Consequences of Cool-Season Drought-Induced Plant Mortality to Chihuahuan Desert Grassland Ecosystem and Soil Respiration Dynamics

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ABSTRACT

Predicted reductions of cool-season rainfall may expand and accelerate drought-induced plant mortality currently unfolding across the Southwest US. To assess how repeated plant mortality affects ecosystem functional attributes, we quantified net ecosystem CO_2 exchange (NEE), ecosystem respiration (R_{eco}), and gross ecosystem photosynthesis (GEP) responses to precipitation (P) at a semidesert grassland over spring (Feb 1–Apr 30) and summer (June 15–Oct 1) plant-active periods across eight years, including two with distinct patterns of extensive species-specific mortality. In addition, we quantified daily soil respiration (R_{soil}) in high- (56–88%) and low-mortality (8–27%) plots the summer following the most recent mortality event. Plant mortality coincided with severely dry cool-season conditions (Dec 1–Apr 30). We found a positive relationship between springtime P and GEP, and that springtime conditions influenced GEP response to summer rainfall. High springtime R_{eco}/GEP ratios followed plant mortality, suggesting increased available carbon after mortality was rapidly decomposed. R_{soil} in low-mortality plots exceeded high-mortality plots over drier summer periods, likely from more root respiration. However, total cumulative R_{soil} did not differ between plots, as variation in surviving plant conditions resulted in high and low C-yielding plots within both plot types. Vegetation status in high C-yielding R_{soil} plots was similar to that across the grassland, suggesting R_{soil} from such areas underlay higher R_{eco}. This, coupled to springtime drought constraints to GEP, resulted in positive NEE under summer P accumulations that previously supported C-sink activity. These findings indicate that predicted lower cool-season precipitation may strongly and negatively affect summer season productivity in these semiarid grasslands.

Key words: climate change; ecosystem respiration; gross ecosystem photosynthesis; net ecosystem carbon dioxide exchange; seasonal precipitation; soil moisture; southern oscillation/El Niño.

INTRODUCTION

Southwestern North America is predicted to become increasingly arid, and is especially expected to experience warmer and drier cool-season (that

is, winter and spring) conditions (Christensen and Hewitson 2007; Seager and others 2007; McAfee and Russell 2008). Severe drought across the southwestern US over the last decade has induced region-wide pulses of plant mortality, even in ecosystems with typically low cool-season rainfall (Pennington and Collins 2007; Breshears and others 2009; McAuliffe and Hamerlynck 2010). Warmer cool-season temperatures are expected to be concurrent with fewer severe cold events across the western US (Diffenbach and others 2005). Warm minimum temperatures shorten critical plant ''cold-hardening'' periods, and can increase effects of extreme cold and cool-season drought (Lambrecht and others 2007). Given that many southwestern North American plant species are of sub-tropical origin, rising minimum temperatures could exacerbate the effects of infrequent extreme cold during cool-season drought (Smith and others 1997; Pockman and Sperry 1997; McDowell and others 2008; though see Mederios and Pockman 2011).

Cool-season climate dynamics play an important role in determining the structure and function of aridland ecosystems. The low intensity, long duration, and large areal extent of cool-season rains, coupled to cooler temperatures and lower soil evaporation, make these rains important in recharging deep soil water (Scott and others 2000; Seyfried and others 2005). This soil water is a critical resource needed to support plant springtime activity (Hamerlynck and others 2012b), and also to survive the 2–3 months of hot, dry late-spring conditions typically preceding summer rains associated with the North American monsoon (Neilson 1987; Adams and Comrie 1997; McAfee and Russell 2008).

Soil respiration is a critical component of aridland ecosystem carbon balance, and is regulated by decomposition of soil organic matter, photosynthate supply to soil biota, and direct root respiration (Knapp and others 1998; Flanagan and others 2002; Frank and others 2002; Pendall and others 2003; Tang and others 2005; Baldocchi and others 2006; Fernandez and others 2006; Sponseller 2007; Fay and others 2008; Cable and others 2008, 2011; Liu and others 2009; Barron-Gafford and others 2011; Thomey and others 2011). Drought induces whole-plant death and partial canopy dieback (McAuliffe and Hamerlynck 2010), both of which could affect soil respiration rates. Whole-plant mortality could increase total carbon available for decomposition, which suggested to underlie increased ecosystem respiratory fluxes observed in semiarid savannas following drought (Scott and

others 2009). However, aridland rainfall regimes are highly ''pulsed,'' with pronounced interstorm dry periods (Loik and others 2004) and plant roots sustain respiration under drier soil moisture conditions that limit microbial activity (Sponseller 2007; Cable and others 2008). Root activity in areas of low-mortality areas might lead to higher respiratory rates and greater cumulative soil CO_2 efflux compared to high-mortality areas because root respiration would continue under drier soil conditions (Flanagan and others 2002; Pendall and others 2003; Baldocchi and others 2006; Cable and others 2008). Also, plant mortality could open soil volumes for rooting of surviving plants. If so, surviving plant canopy condition (that is, degree of dieback) could affect soil respiratory efflux, which can co-vary with plant canopy development (Flanagan and Johnson 2005; Tang and others 2005; Baldocchi and others 2006). Thus, understanding how these distinct aspects of plant mortality affect soil CO_2 efflux could improve understanding of aridland carbon dynamics under future conditions.

Here, we present a study of interannual ecosystem gas exchange in a SE Arizona semidesert grassland watershed that recently experienced two severe plant mortality events. The first occurred in 2006 following several years of protracted drought and higher than average seasonal temperatures, after which the invasive South African bunchgrass, Lehmann lovegrass (*Eragrostis lehmanniana* Nees.) spread and became dominant (Moran and others 2009; Scott and others 2010). The second occurred in 2011, following cool-season drought combined with a severe freeze event that elicited widespread mortality of the exotic bunchgrass. This second event gave us the opportunity to better generalize basic ecosystem functional relationships of desert grasslands in response to drought-induced mortality. Such repeated observations are highly important, given the frequency and severity of drought, especially cool-season drought, is predicted to increase in the future (Christensen and Hewitson 2007; Seager and others 2007; McAfee and Russell 2008). Specifically, we expected drought to result in positive net ecosystem carbon dioxide exchange (NEE), indicating this grassland is acting as a carbon source; higher ecosystem respiration (R_{eco}) compared to gross ecosystem photosynthesis (GEP) has been observed following drought in aridland systems (Scott and others 2009, 2010). Our previous research at this site (Scott and others 2010) did not specifically quantify the sensitivity of NEE constituents R_{eco} and GEP to inter-seasonal variation in precipitation, an important feature in

aridland ecosystem function and resilience (Scott and others 2012). To address this omission, we delineated each observational year into spring and summer periods to determine when the constituent parts of NEE responded most strongly to inter-seasonal precipitation. In addition, we quantified watershed-level plant mortality and canopy die-back, and monitored daily soil respiration (R_{soil}), soil temperature (T_{soil}), and volumetric soil water content (θ) in high- and low-mortality plots over the summer growing season following the most recent plant mortality event. We expected daily and seasonal cumulative R_{soil} in high-mortality plots to be higher, consistent with higher ecosystem respiration. Our results will yield fundamental insight into the effects of climate variation on ecosystem structure and carbon processes in these dynamic, water-limited grasslands.

