Soil Respiration in a Subtropical Savanna Parkland: Response to Water Additions

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Soil respiration (SR) is controlled by abiotic parameters (temperature, water availability) interacting with biotic characteristics of the vegetation (quantity and quality of litter inputs, root respiration) and the soil microbial community. Because SR is a major flux in the C cycle, it is important to understand how vegetation change may interact with predicted climate changes to alter SR and ecosystem C storage. We quantified the SR response to increased soil water availability in a subtropical savanna parkland in the Rio Grande Plains of southern Texas. Diel SR was measured monthly from July 1996 to August 1997 in control and irrigated plots located in grasslands and in three contrasting woody plant communities known to have developed on grassland during the past 100 yr. Irrigation increased SR in all plant community types. Soil respiration in woody communities was higher (12.7 g CO_2 m^{-2} d^{-1} averaged across months and treatments) and more responsive (+103%) to increased water availability than grasslands (9.8 g CO_2 m^{-2} d^{-1} and +48%, respectively). This SR pattern is probably the result of woody communities having greater soil microbial biomass, soil C pools, and root biomass than adjacent grasslands. Irrigation increased the sensitivity of SR to temperature (Q_{10} = 1.6 and 2.6 for control and irrigated plots, respectively), but Q_{10} values were similar in woody communities and grasslands. Results suggest SR is water limited, that sensitivity of SR to soil moisture availability increases with increasing woody plant abundance, and that shifts from grass to shrub dominance may have little impact on SR response to the changes in temperature projected to accompany global warming.

Abbreviations: SR, soil respiration; ST, soil temperature.

FOREST, RANGE & WILDLAND SOILS

Soil respiration is the total efflux of CO_2 produced from soil metabolic processes (Lundegardh, 1927), mainly microbial decomposition of soil organic matter and root respiration (Singh and Gupta, 1977). Thus, the abiotic and biotic factors that influence microbial growth and activity and plant C allocation to roots exert significant control over SR rates (Hibbard et al., 2005). Numerous studies have shown that climatic factors, particularly temperature and precipitation, are major determinants of SR at global (Raich and Schlesinger, 1992; Raich and Potter, 1995), regional (Reichstein et al., 2003; Fierer et al., 2006), and local scales (Davidson et al., 1998; Davidson et al., 2000; Mielnick and Dugas, 2000). Biotic controls on SR have been more difficult to illustrate, in part because plant communities co-vary with patterns in macro- and microclimate (Raich and Tufekcioglu, 2000). By altering organic matter production, litter quality, and belowground C allocation, however, changes in vegetation type can influence microbial decomposition (Hobbie, 1992; Zak et al., 1994) and root respiration (Craine et al., 1999) and therefore total SR rates (Reichstein et al., 2003). As a result of global climate change and alterations in land use (Sala et al., 2000), many ecosystems are currently experiencing concurrent changes in the abiotic and biotic controls on SR. Given the large quantity of CO_2 that soils respire annually and the role CO_2 plays in greenhouse warming, an understanding of SR response to climate change and alterations in vegetation resulting from land use is critical.

One type of land cover change common in dryland regions worldwide during the past two centuries has been the conversion of grasslands and savannas to shrublands or woodlands via woody plant encroachment (van Auken, 2000; Archer et al., 2001). Grasslands are characterized as having some of the largest soil organic C stores and highest SR rates of all terrestrial ecosystem types (Schlesinger, 1997). When woody plants encroach into grasslands, they may promote soil C accumulation and increase SR rates at some sites (McCulley et al., 2004), but cause no net change or declines in others (Kieft et al., 1998; Schlesinger and Pilmanis, 1998; Jackson et al., 2002; Smith and Johnson, 2004). These contrasting effects of woody plant encroachment on soil C pools and SR rates probably reflect the outcomes of interactions between plant species characteristics, climate, edaphic properties, and land use histories (Wessman et al., 2004).

Grassland ecosystem C fluxes are tightly linked to precipitation and water availability (Flanagan et al., 2002; Knapp et al., 2001; McCulley et al., 2005; Meyers, 2001; Risch and Frank, 2006; Sala et al., 1988). This suggests that grassland ecosystem function will track changes in precipitation predicted by global circulation models as a consequence of increasing atmospheric CO_2 concentrations (Intergovernmental Panel on Climate Change, 2001). Both the quantity and timing of rainfall are likely to be altered, however, under future climate change scenarios (Easterling

Soil Sci. Soc. Am. J. 71:820–828
doi:10.2136/sssaj2006.0303
Received 29 Aug. 2006.
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et al., 2000), and recent work from grassland and arid-land ecosystems indicate that the magnitude, timing, and "pulse" nature of precipitation events play important roles in governing the uptake and release of ecosystem C (Huxman et al., 2004; Harper et al., 2005; Potts et al., 2006). When woody plants proliferate in grasslands, they may alter the degree of coupling between ecosystem C fluxes and rainfall by altering rooting depths, leaf area, photosynthetic pathways, phenology, and the size of C and nutrient pools (Ogle and Reynolds, 2004). To identify how water availability and woody plant encroachment might interact to alter SR fluxes, a year-long field irrigation experiment was conducted at the La Copita Research Area in the southern Great Plains. In this experiment, we quantified diel and seasonal SR in control and irrigated plots within remnant grasslands and in three adjacent woody plant community types that have developed on grassland. There are innumerable permutations and combinations of rainfall amount, timing, and frequency that could uniquely affect SR, and there is considerable uncertainty about whether the climate in this region will become wetter or drier (Twilley, 2001). We opted to quantify the upper bounds of the SR response envelope by minimizing soil moisture constraints.

