estimate transpiration ($T = ET - T$).

A split-plot, repeated-measures analysis of variance (STATISTIX v. 8.0, Analytical Software, Tallahassee, FL) was used to test for seasonal differences in leaf-level and whole-plant-level gas exchange of annual and perennial grass plots. The between-treatment, whole-plot effect was cover type (annual or bunchgrass; $n = 4$), using the type-by-replicate interaction as the whole-plot error term to test for differences pooled across all dates, with an associated α of 0·05. Because more bunchgrass plots were sampled ($n = 12$ vs $n = 4$ for annuals), bunchgrass replicates were obtained by pooling across individual species replicates (i.e. first bunchgrass replicate 1 = mean of the first replicate of Lehmann's lovegrass, bush muhly, and Arizona cottontop plots). Within-treatment, subplot effects were sampling date ($n = 6$) and type-by-time interaction, using the type-by-time-by-replicate interaction as the F-test error term. General linear contrasts (Scheffe's F) were used to test for specific contrasts underlying any significant type-by-time interaction. Slopes and intercepts of linear regressions of annual-dominated and bunchgrass-dominated plots were compared to determine R_{eco} and GEP controls to NEE and to estimate and compare WUE_e and WUE_c of annual and bunchgrass plots, using an F-test to statistically compare slopes and intercepts (linear regression, STATISTIX v. 8.0). To see if NEE within annual or perennial plots responded more to changes in GEP or R_{eco}, we compared slopes of $NEE:GEP$ and $NEE:R_{eco}$ within each plot type, using Tukey's test (honestly significant difference, HSD), with an HSD exceeding 3·79 considered significant ($p \leq 0{\cdot}05$; Zar, 1974).

RESULTS

Volumetric soil moisture (θ_{25cm}) was similar between annual and bunchgrass plots (Figure 1). Soil drying rates, as estimated by e-folding times, were similar between annual and perennial plots for the six dry-down periods where both functional types were active, and both types of vegetated plots usually had faster dry-down rates in bare soil plots (Figure 1). Net ecosystem carbon dioxide exchange (*NEE*) was significantly more negative in bunchgrass plots [$-1{\cdot}64\ \mu mol\ m^{-2}\ s^{-1} \pm 0{\cdot}295$ standard error (SE)] compared with annual plots ($-0{\cdot}84\ \mu mol\ m^{-2}\ s^{-1} \pm 0{\cdot}183$ SE) pooled across the study period, with a significant type-by-time interaction (Table I). Initially, *NEE* was more negative in bunchgrass plots (Scheffe's $F = 6{\cdot}16$; $p \leq 0{\cdot}001$) and then was similar to annual plot *NEE* over the first prolonged dry period (14 and 29 Sept; Scheffe's $F = 0{\cdot}06$; $p = 0{\cdot}99$). Across the remaining sampling periods, *NEE* was more negative in bunchgrass plots (Scheffe's $F = 5{\cdot}78$; $p < 0{\cdot}001$), especially following the last rain of the season (11–24 Oct; Figure 1).

Consistent with θ_{25cm}, evapotranspiration (*ET*) and transpiration (*T*) fluxes were statistically indistinguishable between annual and bunchgrass plots (Table I and Figure 2). However, the relative contributions of T to ET differed between plots, with bunchgrass plots having

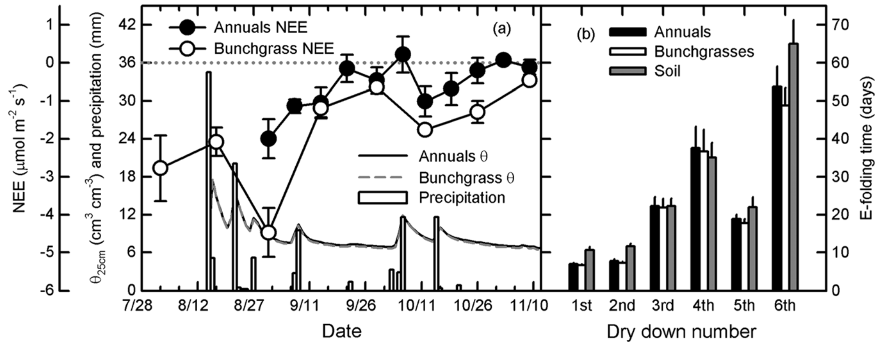

Figure 1. The 2010 monsoon season (a) net ecosystem carbon dioxide exchange (*NEE*), precipitation, soil volumetric water content across 25-cm soil depths (θ_{25cm}) of annual-dominated and bunchgrass-dominated plots; dotted line indicates *NEE* = 0. (b) E-folding times over six soil dry-downs when annuals and bunchgrasses were active. Error bars are ±1 standard error from the nonlinear regression fitted to determine poststorm e-folding dry-down rates.