MATERIALS AND METHODS

Study Site and Climate Conditions

This study was conducted at the Kendall Grassland, in Watershed 112 (109°56′28″W, 31°44′10″N, 1526 m asl) on the Walnut Gulch Experimental Watershed (WGEW), and located approximately 11 km east of Tombstone, Arizona, USA. Kendall Grassland is a typical semidesert grassland, with most annual productivity occurring during the summer monsoon, typically from mid-June through September (Cable 1975), though monsoon rains can be delayed to as late as mid-July, and can continue through October (Adams and Comrie 1997). Desert grasslands can also sustain significant springtime productivity, mainly from February to April, if sufficient rain occurs prior to and during this period (Cable 1975; Scott and others 2010). Historically, Kendall Grassland was dominated by black grama (*Bouteloua eripoides*), side-oats grama (*B. centruipoides*), hairly grama (*B. hirstuta*), tangle-head (*Heteropogon contorta*), and curly mesquite (*Hilaria berlangi*). Following protracted drought between 2000 and 2006, these native grasses experienced extensive mortality and were replaced by the invasive South African grass, Lehmann lovegrass, which invaded in 2006 and became dominant in 2007 (Scott and others 2010).

Mean annual precipitation at Kendall Grassland is 345 mm (1964–2009), with 63% of this coming in the summer months of June–September with the annual recurrence of the North American monsoon (Adams and Comrie 1997; Scott and others 2010). Mean annual temperature is 17.4°C, with summertime highs of approximately 37°C and average monthly minimum wintertime temperature of 3°C (Scott and others 2010). We used half-hourly air temperature data from a fully instrumented weather station established at Kendall Grassland in 1990 (KenMET; Keefer and others 2008) to provide context to the February 2011 freeze event. All observations and associated metadata for this station are available at: ftp://www-ftp.tucson.ars.ag.gov/metDAP/.

We used 1956–2011 monthly precipitation data from rain gauge #60, located 0.5 km NNW of the Kendall eddy covariance (EC) site, to calculate the standardized precipitation index (SPI; McKee and others 1993). This gauge was chosen as it included data from drought conditions in the 1950s and 1970s to provide deeper historical context for recent drought conditions. SPI renders a normalized index, with SPI of zero indicating normal rainfall, and positive and negative SPI, respectively, indicating above- and below-normal precipitation over any time period of interest (McKee and others 1993). We calculated SPI for three specific time spans: (i) April 5-month SPI (Dec 1–April 30), hereafter referred to as *cool-season*, which combines winter (Dec–Feb) and spring (Feb–April) rainfall, (ii) April 3-month SPI (Feb 1–April 30), hereafter referred to as *spring*, the timeframe within which the grassland may have sustained (ca. 4–10 weeks) GEP (Scott and others 2010), and (iii) September 3-month SPI (July 1–Sept 30), hereafter referred to as *summer*, which covers the 3 months receiving the bulk of summer precipitation in the Southwest US during the North American monsoon (Sheppard and others 2002). We used NOAA Climatic Data Center standard SPI range designations for normal (SPI 0 to ±0.5), abnormal (±0.51 to ±0.79), moderate (±0.8 to ±1.29), severe (±1.3 to ±1.59), extreme (±1.6 to ±1.99), or exceptional conditions (SPI exceeding ±2.00; http://www.ncdc.noaa.gov/oa/climate/research/prelim/drought/spi.html).

Ecosystem Gas Exchange

We have measured hydrometerological variables and carbon dioxide and water vapor fluxes using the EC technique continuously since May 2004 at this site. Details of EC instrumentation and flux data are presented in Scott and others (2010). We have recently discovered a specific instrumental bias in the sensitivity of the particular open-path infrared gas analyzer (IRGA) using side-by-side tests with other open-path and closed-path IRGAs. To correct this bias, we multiplied 30-min vertical wind and CO_2 density covariances with a 0.94 correction factor (Scott and others, unpublished).

We partitioned NEE ($\pm$mol m^{-2} s^{-1}) into eco-system photosynthesis (gross ecosystem production: GEP) and ecosystem respiration (R_{eco}). We determined 30-min average R_{eco} by fitting an exponential function of air temperature to night-time NEE data over a moving approximately 5-day window (Reichstein and others 2005). Window size was varied to ensure that data from pre-storm (dry) periods were not grouped together with data following storms. This model was then used to fill missing nighttime NEE data and model daytime respiration. Missing daytime NEE values (ca. 22% of daytime 30-min period) were filled using a sec-ond-order polynomial of incoming PAR fit to morning or afternoon NEE data on a 5-day moving window basis, which better fits NEE to PAR than commonly used higher order light response models (Lasslop and others 2010). GEP was calculated as GEP = R_{eco} − NEE. We used the standard sign convention for NEE with NEE greater than 0 indi-cating a net loss of CO_2 to the atmosphere (source) and NEE less than 0 indicating CO_2 uptake by the ecosystem (sink). R_{eco} and GEP are always positive. For this study, we calculated cumulative P, NEE, GEP, and R_{eco}, and the ratio of cumulative R_{eco} and GEP (R_{eco}/GEP) over spring (Feb 1–April 30) and summer (June 15–Oct 1) periods for each year from 2004 to 2011. As the EC array was deployed May 2004, we could not calculate cumulative NEE, GEP, or R_{eco} over the 2004 spring period. These periods were chosen to envelope the two distinct seasonal periods where the vegetation could be active given sufficient precipitation, and are based on overall seasonal patterns of sustained GEP at the Kendall grassland site (Scott and others 2010), and corre-spond closely to our spring and summer SPI peri-ods.

Uncertainty in seasonal NEE data was computed as the sum of measurement error (Richardson and Hollinger 2007) and gap-filling error, which is dependent on the number of missing observations (Dragoni and others 2007). The average measure-ment error for year-by-year cumulative NEE for spring (Feb 1–April 30) and summer (15 June–Oct 1) was 2.0 and 2.4 g C m^{-2} season^{-1}, respectively. The gap-filling error for these periods averaged 1.3 and 1.6 g C m^{-2} season^{-1}, respectively. Systematic errors are expected to be larger but are largely unknown. We recently conducted a year-long comparison of this EC setup with a parallel closed-path EC system, and found good agreement with spring (8.2 g C m^{-2} season^{-1}—open vs 1.7 g C m^{-2} season^{-1}—closed) and summer NEE (−200.7 and −188.2 g C m^{-2} season^{-1} for open- and closed-path systems, respectively).

Soil Respiration

On June 24, 2011, prior to plant mortality surveys (below), we deployed a multi-chamber soil respira-tion monitoring system (LI-8100, LiCOR Instru-ments, Lincoln, NE), consisting of eight chambers in a 10 × 12 m^2 area within a 900 m^2 grazing enclo-sure on a north-facing (359° mag. N) slope. Four chambers were placed in areas dominated by Leh-mann lovegrass, and four by native bunchgrasses, with the original intent to quantify R_{soil} under exotic and native grass dominance. At the time of installa-tion, all plants were dormant, with no apparent differences in plant condition. All plots were sur-rounded by different individual plants, and no plants co-occurred between plots. After we noted plant mortality, lovegrass plots were designated as "high mortality" and the native grass plots as "low mor-tality." There were not enough lovegrass plants in low-mortality plots, or sufficient native grasses in high-mortality plots (Table 1), to statistically parti-tion species and mortality-level effects to R_{soil}.