Previous work at the La Copita site has demonstrated that woody communities occur in areas recently (<100 yr) dominated by grasses (Boutton et al., 1998), and that woody communities have greater above- and belowground productivity (Hibbard et al., 2001) and larger soil organic C and N pools (Archer et al., 2001, 2004; Liao et al., 2006a, 2006b) than current-day grasslands. A concurrent study also showed that woody plant communities have greater microbial biomass and higher annual SR rates than adjacent grasslands (McCulley et al., 2004). Nothing is known, however, concerning the ability of these different vegetation types to respond to alterations in climate. Thus, the specific objective of this experiment was to determine whether SR fluxes from grasslands and woodlands responded similarly to increases in water availability. Given the semiarid climate of the site, we expected that (i) increased water availability would increase SR rates in all plant community types, but (ii) woody plant communities, with their larger pools of soil organic C, microbial biomass, and root biomass, would exhibit a larger SR response to increased water availability than grasslands.

MATERIALS AND METHODS

Site Description

Research was conducted at the Texas Agricultural Experiment Station La Copita Research Area on the eastern edge of the Central Rio Grande Plains (27°40′ N, 98°12′ W). The climate is subtropical, with a mean annual temperature of 22.4°C and mean annual precipitation of 716 mm. The present vegetation consists of savanna parkland on uplands and closed-canopy woodlands in low-lying drainages (Boutton et al., 1998; Scifres and Koerth, 1987); however, historical accounts, aerial photography, tree ring analyses, and isotopic analyses of plants and soils all indicate that this region was once grassland and open savanna (Archer, 1995).

Our study assessed the response of SR to enhanced water availability in the four dominant plant communities at this site: (i) upland remnant grasslands; (ii) small, discrete shrub clusters comprised of a single *Prosopis glandulosa* var. *glandulosa* (Torr.) plant with 5 to 10 other woody species beneath its canopy; (iii) groves comprised of numerous *Prosopis*–mixed species shrub clusters that have expanded laterally and fused to form these larger woody patches; and (iv) lowland drainage woodlands, which have a species composition similar to upland clusters and groves.

Soil and plant community properties determined from previous work (McCulley et al., 2004) are summarized in Table 1. Soils of all plant community types are classified as Mollisols. The bulk density of surface soils was significantly higher in grasslands (1.47 g cm^{-3}) than in woody communities (1.09–1.27 g cm^{-3}; $P < 0.05$); and upland plant community soils had less clay (12.4–12.9% in grasslands, clusters, and groves) than lowland drainage woodlands (22.2%; $P < 0.001$). Soil organic C and total N pools were significantly larger in drainage woodlands and groves than clusters and grasslands ($P < 0.001$). Mean understory height and species richness were comparable across woody plant community types; however, the mean *P. glandulosa* basal diameter and estimated age of clusters (13.6 cm and 40.3 yr, respectively) were significantly lower than that of groves (38.5 cm and 81.6 yr). Mean grassland herbaceous richness (11.2 species) was higher than understory shrub species richness in the woody communities (5.5–7.0 species). Additional details

Table 1. Soil (0–10 cm) and vegetation characteristics of the plant community types present at La Copita (soils data are extracted from McCulley et al., 2004). Herbaceous and woody understory species richness was determined by inventorying a 2- by 2-m area within each sample plot. Mean understory height and basal diameter of *Prosopis* stems were measured at each wooded site. Age of woody community types was estimated from the basal diameter of the largest *Prosopis* stem in each plot using soil-specific equations (Stoker, 1997).

Characteristic	Grassland	Cluster	Grove	Drainage woodland
Taxonomy†	Typic Argiustoll	Typic Argiustoll	Pachic Haplustoll	Pachic Argiustoll
Texture	fine sandy loam	fine sandy loam	sandy loam	sandy clay loam
Clay, %	12.5 ± 3.5 b‡	12.9 ± 2.2 b	12.4 ± 2.6 b	22.2 ± 4.6 a
Bulk density, g cm^{-3}	1.47 ± 0.06 a	1.27 ± 0.18 ab	1.09 ± 0.12 b	1.13 ± 0.13 b
Organic C, g C m^{-2}	987 ± 170 c	1302 ± 414 b	2153 ± 885 a	2223 ± 823 a
Total Nitrogen , g N m-2	83.7 ± 16.2 c	111.3 ± 35.8 b	192.4 ± 65.6 a	172.3 ± 76.0 a
Basal diameter of *Prosopis*, cm	–	13.6 ± 2.9 b	38.5 ± 20.1 a	24.7 ± 6.3 ab
Estimated age, yr	–	40.3 ± 6.8 b	81.6 ± 38.1 a	61.9 ± 13.6 ab
Mean understory height, m	–	1.8 ± 0.3 a	1.5 ± 0.7 a	1.8 ± 0.3 a
Species richness§	11.2 ± 1.5 a	6.2 ± 1.8 b	5.5 ± 0.8 b	7.0 ± 0.9 b

† From Boutton et al. (1998).

‡ Numerical values are means ± 1 SD. Different letters represent significant differences between means within a row ($P \leq 0.05$).