Table I. Repeated-measures analysis of variance *F*-test results comparing seasonal water and carbon exchanges of annual and perennial bunchgrass-dominated plots.

Variable	$Plot_{(1,6)}$	$Date_{(5,28)}$	$Plot \times date_{(5,28)}$
ET	$0{\cdot}01^{ns}$	90·21**	$1{\cdot}06^{ns}$
T	$0{\cdot}19^{ns}$	44·15**	$1{\cdot}19^{ns}$
% *T* to *ET*	7·48*	40·18**	19·19**
GEP	$0{\cdot}70^{ns}$	135·40**	$0{\cdot}81^{ns}$
R_{eco}	$4{\cdot}48^{ns}$	129·38**	4·51**
NEE	8·08*	46·55**	5·18**

Degrees of freedom are presented parenthetically.
NS, nonsignificant.
F-test results significant at $*p \leq 0{\cdot}05$ and $**p \leq 0{\cdot}01$.

higher *T* contributions (67% ± 1·7 SE) than in annual plots (56% ± 4·4 SE), with a significant type-by-time interaction (Table I). This is due to similar *T* contributions over the first four sampling periods (Scheffe's $F = 0{\cdot}01$; $p = 0{\cdot}999$), followed by significantly lower *T* contributions in annual plots later in the season (Scheffe's $F = 12{\cdot}16$; $p \leq 0{\cdot}001$), when soil drying was more pronounced (Figure 1), whereas *T* : *ET* remained consistent in bunchgrass plots (Figure 2).

Gross ecosystem photosynthesis (*GEP*) did not significantly differ between annual-dominated and bunchgrass-dominated plots pooled across the study, with no type-by-time interaction (Table I), despite some sampling periods with higher *GEP* in bunchgrass plots (Figure 3). Ecosystem respiration (R_{eco}) was higher in annual plots pooled across the study ($2{\cdot}40\ \mu mol\ m^{-2}\ s^{-1} \pm 0{\cdot}421$ SE) compared with that in bunchgrass plots ($1{\cdot}99\ \mu mol\ m^{-2}\ s^{-1} \pm 0{\cdot}291$ SE), but this was not statistically significant at $p \leq 0{\cdot}05$ ($p = 0{\cdot}078$; Table I). R_{eco} did show a significant type-by-time interaction, likely owing to much higher R_{eco} in annual plots on the first sampling date (Scheffe's $F = 6{\cdot}81$; $p \leq 0{\cdot}001$), after which declining R_{eco} was similar between annual and bunchgrass plots (Figure 3). Both annual and bunchgrass plots attained similar *GEP* and R_{eco} after the first long dry-down (third period; Figure 3), and both responded positively to rain and remained at fairly high levels for 4 weeks following the rain that broke this dry spell (Figure 1).

Overall, *GEP* explained more of variation in *NEE* than R_{eco} pooled across plots (Table II). In annual plots, *GEP* was a considerably stronger predictor of *NEE*, explaining ~19% more variation in *NEE* than R_{eco} (Figure 4 and Table II). In bunchgrass plots, R_{eco} and *GEP* were strong predictors of *NEE*. Slopes and intercepts of *NEE* versus R_{eco} and *GEP* were lower in annual than in bunchgrass plots (Table II). However, *NEE* did not change proportionally more with *GEP* or R_{eco} in annual plots (Tukey $HSD = 0{\cdot}49$), whereas *NEE* changed more in response to R_{eco} than *GEP* in bunchgrass plots (Tukey $HSD = 5{\cdot}75$). WUE_e (*NEE* : *ET*) was higher in bunchgrass plots (Figure 5), with significantly greater slopes than in annual plots (Table II). In contrast, WUE_c (*GEP* : *T*) was identical between annual and bunchgrass plots (Table II and Figure 5).