Soil collars were inserted 8–9 cm into the soil surface, leaving 2–3 cm of the collar exposed; this exposed height was used to calculate chamber volume needed to estimate R_{soil}. Soil CO_2 efflux was measured every 3 h by enclosing the chamber and measuring [CO_2] every second over a 2-min measuring interval following a 45-s pre-measure-ment purge. Soil respiratory CO_2 efflux (µmol m^{-2} s^{-1}) was calculated from an exponential or linear regression of [CO_2] on time after selecting the regression technique with the lowest number of iterations and highest coefficient of determina-tion (R^2; File Viewer v3.0, LiCOR Instruments). Concurrent with [CO_2] sampling, chamber air temperature (T_{cham}) was measured with a therm-istor attached to the chamber housing. Soil tem-perature (T_{soil}) was measured with a LiCOR temperature probe and volumetric soil moisture (θ, cm^3 cm^{-3}) with a Decagon ECH$_2$O 5-cm probe in-serted horizontally at 15 cm depth into a trench face dug adjacent to the monitored soil plot and subsequently reburied. T_{cham}, T_{soil}, and θ were averaged over each 2-min efflux measurement. High- and low-mortality plots were paired for concurrent sampling to insure diel temperature effects that were spread evenly across plot types. Daily molar soil efflux (mol CO_2 m^{-2} d^{-1}) was estimated by determining the area under each diel efflux curve (Area-transform function, SigmaPlot v10.0). Molar R_{soil} was used to calculate daily soil-respired carbon (R_{soil} in g C m^{-2} d^{-1}) and cumu-lative seasonal R_{soil}, calculated by summing g C m^{-2} d^{-1} from June 30 to Oct 30, 2011, for each plot.

Table 1. Percent Plant Mortality and Canopy Condition Classes for Exotic Lehmann Lovegrass and Native Grasses, and the Density and Proportion of All Dead and Live Grasses across the Kendall Grassland Watershed, and Within High- and Low-Mortality Soil Respiration Plots

	Watershed		R_{soil} High mortality		R_{soil} Low-mortality	
	Exotic	Native	Exotic	Native	Exotic	Native
Dead (0% live)	77.6 (4.54)	40.8 (14.28)	78.2 (8.27)	0.0	50.0*	12.9 (4.07)
Class 1 (<25% live)	15.2 (2.79)	13.6 (2.84)	20.7 (8.61)	0.0	50.0*	3.4 (2.30)
Class 2 (25–50% live)	3.1 (1.36)	10.4 (1.84)	1.1 (1.26)	33.3*	0.0	14.8 (3.08)
Class 3 (50–75% live)	2.6 (0.53)	13.6 (4.72)	0.0	0.0	0.0	19.2 (4.53)
Class 4 (>75% live)	1.5 (0.97)	21.6 (12.07)	0.0	66.7*	0.0	49.7 (11.75)
Density dead (# m^{-2})	2.6 (0.39)	1.4 (0.82)	5.8 (0.59)	0.0 (0.00)	0.1 (0.09)	0.6 (0.15)
Density live (# m^{-2})	0.9 (0.29)	1.6 (0.63)	1.6 (0.63)	0.6 (0.29)	0.1 (0.09)	4.4 (0.70)
% Total grasses dead	43.1 (7.97)	18.3 (8.13)	72.0 (6.00)	0.0 (0.00)	1.7 (1.92)	12.2 (3.14)
% Total grasses live	14.7 (4.90)	23.9 (6.26)	20.5 (7.90)	7.5 (3.38)	1.7 (1.92)	84.4 (6.90)

Watershed values are the mean of five 50-m^2 transects, and soil respiration plot values are the mean of four plot characterizations; SE of the mean in parentheses. R_{soil} plot values with an asterisk are for individuals pooled across all plots due to low frequency (native* n = 9 and exotic* n = 2 plants total).

Mortality and Canopy Dieback

Widespread perennial grass mortality was noticed about 2 weeks after the first significant rains of the summer monsoon, which started July 7, 2011. Plant mortality surveys were performed in August during peak biomass and canopy development (Cable 1975) to insure accurate determination of whole-plant death (McAuliffe and Hamerlynck 2010). On August 10, we quantified watershed-level plant mortality and surviving plant condition in 5-, 50-m^2 transects, each a 1-m swath on the N-side of a 50-m-long transect line. Within each transect, we identified all plants to species, and classified individuals into canopy dieback categories, with 0 representing all dead, with no green tissue, 1 equal to less than 25%, 2 equal to 25–50%, 3 equal to 50–75%, and 4 equal to greater than 75% live canopy (McAuliffe and Hamerlynck 2010). On August 22, 2011, we classified all plants within a 1-m swath around the soil collar of each R_{soil} plot. These provided plant density, % mortality, and plant condition data to generalize R_{soil} results across the watershed and EC tower footprint.

Statistical Analyses

We used linear regression (Statistix v8.0, Analytical Software, Tallahassee, Florida, USA) to determine the strength of the relationship between R_{eco} and GEP to cumulative precipitation during the spring (Feb 1–April 30) and summer (June 15–Oct 1) periods. Specific pairwise slope comparisons were made using Tukey's Honestly Significant Differences (HSD) test if F test criteria for comparing slope differences were met (Zar 1974). Standard errors to calculate HSD were made using the pooled sum of squares, with HSD scores exceeding 4.33 considered significant at $p \leq 0.05$. We did a full pairwise comparison of spring and summer GEP/P and R_{eco}/P slopes to determine which of these processes were most sensitive to precipitation and when.

We tested for differences in daily soil-respired carbon (R_{soil} g C m^{-2} d^{-1}), volumetric soil moisture (θ), T_{soil}, and T_{cham} between collars surrounded by high- and low-mortality levels, using split-plot repeated measures analysis of variance (RM-ANOVA; Statistix v8.0) across the 2011 monsoon season. The whole-plot, between treatment factor was mortality (high vs low, $n = 4$), with the mortality-by-replicate collar interaction as the whole-plot F test error term. We use day of year and the day-by-mortality interaction as the sub-plot factors, with the nested day-by-mortality-by-replicate interaction as the sub-plot F test error term. The day-by-mortality interaction effect was of particular interest, as this would indicate mortality-specific responses over time. All whole- and sub-plot effects were considered significant at $\alpha = 0.05$. To determine underlying causes of significant two-way interactions, pairwise post hoc mean tests were made using α-adjusted general linear contrasts (Scheffe's F) between high- and low-mortality collars within a given day. θ data were arcsine transformed to meet ANOVA data distribution assumptions (Zar 1974). One-way ANOVA (Statistix v8.0) was used to compare average total R_{soil} carbon yields (daily g C m^{-2} summed across June 30–October 30) of high- and low-mortality collars, using the mortality-by-replicate interaction as the F test error term.