§ Number of understory shrub species in woody communities and herbaceous species in grasslands in a 4 m^2 area.

on the plant communities and soils of the site are available elsewhere (Archer, 1995; Boutton et al., 1998; McCulley et al., 2004).

Experimental Design and Implementation

Twelve replicates (each 4 by 5 m) of the different plant communities (grassland, cluster, grove, and drainage woodland) were identified within a 1-km^2 area. Half of these replicates were randomly selected to receive the irrigation treatment (n = 6 per treatment for each plant community). Measurements of SR taken the day before irrigation began were not significantly different between the designated irrigated and unirrigated control replicates for any plant community type. Irrigation began in July 1996 and consisted of weekly applications of 30 to 50 mm of water throughout the year. Water was applied via timers on an irrigation system that supplied water to four commercially produced, 90° shrub-type sprayer heads situated at 0.45-m height in the corners of each plot. Rates of water application were measured with randomly placed ground-level rain gauges during the first irrigation event. The rate of water application (30–50 mm) varied across plots, probably as a function of the rate of interception of water by aboveground biomass or wind. Given the range in application rates, we estimated that irrigation treatments delivered two to four times more water than the long-term annual mean rainfall. During sampling weeks, irrigation was applied the day before measurements began. The unirrigated controls received only natural rainfall that was recorded daily at the site by an automated weather station.

Soil respiration, soil temperature, and moisture were measured monthly from July 1996 through August 1997. Irrigation malfunctions in October 1996 and January 1997 prevented data collection in the upland plant communities (grassland, cluster, and grove), and inclement weather prevented data collection in all community types in August 1996 and March and April 1997. In plots representing woody community types (cluster, grove, and drainage woodland), all measurements were conducted within 1.5 m of the bole of the largest *Prosopis* tree. This locational constraint was used to minimize potentially confounding effects that might occur if bole-to-canopy dripline gradients exist and to ensure that the soils sampled would have been near-maximally affected by woody vegetation.

Soil Respiration and Temperature

Diel measurements of SR were made monthly in the field, starting ~12 h after irrigation, using a soil respiration chamber (LI-6000–09, LICOR, Lincoln, NE) attached to an infrared gas analyzer (IRGA; LICOR 6200) (Norman et al., 1992). Some of the soil respiration measurements on the control plots have been published previously (McCulley et al., 2004), but are included here as a necessary point of comparison with the irrigated plots. At each measurement period, polyvinyl chloride collars (10 cm diameter by 7 cm tall, one per plot) were inserted in the soil to a depth of 2.5 cm in the evening, and SR rates were measured at 04:00, 09:00, 14:30, and 22:00 h the following day. Plots were visited in the same sequence during the 24-h period. Soil temperatures were recorded concurrent with SR measurements using a probe inserted 5 cm into the soil and interfaced with the LICOR unit. The IRGA was calibrated with a standard (501 mmol mol^{-1} CO_2 in air) before every measurement period.

To derive a daily SR, the trapezoidal rule was used to calculate the area under the curve (AUC) produced by the diel measurements of instantaneous respiration rates:

$$\begin{aligned}\mathrm{AUC} = {} & \mathrm{mean}(\mathrm{SR}_1,\mathrm{SR}_2)(\mathrm{t}_2 - \mathrm{t}_1) + \mathrm{mean}(\mathrm{SR}_2,\mathrm{SR}_3)(\mathrm{t}_3 - \mathrm{t}_2) + \\ & \mathrm{mean}(\mathrm{SR}_3,\mathrm{SR}_4)(\mathrm{t}_4 - \mathrm{t}_3) + \mathrm{mean}(\mathrm{SR}_4,\mathrm{SR}_1)(\mathrm{t}_4 - \mathrm{t}_1)\end{aligned} \qquad [1]$$

where SR_x were the SR rates measured at times t_1, t_2, t_3, and t_4 (04:00, 09:00, 14:30, and 22:00 h, respectively).

Soil Collection and Characterization

The day following completion of diel SR measurements, a soil core (5-cm diameter by 10 cm deep) was extracted from each SR collar and was sealed in a tin for determination of gravimetric soil moisture content, which was later converted to a volumetric basis. The characterization of soils associated with each plant community type occurred as part of a concurrent study (see McCulley et al. [2004] for methodology).

Statistical Analyses

Statistical differences in soil parameters across plant community types and between irrigated and unirrigated control plots were assessed using SAS (SAS Institute, 1996). Daily SR data were log transformed before statistical analysis. A repeated measures general linear model (GLM) was used to test for differences in SR and soil temperature and moisture attributable to season (month), plant community type, irrigation treatment, and their interactions. For significant main effects, Tukey's mean separation tests were performed. Analysis of variance was used to assess the effects of plant community type on site characteristic data. To determine the primary variables controlling SR, we ran a multiple linear regression (stepwise, using a GLM) with each of the control and irrigated daily SR data sets and measurements of precipitation, volumetric soil moisture, soil temperature, soil organic C and total N pools, and a categorical variable called "plant community type," which represented the collective biotic differences between the plant community types (e.g., differences in root biomass, litter quality, etc.).