DISCUSSION

Unlike other studies that found reduced soil water content under annual dominance (Holmes and Rice, 1996; Specht, 2000; Booth *et al*., 2003; Enloe *et al*., 2004; Ogle *et al*., 2004), our study found that root zone soil moisture (θ_{25cm}) did not differ between annual-dominated and bunchgrass-dominated plots and showed similar dry-down characteristics (Figure 1). In addition, annual and bunchgrass plots had similar *ET* and *T* (Figure 2). Annual plots did not show greater proportional *T* contributions to *ET*, contrary to our hypothesis, but these differences varied through the study (Table I). When θ_{25cm} was high earlier in the study period (Figure 1), *T* : *ET* was similar between annual and bunchgrass plots (Figure 2). These indicate that when perennial and annual grass activity was high, controls to intercanopy water balance were consistent between annual-dominated and bunchgrass-dominated plots, suggesting that ecological processes tied to water balance may not be strongly affected by community composition during these periods. But, as soil drying

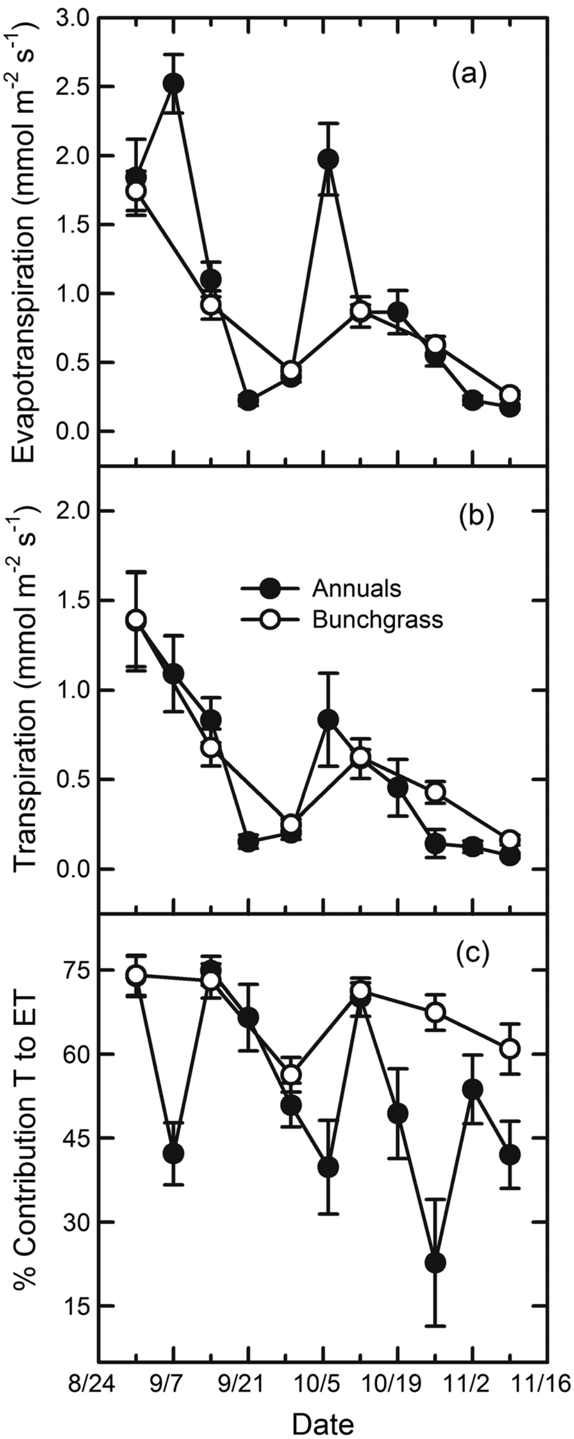

Figure 2. (a) Evapotranspiration, (b) transpiration, and (c) per cent contribution of *T* to *ET* of annual-dominated and bunchgrass-dominated plots over the course of the 2010 summer growing season. Each point is the mean of four measurements, error bars are ±1 standard error.

progressed, *T* contributed proportionally less to *ET* in annual plots compared with bunchgrass plots (Figure 2). This indicates that the similar *ET* between our plots under more water-limited conditions was due to higher soil *E* in annual