We used χ^2 analysis to test for differences in proportions of mortality class scores (0–4) between native bunchgrasses and Lehmann lovegrass across the watershed and between soil respiration plots. To see if vegetation conditions pooled across the R_{soil} plots differed from those across the watershed, one-way ANOVA (Statistix v8.0) was used to test for differences in plant density, average living plant canopy condition, and percent contributions of live and dead native and exotic grasses to total grass density. Plant mortality and percent density contributions were arcsine transformed and canopy class data were log transformed to meet ANOVA data distribution assumptions, post hoc mean testing using least significant difference, with an adjusted α of 0.05.

RESULTS

SPI analysis showed two years with documented plant mortality, 2006 had extreme (11.4 mm; SPI = −1.79) and 2011 had severe (15.6 mm; SPI = −1.53) cool-season rainfall deficits (Figure 1A). Three other years had cool-season SPI within this range; 1959 (13.2 mm; SPI = −1.65), 1967 (14.2 mm; SPI = −1.53), and 2000 (10.9 mm; SPI = −1.79), and two others, 1961 (18.8 mm; SPI =
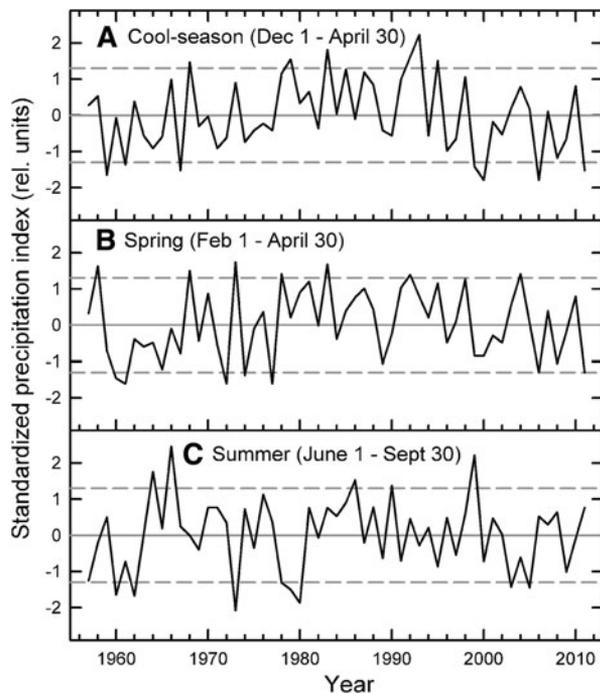

Figure 1. Standardized precipitation index (SPI) for **A** cool-season (Dec 1–April 30), **B** spring (Feb 1–April 30), and **C** summer plant-active periods (June 1–Sept 30) at the Kendall Grassland site. *Solid lines* Severely wet (SPI > +1.3) and dry conditions (SPI < 1.3).

−1.37) and 1999 (17.0 mm; SPI = −1.42), experienced severe cool-season deficits (Figure 1A). Of the seven years with severe to extreme cool-season drought, only three had severe rainfall deficits during the spring February–April plant-active period: 1961 (0 mm; SPI = −1.61), 2006 (5.3 mm; SPI = −1.30), and 2011 (4.8 mm; SPI = −1.30) (Figure 1B). Strong interannual swings in summer SPI (July–Sept) were common over the entire data set (Figure 1C). Summer accumulations in 2006 and 2011 were 225 and 243 mm, respectively, giving SPI of +0.52 and +0.77, indicative of above-normal rainfall (Figure 1C). The dry 2006 cool season was preceded by a severely dry 2005 summer monsoon season (SPI = −1.45), whereas summer rains preceding the 2011 cool season were near normal (SPI = 0.09; Figure 1C).

In 2011, one of the two years where plant mortality occurred, an extreme freeze event occurred. The freeze event spanned Feb 2–4, during which maximum air temperature did not exceed −0.9°C over 2 days, with prolonged (6–9 h) minimum temperatures of −10 to −16.3°C, the coldest recorded over the 22 year data set. One month prior to the freeze event, nighttime lows ranged between −1.1 and 6.5°C, and daytime highs from 8.5°C to as high as 21.2°C. The freeze event occurred after 10.8 mm of the 15.6 mm total cool-season rainfall had fallen, with most of this rain (8.9 mm) falling by Jan 2, 2011.

Spring (Feb 1–April 30) precipitation (P) at the EC site showed accumulations of 6.2 and 5.2 mm for 2006 and 2011, respectively (Figure 2A), in close agreement with spring accumulations at the rain gauge used to calculate spring SPI. NEE was strongly dependent on seasonal P; spring NEE was generally close to zero (Figure 2B), with similar low levels of R_{eco} and GEP, except for years such as 2005, 2007, and 2010 when spring rains were sufficient to stimulate sustained springtime photosynthetic activity (Figure 2D), and the grassland acted as a sink (Figure 2B). For the two years with observed plant mortality (2006 and 2011), spring NEE was positive, because of very low GEP (Figure 2B, D). Over most summers (June 15–Oct 1), the grassland acted as a C-sink, but was a net C-source during dry summers (2004, 2005; Figure 2B), and in 2011, even though summer rainfall accumulations in 2011 were at levels supporting sink activity in previous years (Figure 2B). In 2004 and 2005, highly constrained GEP did not match relatively strong R_{eco} responses to limited summer rains, while in 2011, summer rainfall, GEP and R_{eco} were all higher, but GEP was again more constrained than R_{eco} (Figure 2C, D).
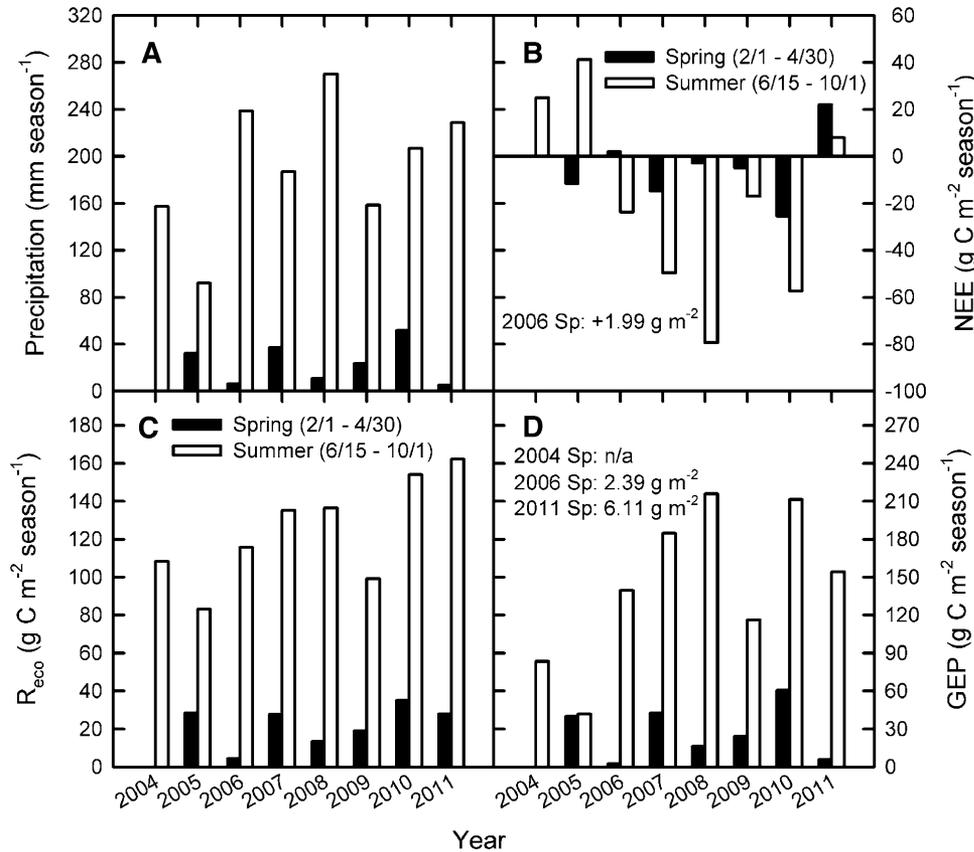
Figure 2. Total spring (Feb 1–April 30) and summer (June 15–Oct 1) plant-active period **A** precipitation, **B** net ecosystem carbon dioxide exchange (NEE), **C** ecosystem respiration (R_{eco}), and **D** gross ecosystem photosynthesis (GEP) from 2004 to 2011 at the Kendall Grassland site.