The multiple linear regressions for both control and irrigated data sets indicated a significant relationship between SR and soil temperature. To further explore this relationship, we fit our data to the empirically derived van't Hoff function as expressed in Lloyd and Taylor (1994):

$$\mathrm{SR} = A\exp(B\times \mathrm{ST}) \qquad [2]$$

where SR is the soil respiration rate standardized for soil C content to 10-cm depth [g CO_2–C (kg soil C)$^{-1}$ d^{-1}], ST is the soil temperature at 5-cm depth (°C), and A and B are constants. Because microbial respiration is dependent on substrate availability, SR rates are expressed per kilogram of soil C to facilitate comparison of the ST relationship across plant community types that differ in soil C pool size (Table 1). From Eq. [2], the response of SR to a 10°C change in ST (Q_{10},) can be calculated as:

$$Q_{10} = \exp(10\times B) \qquad [3]$$

We fit Eq. [2] to both the control and irrigated SR data collectively and by plant community type. For plant communities with significant exponential relationships between SR and ST, we calculated Q_{10} for each replicate within the plant community type and tested for significant plant community type and treatment main effects on Q_{10} using an ANOVA.

RESULTS

Rainfall, Soil Moisture, and Temperature

Rainfall during the study (July 1996–August 1997, 645 mm) was 82% of the long-term (1911–1985) average recorded at nearby Alice, TX (785 mm). All months of the study had less rain than the long-term average except August

1996 and March, April, and May 1997, which received 40 to 60 mm mo^{-1} more than average. Volumetric soil moisture quantified the day following irrigation events ranged from 0.22 m^3 m^{-3} in irrigated drainage woodlands (sandy clay loams) to 0.01 m^3 m^{-3} in unirrigated grasslands (fine sandy loams; Fig. 1). Repeated measures ANOVA revealed that soil moisture differed significantly across the months sampled ($P < 0.0001$), the plant community types ($P < 0.001$), and the treatment ($P < 0.0001$). Small differences in seasonal soil moisture patterns between treatments and across plant community types during May to August 1997 resulted in significant month × treatment and month × community × treatment interactions ($P < 0.0001$ and $P < 0.001$, respectively). A significant community × treatment interaction ($P < 0.05$) was also found. In unirrigated control plots, lowland drainage woodlands had, on average, higher soil moisture than upland groves, clusters, and grasslands (Table 2). In irrigated plots, however, drainage woodlands (0.168 m^3 m^{-3}) and grasslands (0.179 m^3 m^{-3}) had higher soil moisture values than clusters (0.143 m^3 m^{-3}) and groves (0.138 m^3 m^{-3}). Thus, although the irrigation treatment resulted in a significant increase in soil moisture across all plant community types ($P < 0.0001$), grassland soil moisture values were more impacted by the treatment than the woody communities. Average soil moisture for all irrigated plots during the study (0.204 m^3 m^{-3}) was 0.141 m^3 m^{-3} higher than the average unirrigated control plots.

Mean daily soil temperatures during the measurement period ranged from 16 to 31°C in irrigated plots and from 15 to 38°C in unirrigated controls, with maximum and minimum temperatures for both treatments occurring in July 1996 and February 1997, respectively (Fig. 1). All main effects and interaction terms from the soil temperature repeated measures ANOVA were significant. Averaged across the study, irrigated plots were ~2°C cooler than unirrigated controls during the day following water application (Table 2). This effect was particularly apparent during the summer months (June–October, Fig. 1). In general, grasslands tended to have higher soil temperatures than woody community types in both control and irrigated treatments (Table 2).

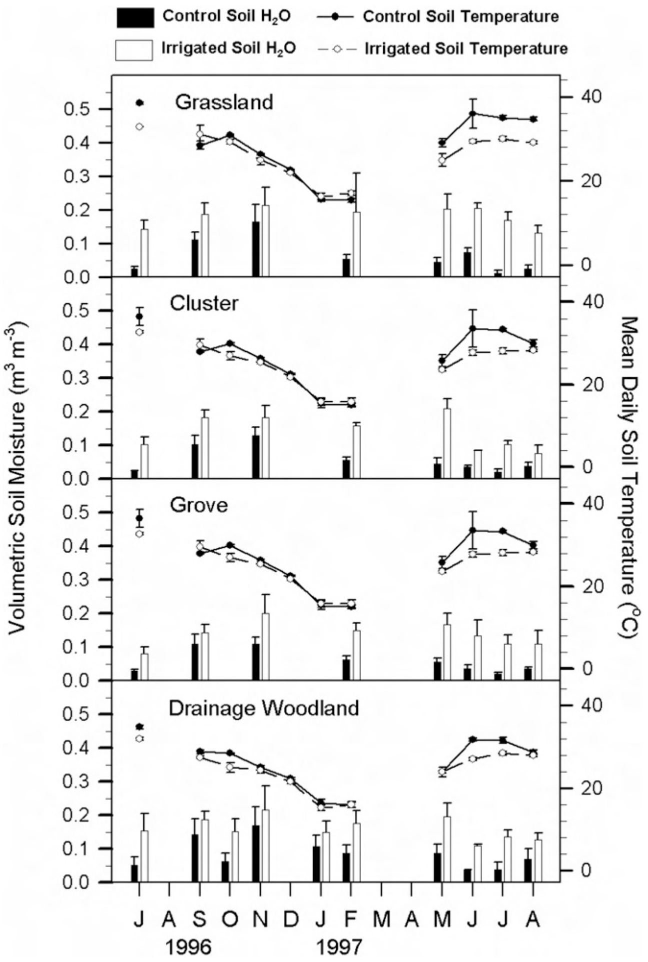

Fig. 1. Mean (±1 SD) volumetric soil moisture (0–10-cm depth) and daily soil temperature (5-cm depth) for control and irrigated plots in each plant community type.