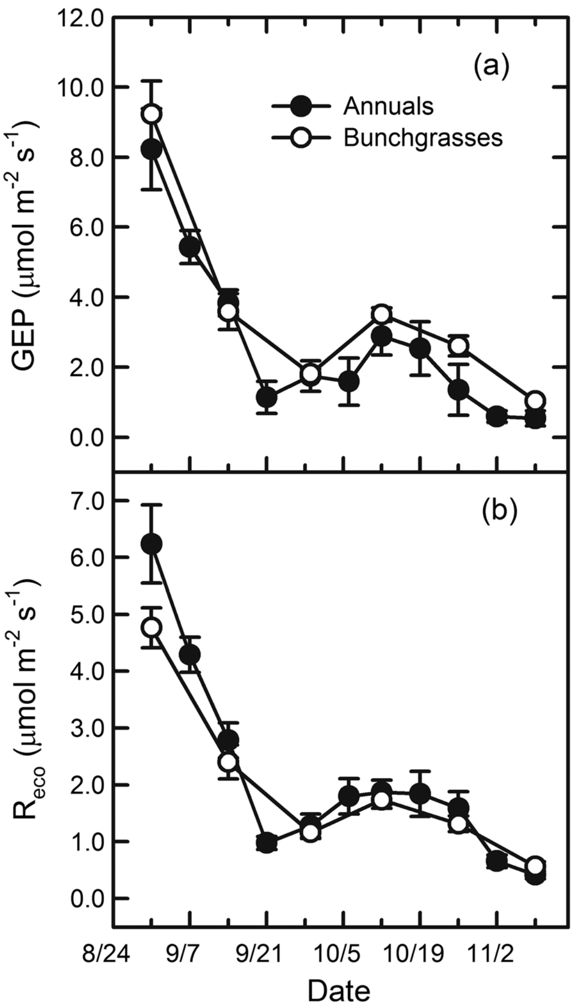

Figure 3. (a) Gross ecosystem photosynthesis (*GEP*) and (b) ecosystem respiration (R_{eco}) of annual-dominated and bunchgrass-dominated plots over the 2010 summer growing season. Each point is the mean of four measurements, error bars are ±1 standard error.

Table II. Coefficients of determination (R^2) and slopes and intercepts of linear regressions fit to *NEE* and R_{eco} and *GEP*, and ecosystem (*NEE* : *ET*) and community-level water use efficiency (*GEP* : *T*) of annual-dominated and bunchgrass-dominated plots.

Relationship	R^2	Comparison	Annual	Bunchgrass
$NEE : R_{eco}$	0·54	Slope	**−0·37**	**−0·93***
		Intercept	**$6{\cdot}04 \times 10^{-4}$**	**0·21**
NEE : *GEP*	0·83	Slope	**−0·30**	**−0·50***
		Intercept	**0·08**	**0·19**
NEE : *ET*	0·61	Slope	**−1·14**	**−2·71**
		Intercept	**−0·11**	**−0·56**
GEP : *T*	0·86	Slope	5·04	5·83
		Intercept	0·47	0·20

Reported R^2 are significant at $p \leq 0{\cdot}05$; significant differences between slopes or intercepts of annual and bunchgrass plots are highlighted in bold ($p \leq 0{\cdot}05$).
*Significantly different slopes between $NEE : R_{eco}$ and *NEE* : *GEP* within a plot type (Tukey *HSD*; $p \leq 0{\cdot}05$).

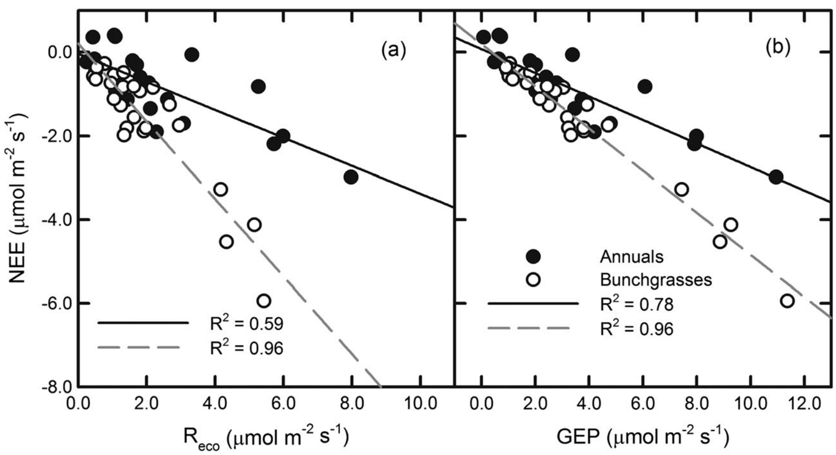

Figure 4. Relationship of net ecosystem carbon dioxide exchange (*NEE*) and (a) ecosystem respiration and (b) gross ecosystem photosynthesis in annual and perennial bunchgrass-dominated plots. All fitted regressions are significant at $p \leq 0{\cdot}05$.