Linear regression showed that interannual GEP was most sensitive to spring P, but not significantly more so than GEP responses to summer rain (Figure 3A, B). Ecosystem respiration had similar sensitivity to spring and summer P, with similar R_{eco}/P slopes between these two periods (Figure 3C, D). Springtime GEP responded more strongly to P than springtime R_{eco} (HSD = 5.56; $p \leq 0.05$) and summer R_{eco} (HSD = 6.16; $p \leq 0.05$), whereas the summer GEP/P relationship had a slope similar to spring and summer R_{eco}/P relationships (Figure 3C, D).

Springtime R_{eco}/GEP ratios were highest in the two years with extensive plant mortality, 2006 (1.83) and especially 2011 (4.57; Figure 4). In contrast, springtime ratios in other years were lower and more constrained (0.58–0.83; Figure 4). The highest summer R_{eco}/GEP ratios occurred under dry conditions in 2004 (1.30) and 2005 (1.98), with ratios for other years similar to the lowest ratios attained in springtime (0.63–0.85; Figure 4).

Mortality and living plant canopy dieback in 2011 was significantly higher in Lehmann lovegrass than in native grasses across the watershed ($\chi^2 = 3787.1$; $p < 0.01$) and in the R_{soil} plots

($\chi^2 = 525.2$; $p < 0.01$; Table 1). High-mortality R_{soil} plots had significantly higher grass densities than low-mortality plots ($F_{1,6} = 29.3$; $p = 0.002$), with the greatest proportion of these being dead Lehmann lovegrass (Table 1). For grasses as a whole, lovegrass was dominant in high-mortality respiration plots (92.5%) and native grasses dominated low-mortality plots (96.6%; Table 1). Mortality and dieback within the dominant grass types in the respiration plots were similar to those across the watershed, though the native grasses in the low-mortality R_{soil} plots had markedly less mortality (12.9%) than natives grasses across the watershed (40.8%; Table 1).

Plant mortality pooled across the R_{soil} plots (43.2%, +11.6%) was lower than across the watershed (61.4%, ±3.1%), but not significantly so (ANOVA $F_{1,11} = 0.87$; $p = 0.37$). Total plant densities were the same for watershed transects and pooled soil respiration plots (ca. 6.6 plants m^{-2}; $F_{1,11} = 0.001$; $p = 0.98$). R_{soil} plots also had similar average canopy condition of live plants (2.6, ±0.34 SE) compared to those across the watershed (2.2, ±0.19 SE; log-transformed ANOVA $F_{1,11} = 0.21$; $p = 0.65$). The percent contribution of dead native grasses to total grass density was lower in the R_{soil}
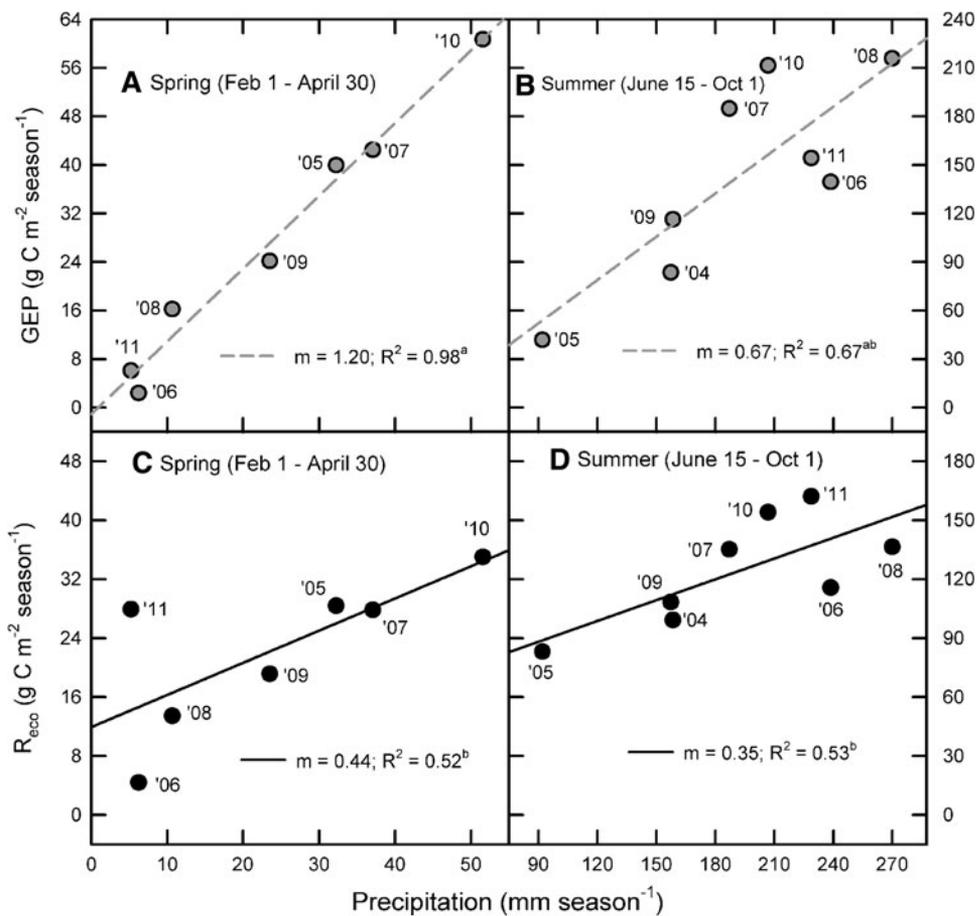
Figure 3. Interannual spring (Feb 1–April 30) and summer (June 15–Oct 1) precipitation relationships with seasonal total gross ecosystem productivity (GEP; **A**, **B**) and ecosystem respiration (R_{eco}; **C**, **D**) at the Kendall Grassland site. *Numbers* next to *symbols* indicate year of sampling. Please note different *x*- and *y*-axis scales. All regressions are significant at $p \leq 0.05$; R^2 with different *superscripts* indicating provided slope values differ significantly ($p \leq 0.05$; all pairwise Tukey's HSD).
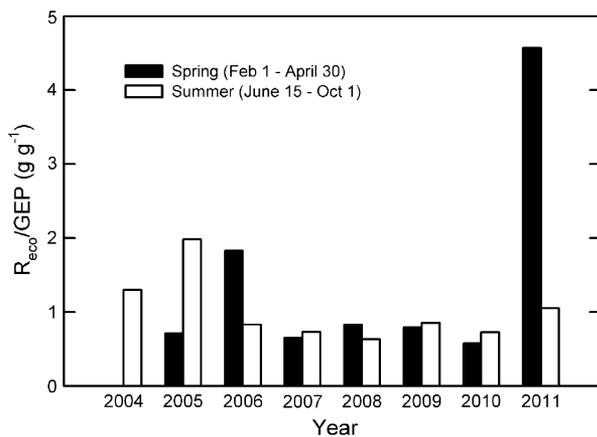