Soil Respiration (SR)

Diel changes in SR were small (<4 μmol CO_2 m^{-2} s^{-1}) across all plant communities and treatments, but were more pronounced in the irrigated treatment (averaged across months, diel range = 1.4 and 0.55 μmol CO_2 m^{-2} s^{-1} for irrigated and control plots

Table 2. Volumetric soil moisture (0–10-cm depth), temperature (5-cm depth), and daily soil respiration (SR) rates on the day following irrigation, averaged across all sample dates in 1996 to 1997.

Parameter	Grassland	Cluster	Grove	Drainage woodland
Soil moisture, m^3 m^{-3}				
Control	0.063 ± 0.055 b†	0.058 ± 0.41 b	0.059 ± 0.037 b	0.090 ± 0.055 a
Irrigated	0.179 ± 0.057 a	0.143 ± 0.053 c	0.138 ± 0.048 c	0.168 ± 0.049 b
Soil temperature, °C				
Control	28.9 ± 7.80 a	27.3 ± 7.10 b	26.6 ± 6.56 c	26.5 ± 6.08 c
Irrigated	26.4 ± 5.55 a	25.3 ± 5.42 b	25.7 ± 5.44 b	24.7 ± 5.16 c
Soil respiration, g CO_2 m^{-2} d^{-1}				
Control	7.9 ± 6.2 b	7.1 ± 5.8 b	9.0 ± 6.9 a	8.8 ± 6.2 a
Irrigated	11.7 ± 7.4 c	12.3 ± 6.5 c	20.8 ± 11.6 a	18.1 ± 10.6 b
Q_{10}‡				
Control	1.43 ± 0.29	1.39 ± 0.17	1.65 ± 0.11	1.78 ± 0.17
Irrigated	2.89 ± 1.85	2.08 ± 0.55	3.27 ± 1.26	2.28 ± 1.30

† Numerical values are means ± 1 SD. Different letters represent significant differences between means within a row ($P \leq 0.05$), as determined by repeated measures tests for parameters with seasonal time-courses of data and ANOVA for derived Q_{10} values.

‡ Q_{10} values were derived using the Van't Hoff exponential equation (see Eq. [2] and [3]) and represent the response of SR to a 10°C change in soil temperature. No significant differences between plant community types were found for either the irrigated or control Q_{10} data.

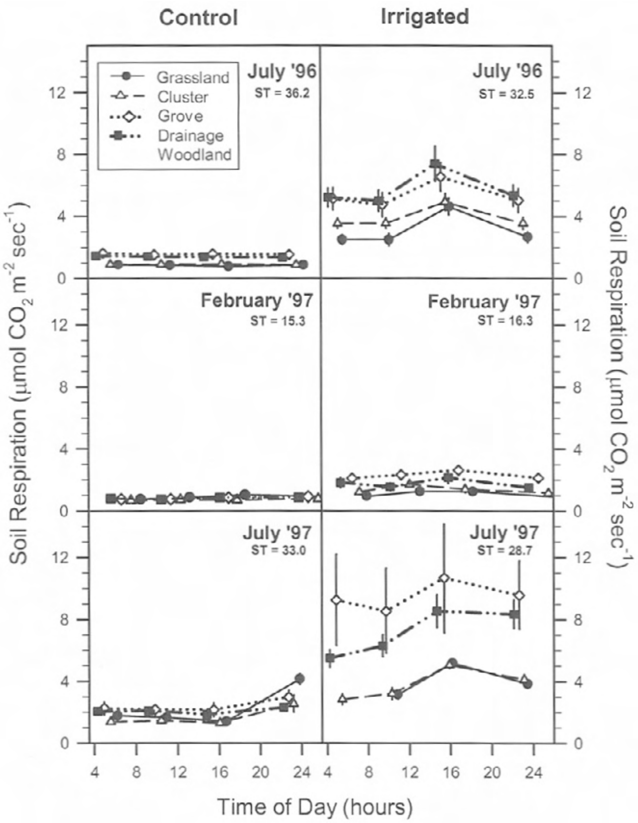

Fig. 2. Diurnal soil respiration curves for control and irrigated plots in each plant community type from the first month of water application (July 1996), a cold month (February 1997), and a hot month 1 yr after continuous irrigation (July 1997). Data are means ± 1 SE. Mean daily soil temperature (ST, °C) averaged across plant communities is shown for each sampling period and treatment.