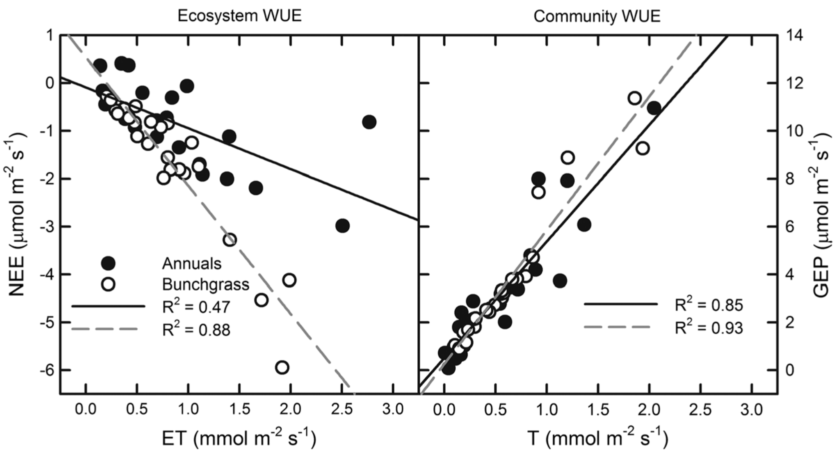

Figure 5. Linear regression determined ecosystem-level (*NEE* : *ET*) and community-level (*GEP* : *T*) water use efficiency of annual-dominated and bunchgrass-dominated plots. All fitted regressions are significant at $p \leq 0{\cdot}05$.

plots. Altered *ET* partitioning can have cascading effects that can affect ecosystem nutrient dynamics, primarily by altering surface soil moisture (Holmes and Rice, 1996; Prater *et al*., 2006). Our findings suggest that any consequences of shifts in *ET* partitioning associated with altered community composition will likely be more pronounced when water limitations are more pronounced, not when water is more available, as found in studies from other arid-land systems (Holmes and Rice, 1996; Specht, 2000; Prater *et al*., 2006).

The *NEE* dynamics were consistent with changes in *T* : *ET* with similar *NEE* in perennial grass and annual grass plots when soil moisture was not limiting and then higher in perennial grass plots when soil moisture declined later in the study, leading to overall higher *NEE* in bunchgrass plots (Figure 1). Initially, less negative *NEE* (i.e. lower net carbon uptake) in annual plots was due to markedly higher R_{eco}, as seen in perennial grass plots after the first significant summer rain (Potts *et al*., 2006; Hamerlynck *et al*., 2010). Such 'respiratory bursts' have been associated with stimulation of microbial activity, as roots respond more slowly to rewetting (Jarvis *et al*., 2007). However, both types of plot had been exposed to several strong wetting and drying cycles prior to the onset of annual plant activity (Figure 1). Thus, it seems unlikely that microbial activity drove the observed high initial R_{eco} in annual plots, although it may be that previous wet/dry cycles resulted in different microbial community structure, which can affect R_{eco} (Schimel *et al*., 2007; Sponseller 2007). More likely, the high initial R_{eco} in annual plots is a result of rapid plant growth over the week following the rain that triggered development (Flanagan and Johnson, 2005).

Surprisingly, *GEP* and *T* did not significantly differ between annual and bunchgrass plots (Figures 3 and 2, respectively). It may be that higher leaf-level *T* and photosynthesis typical of desert annual plants (Smith *et al*., 1997) may have offset lower plot-level *LAI*. Or it may be that *LAI* and photosynthetic gas exchange rates were similar between annual and perennial grass plots. If so, the higher initial R_{eco} in annual plots may be due to these plants having younger tissue with limited exposure to water stress, which may have affected bunchgrass physiological capacity (Constable and Rawson, 1980; Flanagan *et al*., 2002). Visually, annual plots appeared to have a lower *LAI* than bunchgrass plots, favouring higher leaf-level gas exchange in annual plots in maintaining similar plot-level *T* and *GEP* between plot types. But, as bunchgrass plots had leaf area concentrated within discrete canopies, and leaf area was more diffusely spread in annual plots, we cannot fully ascertain if visual differences were quantitatively different. Concurrent quantification of plot-level *LAI* and leaf-level gas exchange would be needed to fully discriminate between these two processes in determining plot-level carbon and water flux.