Figure 4. Ecosystem respiration per gross ecosystem photosynthesis at the Kendall Grassland site over 2005–2011 spring (Feb 1–April 30) and 2004–2011 summer (June 15–Oct 1) plant-active periods.

plots (6.1%, ±4.05 SE) compared to watershed levels (18.3%, ±5.13 SE), as were contributions of dead lovegrass (27.3%, ±10.84 SE in R_{soil} plots compared to 43.1%, ±13.72 SE across the watershed). Though these differences were not significant accounting for type I error (ANOVA $F_{1,11} = 3.45$; $p = 0.09$ for native grasses, $F_{1,11} = 0.54$; $p = 0.48$ for exotic grasses), we did not have the statistical power needed to determine if native grass mortality in R_{soil} and watershed plots were truly the same (that is type II error). Therefore, we cannot claim with full certainty the R_{soil} plots are fully representative of vegetation conditions across the watershed. However, the under-representation of dead native grasses in the respiration plots could not have been foreseen because evidence of mortality arose during the experiment, not as part of the experimental design.

Pooled across the 2011 summer monsoon season, daily R_{soil} did not significantly differ between high- and low-mortality collars, nor did volumetric soil moisture, chamber air temperature, or soil temperature at 15 cm (Table 2; Figure 5). Only R_{soil} had a significant day-by-plot interaction (Table 2; $F = 1.64$; $p \leq 0.001$). After the first summer rains, the peak R_{soil} attained following rain was significantly higher in high-mortality than in low-mortality collars (July 9 and 24–25; Figure 5A), with R_{soil} of high- and low-mortality collars converging to similar levels over interstorm periods (Figure 5A,

Table 2. Split-Plot Repeated Measures Analysis of Variance (RM-ANOVA) Mean Square Error Results (MSE) Comparing Seasonal Daily Soil Respiration (R_{soil}), Volumetric Soil Water Content at 15 cm (θ), Respiration Chamber Air Temperature (T_{cham}), and Soil Temperature at 15 cm (T_{soil}) for R_{soil} Collars Placed in High- and Low-Mortality Desert Grassland Plots

Effect$_{(df)}$	R_{soil}	θ	T_{cham}	T_{soil}
Mortality$_{(1)}$	10.18	9.2×10^{-4}	4.08	48.65
Error$_{a(6)}$	*12.98*	*0.071*	*1.43*	*8.98*
Day of year$_{(122)}$	**7.9**	**0.023**	**162.71**	**154.65**
DOY × Mort$_{(122)}$	**0.24**	2.4×10^{-4}	0.0459	0.17
Error$_{b(732)}$	*0.14*	*0.96*	*0.146*	*0.18*

Significant effects are highlighted in bold (p $\leq$ 0.05), F test error terms are in italics; degrees of freedom are presented in parentheses.

B). Following this, the highest post-rain R_{soil} occurred in low-mortality collars, usually under drying soil conditions 2–3 days after the highest θ_{soil} (Figure 5B). Daily R_{soil} were similar over a prolonged dry spell from Aug 22 to Sept 7, which was followed by a period of sustained higher R_{soil} from low-mortality collars from Sept 17 to 27 following the last summer rains (Figure 5A).

Despite these periods of higher daily R_{soil} in high-mortality collars (Figure 5A), total seasonal soil-respired carbon yields did not differ between high- and low-mortality collars ($F_{1,6} = 0.78$; $p = 0.41$; Figure 6A). However, high-yielding high-mortality collars were in plots with surviving plants with less dieback compared to those with lower overall plant mortality but poorer plant condition (Figure 6B). In low-mortality plots, the one collar with high C-yields was in a plot with higher plant mortality and poorer plant condition compared to those with lower yielding R_{soil} collars (Figure 6C).

DISCUSSION

Ecosystem Gas Exchange, Precipitation, and Plant Mortality

NEE, as expected, was positive under dry conditions in the spring or during the summer monsoon (Figure 2), highlighting the importance of precipitation and soil water to the functionality of this desert grassland ecosystem (Scott and others 2010). The plant mortality events of 2006 and 2011 were associated with severely dry springtime conditions (Figure 1B), and these were associated with extremely low GEP (Figure 2D). Grassland GEP is tightly coupled to canopy development and aboveground productivity (Flanagan and others 2002; Hu and others 2008; Bachman and others 2010). Kendall Grassland is a typical Chihuahuan

Desert grassland, receiving the bulk of its annual rainfall and highest productivity during the summer monsoon (Pennington and Collins 2007; Muldavin and others 2008; Collins and others 2009; Thomey and others 2011). Importantly, however, our results suggest that, though summer GEP was markedly higher and did vary strongly with monsoon season P (Figure 2), spring-time conditions may modulate summer season aboveground processes.