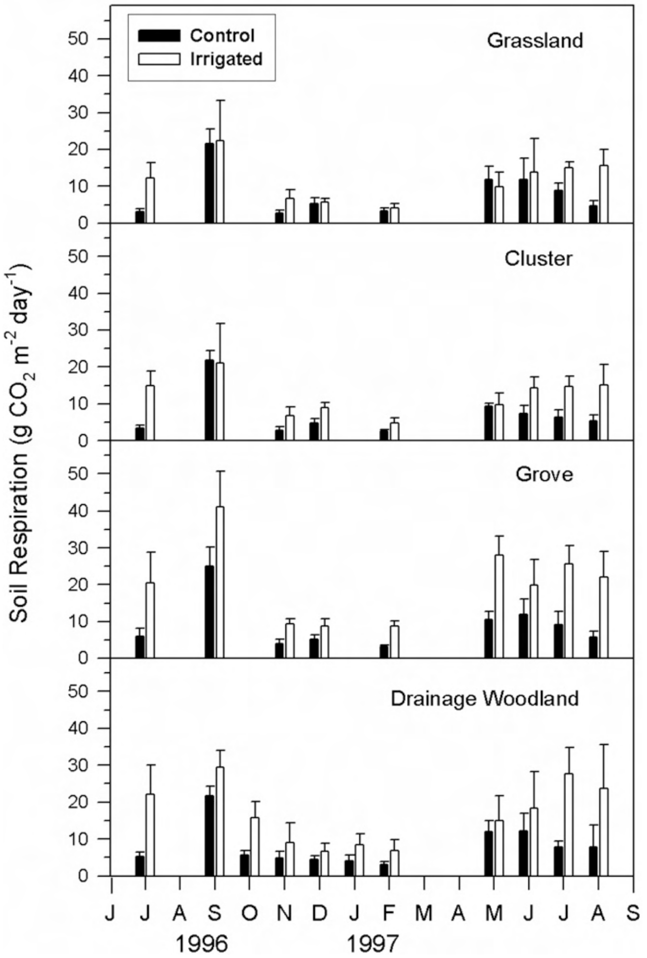

Fig. 3. Seasonal pattern of daily soil respiration rates in control and irrigated plots for each plant community type. Data are means ± 1 SD.

respectively; Fig. 2). Soil respiration rates were generally highest at the 14:30 h reading on any given sample date, except when small rainfall events occurred during the measurement period, thereby temporarily alleviating water stress in the control treatments (such as occurred before the last reading in July 1997, Fig. 2). The most dramatic diel SR cycles occurred during the warm summer months (May–August 1997) for all plant community types and both treatments (typical months are shown in Fig. 2; for the complete data set see McCulley, 1998). During the study, unirrigated grassland diel SR flux was more variable (mean range of 0.76 µmol CO_2 m^{-2} s^{-1} across all diel measurement cycles) than SR from unirrigated woody plant community types (average SR range 0.48 µmol CO_2 m^{-2} s^{-1}). With irrigation, however, drainage woodlands had higher average absolute magnitudes of response (1.72 vs. 1.37 µmol CO_2 m^{-2} s^{-1} for drainage woodland and grassland, respectively).

Seasonal trends in SR were generally similar across plant community types and treatments (Fig. 3). Maximum rates occurred in September 1996 in both irrigated and control plots, and ranged from 21.2 g CO_2 m^{-2} d^{-1} in irrigated clusters to 41.0 g CO_2 m^{-2} d^{-1} in irrigated groves. All main effects and interaction terms were significant in the repeated measures ANOVA on daily SR rates. The significant interactions are the result of small differences in the seasonal SR pattern (specifically May–August 1997) across plant community types and treatment (month × community, $P < 0.05$; month × treatment, $P < 0.0001$) and the lack of a significant irrigation effect on grassland and cluster SR rates in September 1996 (community × treatment, $P < 0.01$).

Irrigation significantly increased SR rates in all community types ($P < 0.0001$; Table 2), with the average daily SR for the study period ranging from 7.1 g CO_2 m^{-2} d^{-1} for unirrigated clusters to 20.8 g CO_2 m^{-2} d^{-1} for irrigated groves. Drainage woodlands and upland groves had significantly higher average daily SR rates than clusters and grasslands in both control and irrigated plots ($P < 0.0001$; Table 2). Grasslands tended to be the least responsive (49% increase), and groves and woodlands the most responsive to additional water inputs (132 and 104% increases, respectively).

Stepwise multiple linear regression models indicated that precipitation, soil moisture, and ST accounted for 75.6% of the variability in daily SR rates of unirrigated control plots (Table 3). Of these three significant environmental variables, total precipitation during the 2 wk before measurement accounted for more of the variability in the data than either ST or soil moisture (63.1, 8.4, and 4.1%, respectively). The regression model for irrigated plots was similar to the control model in that ST, soil moisture, and precipitation emerged as significant predictors, explaining 29.9, 10.7, and 11.4% of the total explained variance, respectively. The irrigated plot model, however, differed from the control model in that the categorical "plant community type" variable, which collapses

Table 3. Regression equations for predicting daily soil respiration in unirrigated and irrigated treatments. Plant community type was run as a categorical variable in both regression models but was only significant in the irrigated data set; therefore, plant-community-specific regression equations are presented for only the irrigated data. Because all plant community types were run in one model, only one R^2 value was generated.

Treatment	Plant community type	Regression equation†	R^2
Unirrigated	all community types	SR = -16978 + 335(ST) + 56099(H_2O) + 8393(PPT)	75.6%
Irrigated	drainage woodland	SR = -9150 + 1254(ST) – 28781(H_2O) + 5670(PPT)	66.4%
	grove	SR = -39239 + 1578(ST) + 147420(H_2O) + 5670(PPT)	
	cluster	SR = -4167 + 670(ST) – 15865(H_2O) + 5670(PPT)	
	grassland	SR = -9335 + 818(ST) – 11653(H_2O) + 5670(PPT)	

† SR = soil respiration (mg CO_2 m^{-2} d^{-1}), ST = mean daily soil temperature (°C), H_2O = volumetric soil moisture (m^3 m^{-3}) in the 0- to 10-cm depth, PPT = precipitation (mm) 2 wk before diurnal SR measurements. All variables included in model were significant ($P \leq 0.05$).

the vegetation and soil differences between the community types into a single dummy variable, emerged as significant, accounting for 14.4% of the explained variance.