After the last rain of the season, *T*:*ET* (Figure 2c) and R_{eco} and *GEP* tended to be lower in annual plots than in bunchgrass plot levels (Figure 3). These might reflect physiological downregulation in annual plants as they entered the grain filling and senescence portion of their life cycle, indicative of a stronger phenological constraint to fluxes in annual plots. However, prior to this late-season rain, annual grass plots showed a remarkably similar ability to upregulate flux activity as bunchgrasses in *NEE* (Figure 1), *T* (Figure 2), and R_{eco} and *GEP* (Figure 3) following rainfall events. This suggests that the *NEE* in annual plots following the last rainfall is more likely due to plant mortality and loss of active leaf area in the dry spell preceding this rain, rather than completion of plant life cycles.

As expected, *GEP* was a better predictor of *NEE* than R_{eco}, especially in annual-dominated plots (Figure 4). Annual plants are known to allocate more to aboveground biomass and photosynthetic capacity than perennials (Smith *et al*., 1997; Monaco *et al*., 2003). Although *NEE* had a strong relationship with *GEP* in annual plots, annual plot *NEE* responded similarly to *GEP* and R_{eco}, contrary to our expectations (Table II). It may be that aboveground respiration dominates R_{eco}, leading to a more even response of *NEE* to *GEP* and R_{eco} (Figure 4). In contrast, although similar in strength, bunchgrass *NEE* responded more strongly to R_{eco} than *GEP* (Table I and Figure 4). This likely follows greater contributions of root respiration, the primary component of R_{eco} in most grassland systems (Knapp *et al*., 1998; Flanagan *et al*., 2002), although greater allocation to belowground biomass also supports more extensive heterotrophic soil biota activity (Sponseller, 2007).

As expected, WUE_e was lower in annual plots than in bunchgrass plots, but this was not due to lower community water use efficiency (Figure 5b), contrary to our expectations. As mentioned previously, bunchgrass plots have leaf area concentrated into distinct individual canopies, whereas in annual-dominated plots, leaf area is diffused throughout the plot, likely resulting in a more open plot-level canopy. These structural differences could very likely alter the relative contributions of soil evaporation, especially when water became more limiting (Figure 2c), thereby affecting *NEE*:*ET* (Figure 5a). In addition, lower *NEE* in annual plots earlier in the study when more water was available was due to higher R_{eco} (Figure 3). This higher R_{eco} could reflect rapid aboveground growth rates early in the study (Flanagan and Johnson, 2005) when *ET* was also high (Figure 2). These findings are consistent with those showing variation in the physical structure and distribution of belowground and aboveground biomass as critical to controls of material and energy exchange within and between ecological systems (Prater *et al*., 2006; Hu *et al*., 2008; Moran *et al*., 2009; Monson *et al*., 2010).

In conclusion, we found it remarkable that although overall rates and rainfall responses of *ET* and *T* (Figure 2), R_{eco} and *GEP* (Figure 3), and WUE_c (Figure 5) did not differ dramatically between annual and bunchgrass plots, the net effects of relatively small differences in these resulted in lower *NEE* (Figure 1) and reduced WUE_e (Figure 5). The lower *NEE* and WUE_e observed in our study indicate that annual plant dominance could result in a less ‘buffered’ system, with the potential for lower productivity in the intercanopy being tightly coupled to intraseasonal rainfall dynamics. In our case, lower annual plot WUE_e (Figure 5) was linked to higher soil evaporation over longer dry periods (Figure 2c). This suggests growing seasons with similar total rainfall amounts, but different rainfall distributions, could have greater variation and lower productivity than would occur under perennial bunchgrass dominance. This, in addition to periods of low cover when annuals are dormant as seeds, could accelerate woody plant encroachment (Scholes and Archer, 1997), affecting ecosystem ecohydrological function (Huxman *et al*., 2005) and watershed surface processes (Polyakov *et al*., 2010) under the warmer temperatures and lower and more variable summer rainfall regimes predicted for this region (Seager *et al*., 2007).

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