Interannual springtime GEP was tightly coupled to P (Figure 3A), and this relationship was anchored by three years: at the high end in 2010, when spring GEP was high following El Niño-Southern Oscillation (ENSO) enhanced cool-season precipitation (SPI 0.81; Figure 1A), and for two years at the low end; (i) 2006, when drought induced widespread native grass mortality (Scott and others 2010) and (ii) 2011, when GEP was strongly constrained by Lehmann lovegrass mortality and canopy dieback (Figure 3A). The reduced coefficient of determination in the monsoon season GEP/P relationship likely stems from the carry over effects of plant responses to springtime conditions, much as antecedent conditions affect intra-seasonal desert grassland ecosystem gas exchange dynamics (Potts and others 2006). For example, 2007 and 2010 had the highest springtime P and GEP (Figure 3A), and these were followed by proportionally higher GEP the following monsoon (Figure 3B). In contrast, low GEP in the dry springs of 2006 and 2011 (Figure 3A) were followed by lower summer GEP at greater rainfall accumulations compared to 2007 and 2010 levels (Figure 3B). In addition, monsoon conditions can counteract springtime gains or losses. The highest and lowest summer GEP were 2008 and 2005, respectively (Figure 3B). High summer precipitation in 2008 offset low springtime GEP (Figure 3A, B), whereas low
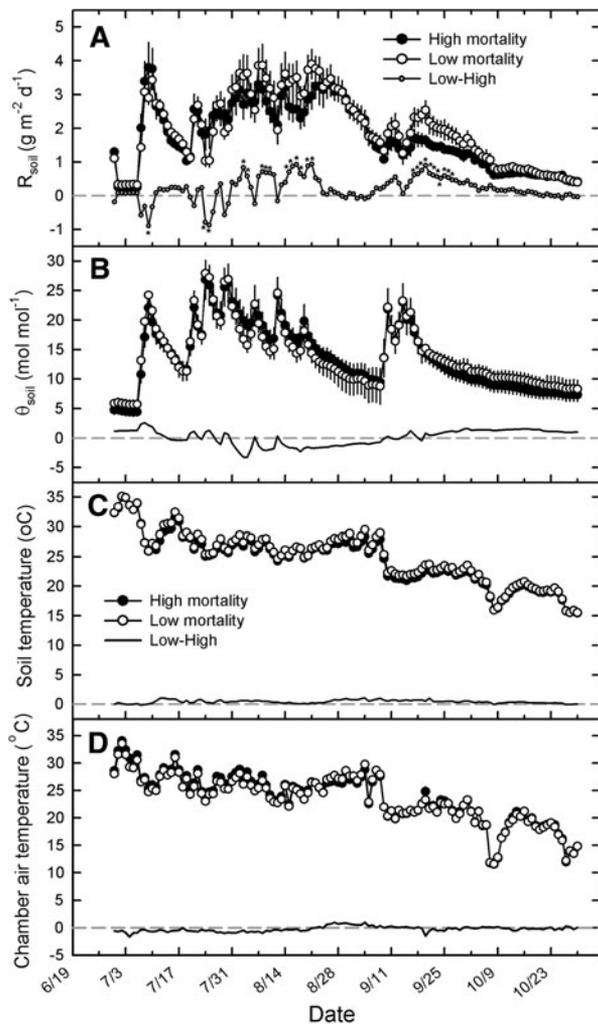
Figure 5. Monsoon season 2011 **A** daily soil respiration (R_{soil}), **B** volumetric soil moisture (θ), **C** soil temperature at 15 cm, and **D** soil respiration chamber air temperature in soil respiration collars in desert grassland plots with high (*closed symbols*) and low plant mortality (*open symbols*). Each point is the mean of four independent measurements, *error bars* ±1 SE; *asterisks* significant differences in R_{soil} between low- and high-mortality collars within a day (Scheffe's *F*, $p \leq 0.05$), error bars for chamber and soil temperature are smaller than the symbols.

summer rains in 2005 offset moderately high GEP attained the previous spring (Figure 3A, B). These findings suggest processes underlying aboveground productivity in this semiarid grassland during the cool season can, in some instances, affect subsequent aboveground productivity during the summer growing season.

The relationship of R_{eco} with seasonal *P* was not as strong as GEP (Figure 3C, D). Grasslands typically have high allocation to belowground biomass, and grassland R_{eco} and R_{soil} are strongly determined
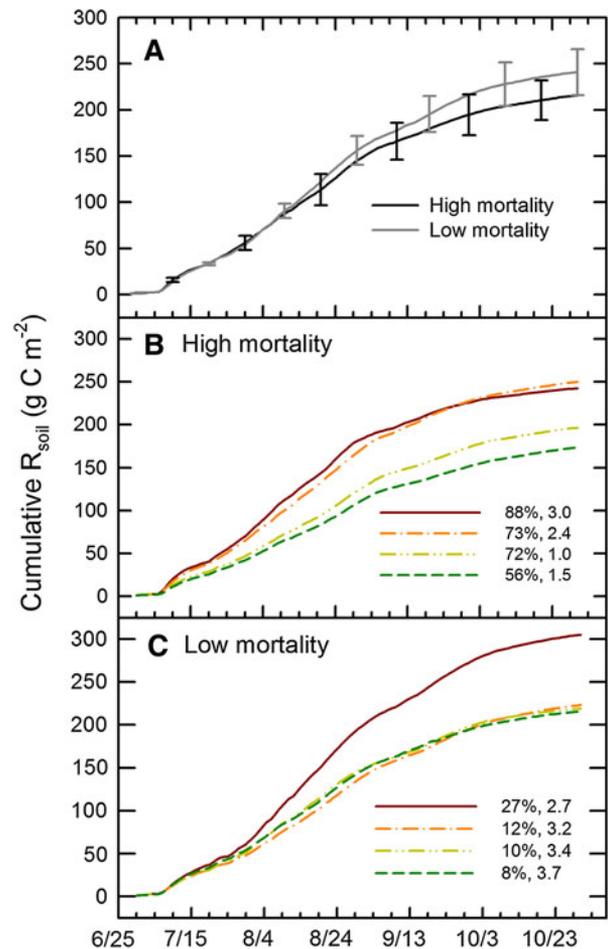

Figure 6. **A** Seasonal soil respiration carbon yields of high- and low-mortality plots across the 2011 summer monsoon season at the Kendall Grassland site. Each point is the mean of four independent measurements, *error bars* ±1 SE. R_{soil} carbon yields of individual **B** high-mortality and **C** low-mortality plots; *numbers* in the *legend* percent plant mortality and average canopy condition class score (Table 1) of all living plants in each plot (grasses, shrubs, and forbs).

by root biomass (Knapp and others 1998; Flanagan and others 2002; Thomey and others 2011). Also, belowground allocation in grasslands tends to be relatively invariant, even across precipitation gradients (Zhou and others 2009). Thus, the lower sensitivity of R_{eco} to seasonal precipitation may reflect greater seasonal carryover of living belowground biomass, whereas the higher sensitivity of GEP to *P* reflects the proportionally greater aboveground senescence typical of grasslands during drought or seasonal dormancy (Heisler-White and others 2008). However, the lower slope and smaller coefficient of determination in the interannual springtime R_{eco}/P relationship was due to high R_{eco} yields per unit precipitation in the spring of 2011, a

year with clearly expressed perennial grass mortality (Figure 3C). The increased precipitation sensitivity of R_{eco} in spring 2011 could reflect increased carbon availability and rapid microbial use over those few periods of sufficient precipitation and soil moisture (Sponseller 2007; Cable and others 2008) and possibly an increased availability of aboveground plant matter to photodegradation (Austin and Vivanco 2006). Direct root respiratory contributions would likely be low, because low springtime GEP in 2011 (Figure 2D) indicate very limited aboveground active biomass that would limit concurrent belowground activity (Flanagan and others 2002; Xu and others 2004; Flanagan and Johnson 2005; Baldocchi and others 2006; Fernandez and others 2006; Tang and others 2005; Sponseller 2007; Cable and others 2008, 2011; Liu and others 2009).

R_{eco}/GEP ratios were elevated during the 2004 and 2005 summer seasons (Figure 4), and were associated with low P, NEE, R_{eco}, and GEP (Figure 2). This is likely driven by low summer monsoon season P limiting aboveground growth, which would have a strong effect on GEP (Pennington and Collins; Scott and others 2010). More important were high springtime R_{eco}/GEP ratios apparent in 2006 and especially 2011 (Figure 4). This disproportionate response of R_{eco}/GEP supports the idea that high ecosystem respiration sensitivity to precipitation in 2011 was due to rapid decomposition associated with increased availability of labile carbon to sustain higher soil microbial activity during the limited period of sufficient soil moisture following springtime rains. Therefore, much of the monitoring of R_{soil} across the 2011 monsoon season likely follows surviving plant activity following a microbially dominated springtime respiratory pulse. In addition, for the two years with plant mortality, cumulative summer R_{eco} in 2011 was 27.5% higher than in 2006 despite only 5 mm difference in precipitation (Figure 3D). In 2006, the plant community was in transition, with reduced plant cover dominated by annual forbs and establishing Lehmann lovegrass plants (Scott and others 2010). In 2011, the plant community was in recovery, with similar overall plant cover and composition to previous years and limited proliferation of forbs (Hamerlynck, personal observation). Low plant cover can strongly limit R_{eco} response to high moisture in desert grasslands (Hamerlynck and others 2012a), and forbs and perennial grasses differ in allocation patterns (Smith and others 1997). This suggests differences in cover and community structure likely underlie the differences in total R_{eco} between 2006 and 2011.