The relative importance of ST and soil moisture as predictors of SR rates are also illustrated in Fig. 4. Both control and irrigated plots exhibited a significant relationship between ST and SR, but the proportion of variability accounted for by the van't Hoff function (Eq. [2]) was higher in irrigated (23.8%) than control plots (15.2%). As irrigation increased soil moisture, ST effects on SR were more apparent. All individual plant community types in both control and irrigated treatments exhibited significant exponential relationships between ST and SR (Table 2). The Q_{10} values derived from the exponential relationships ranged from 1.39 in unirrigated clusters to 3.27 in irrigated groves (Table 2). Irrigation significantly increased Q_{10} values (Q_{10} = 1.56 and 2.63 averaged across all control and irrigated plots, respectively, $P < 0.001$), but there were no significant differences between plant community types for either treatment.

DISCUSSION

Water Supplementation and Soil Respiration

Diel variation in SR (range <4 μmol CO_2 $m^{-2}s^{-1}$) measured in this study was comparable to that which has been reported for temperate grassland (~2 μmol CO_2 m^{-2} s^{-1}; Redmann, 1978; Dugas, 1993) but substantially less than what has been observed in Sahelian savanna (~9 μmol CO_2 m^{-2} s^{-1}; Verhoef et al., 1996). Weekly irrigation increased average daily SR rates across all plant community types in this semiarid savanna parkland (Table 2), primarily by increasing SR rates during the warm summer months of June, July, and August (Fig. 3). The fact that water supplementation increased the amplitude of the diel SR curves in all plant community types during these months (Fig. 2) and that precipitation accounted for the majority of the explained variance in daily SR rates in unirrigated plots suggests that SR is water limited at this site. This is consistent with results from other savanna and grassland ecosystems where rainfall events or experimental additions of water can increase SR two- to ninefold (Hao et al., 1988; Liu et al., 2002; Zepp et al., 1996).

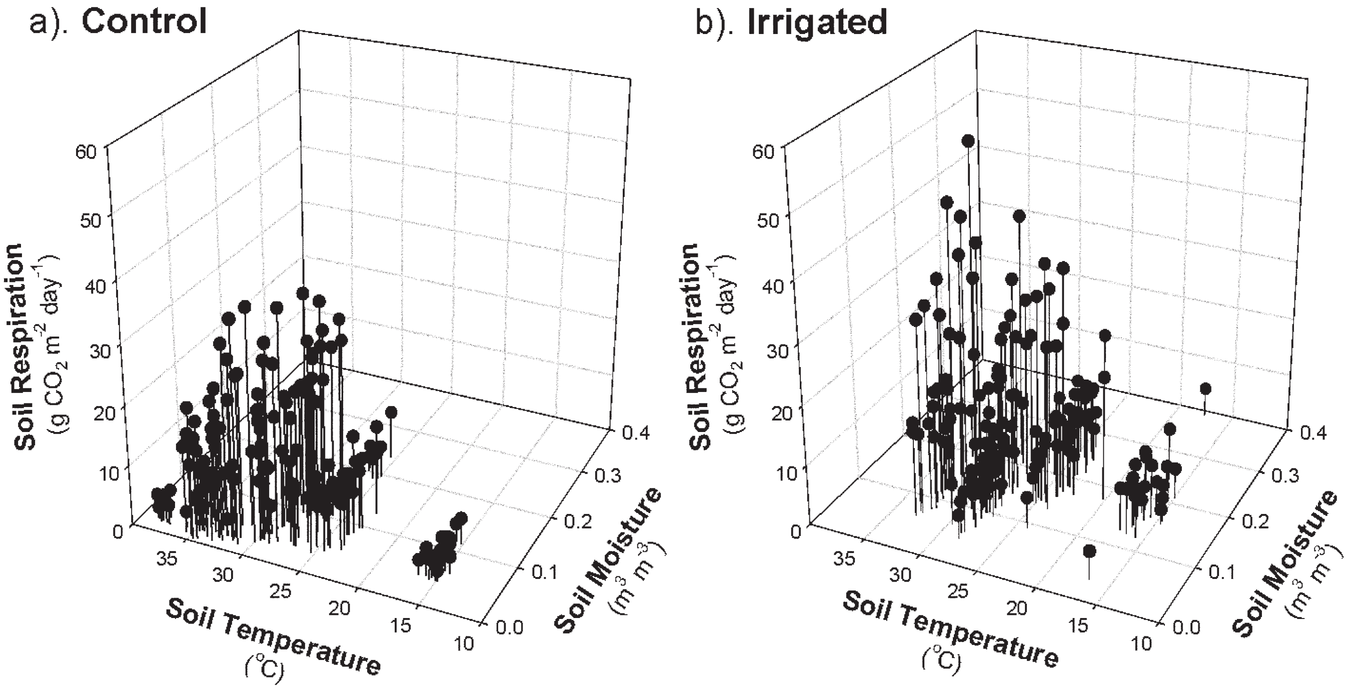

Fig. 4. Relationship between daily soil respiration, volumetric soil moisture (0–10-cm depth), and soil temperature (0–5-cm depth) from (a) control and (b) irrigated plots in all plant community types during the study.