Soil Respiration and Plant Mortality

Overall plant mortality did not have as strong an effect on soil respiration as we expected, with daily R_{soil} usually similar in collars in high- and low-mortality plots (Figure 5A). Following release from very dry pre-monsoon soil moisture levels, the higher R_{soil} we expected in high-mortality plot collars occurred only twice, and then only over one or two days (Figure 5A). This suggests higher plant mortality only moderately enhanced microbial activity and soil organic material turnover that typically follow long dry spells before plant activity increasingly dominates R_{soil} (Sponseller 2007; Cable and others 2011). However, later in the season when soil drying cycles were more pronounced (Figure 5B), daily R_{soil} in low-mortality plots was frequently higher than in high-mortality plots (Figure 5A), but these did not result in different total seasonal soil-respired carbon (Figure 6A). Importantly, seasonal soil-respired carbon yields depended more on the condition of surviving plants surrounding the soil respiration collars, rather than overall plant mortality (Figure 6). In high-mortality plots, collars surrounded by surviving plants in relatively good condition had the greatest total soil respiratory C-yields, whereas collars surrounded by surviving plants in poor condition, even with lower whole-plant mortality, had lower yields (Figure 6B). In low-mortality plots, R_{soil} dynamics were more constrained; the plots with similar low mortality and plant condition having similar cumulative efflux, whereas the collar in the one plot with higher plant mortality and lower canopy condition had markedly higher cumulative efflux (Figure 6C).

Plant mortality and average canopy condition across the Kendall grassland watershed was 60.4% and 2.2, very similar to values pooled across all soil respiration plots (43.2% and 2.6), and within the range of values associated with high seasonal R_{soil} carbon yields (Figure 6B, C). Seastedt and Knapp (1993) suggested transient maxima in grassland ecological processes reflect shifts in multiple limiting resources, which become smaller in number but stronger in effect as conditions near equilibrium. It may be the low R_{soil} yields in plots at opposite extremes in total plant mortality and surviving plant condition, that is, high mortality/poor condition (Figure 6B) and low mortality/good condition (Figure 6C), reflect stronger equilibrium-condition limitations to soil biotic activity. In contrast, high R_{soil} yields from high mortality/good condition (Figure 6B) and low mortality/poor condition plots (Figure 6C) may reflect a transient

release from these equilibrium-condition limitations. Higher seasonal cumulative R_{soil} carbon in these high-yielding plots may reflect root growth accompanying recovery and growth of the plant canopy, much as in soil respiration increases with canopy development and photosynthetic activity in forest systems (Xu and others 2004; Tang and others 2005; Baldocchi and others 2006), which act in combination with microbial use of soil organic matter not consumed during more water-limited springtime conditions (Sponseller 2007; Cable and others 2008, 2011).

Species-level effects do contribute some uncertainty to these assertions. Native grass mortality in R_{soil} plots was lower than observed in the watershed-level plots (Table 1). Our original intent was to test for R_{soil} differences in native- and exotic grass-dominated areas. The underrepresentation of dead native grasses could not have been foreseen, as evidence of mortality arose during the experiment, and was not part of our original experimental design. Therefore, we do not know if areas dominated by native grasses in similar condition to our high-mortality, but lovegrass-dominated, plots had similar survivor condition-dependent R_{soil} yields (Figure 6B). Native grasses across the watershed had similar mortality and canopy condition score (40.9% and 2.6) to the one native-dominated, low-mortality plot with high R_{soil} yield (Figure 6C), but lack of replication makes extrapolation across the watershed problematic. However, as R_{soil} is a dominant contributor to semi-arid and aridland R_{eco} flux (Flanagan and others 2002; Flanagan and Johnson 2005; Barron-Gafford and others 2011; Cable and others 2011), the higher relative summer R_{eco} in 2011 (Figures 2C, 3D) likely reflects higher R_{soil} contributions, possibly from areas with vegetation conditions similar to those we found associated with enhanced R_{soil} yields (Figure 6B, C). This coupled with constraining effects of springtime conditions on summertime GEP (Figures 2D, 3B) likely led to the unusually high, positive NEE of the Kendall grassland over the 2011 summer growing season (Figure 2B).

Past monsoon season research has demonstrated Lehmann lovegrass dominance increased net carbon uptake in drier conditions (Hamerlynck and others 2010; Scott and others 2010). Although Lehmann lovegrass has whole-plant carbon uptake capability similar to native grasses under "typical" cool-season conditions, it performs poorly under colder, wetter ENSO-associated conditions (Hamerlynck and others 2012b). Our current study expands these findings, showing that La

Niña-Southern Oscillation (LNSO) associated cool-season drought, coupled with strong freezing events, can induce greater mortality in this invasive grass compared to native species (Table 1). Indeed, cool-season conditions in 2011 whereas dry were not as severe as in 2006 (Figure 1A). Thus, the 2011 extreme freeze event may have enhanced the effects of these slightly milder drought conditions, leading to the widespread Lehmann lovegrass mortality. However, we do not know if these extremely cold temperatures exceeded the cold-tolerance of this species regardless of soil water status. Disappearance of Lehmann lovegrass was observed in the mid 1970s, a period characterized by protracted drought (Cox and others 1990). So, in addition to cool-season drought effects hypothesized by Cox and others (1990), severe freezes may also have contributed to the 1970s disappearance of Lehmann lovegrass. Some climate predictions suggest lower frequencies of severe cold events will accompany disproportionate rises in minimum temperatures compared to maximum temperatures across western North America (Diffenbach and others 2005; Christensen and Hewitson 2007). If so, the reduced frequency of severe cold snaps and warmer future ENSO with enhanced cool-season rainfall may facilitate the continued dominance and spread of this grass into Southwest US grassland systems.

CONCLUSION

The recent Southwestern US drought has been characterized as a "warm drought," with higher than-average temperatures aggravating growing season drought-stress (Breshears and others 2009). However, the dieback observed in this study occurred under "off-season" conditions of chronic drought and acute freezing under regionally warming conditions, and coincides with 332 consecutive months with above-average global terrestrial temperatures (NOAA 2012). Warming conditions may reduce the frequency and duration of physiological "cold-hardening" periods needed by aridland plants to survive subsequent prolonged cold periods, especially under dry cool-season conditions (Lambrecht and others 2007). Thus, as cool-season climate becomes increasingly arid and variable (Seager and others 2007), and as climate extremes become more pronounced (Easterling and others 2000a, b; Diffenbach and others 2005), cool-season conditions are likely to have increasing and potentially more negative influences on productivity attained during the summer rainy season in these water-limited grassland ecosystems.

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