Increased SR following water additions can result from CO_2 displacement from soil pore space by infiltrating water (Kiefer and Amey, 1992; Smart and Peñuelas, 2005), increases in microbial biomass and activity (Orchard and Cook, 1983), or increases in root respiration associated with enhanced plant photosynthesis (Hao et al., 1988). In this study, water was applied ~12 h before measurement, so displacement of CO_2 from soil pore space should have already occurred by the time measurements took place. This supposition is supported by the diel SR curves for irrigated plots, which show that instantaneous SR rates often peaked at the 14:30 h readings (Fig. 2), ~24 h after irrigation. The fact that SR rates peaked at 14:30 h suggests links to biotic processes sensitive to temperature or light availability, such as microbial decomposition or root respiration coupled to photosynthesis.

Separating microbial and root contributions to SR in the field is problematic (Hanson et al., 2000; Subke et al., 2006) and was not attempted in this study. Drying and rewetting cycles within soil, such as those induced by our irrigation experiment, can significantly impact the soil microbial community and C availability (Lundquist et al., 1999). Microbial biomass can increase (Orchard and Cook, 1983; Magid et al., 1999; Fierer and Schimel, 2003), decrease (Kieft et al., 1987; Zhang and Zak, 1998), or have no net response (Fierer and Schimel, 2002) to rapid changes in water availability, depending on the soil nutrient status, the normal climatic regime experienced at the site, and the time between water additions and microbial sampling. Water availability, by controlling plant C uptake, can also influence root respiration. A previous irrigation experiment at this site found that plant shoot elongation, leaf biomass, and the diurnal period of active C gain increased with increased water availability (McMurtry, 1997; Nelson et al., 2002). Given that some ecosystems show tight linkages between plant photosynthetic activity and root respiration (Craine et al., 1999; Wan and Luo, 2003), it seems likely that our irrigation experiment increased the root respiration component of the SR flux. Without specific measurements of microbial and root responses, however, it is impossible to infer whether the increased SR response to enhanced water availability was primarily of root or microbial origins.

In this study, we measured diel SR 12 to 36 h after supplemental watering. Comparing our results with similar water additions in Liu et al. (2002; 50 mm), it is likely that our SR rates on irrigated plots represent a near-peak flux that would decline exponentially with time without further water additions. Logistical constraints prevented us from obtaining dry-down data, but it would be interesting to know how these might differ between the community types. The fact that both precipitation received the 2 wk before measurement and soil moisture at the time of measurement emerged as significant in the regression analyses (the former more so than the latter) suggests antecedent soil moisture conditions play a role in the extent to which SR can regulate upward in response to a water pulse (e.g., Huxman et al., 2004).

Comparison of Grassland vs. Woody Plant Communities

Woody plants establishing on grassland soils may have negative, neutral, or positive effects on SR (Wessman et al., 2004). In our subtropical savanna parkland and woodland, soils associated with woody plant communities developing on former grassland had higher rates of SR than remnant grasslands in both control and irrigated treatments (Table 2). In addition, woody plant communities were also more responsive to irrigation (73, 106, and 131% increases in clusters, drainage woodlands, and groves, respectively) than grasslands (48% increase; Table 2). Our field data are consistent with results from lab incubations of soils from this site (Holland et al., 2000) and sites in New Mexico (Kieft et al., 1998) and California (Fierer and Schimel, 2002). Enhanced CO_2 efflux in lab incubations in which coarse plant roots were removed point to greater substrate availability and microbial biomass as the basis for enhanced SR in soils of woody plant communities compared with grasslands. Woody plant communities at La Copita have larger recalcitrant and labile soil C and N pools (Liao et al., 2006a, 2006b), higher root biomass and turnover (Boutton et al., 1998; Hibbard et al., 2001), and greater soil microbial biomass and potential mineralization activity (McCulley et al., 2004) than adjacent grasslands. Thus, higher SR rates in woody communities could be the result of larger substrate pools supporting a larger and more active microbial biomass or a higher root biomass, and the greater responsiveness of SR to irrigation may result from root and microbial respiratory pathways in these woody communities being better able to take advantage of the relaxation of water limitations.

Biotic vs. Abiotic Controls on Soil Respiration

Despite finding significant differences in SR rates across plant community types, regression analyses suggest that the majority of variability in SR at this site is related to abiotic parameters such as precipitation, soil moisture, and ST (Table 3). Our categorical variable, meant as a composite representation of biotic differences between plant community types that were not measured (e.g., root biomass, litter quantity and quality, etc.), was only significant in the irrigated plots. This result implies that the substantial differences in root biomass and litter quality and quantity known to exist between grasslands and woody communities at this site (Watts, 1993; Hibbard et al., 2001; Boutton et al., 1998) may only impact SR rates when climatic limitations (moisture in this case) are alleviated.

Our regression results concur with those from a global-scale study that found vegetation controls on SR to be secondary to climatic controls (Raich and Tufekcioglu, 2000); however, separating vegetation and biotic controls from those resulting from small but significant alterations in microclimate caused by plants is a well-known difficulty associated with vegetation type comparisons (Davidson et al., 1998, 2000; Raich and Tufekcioglu, 2000). In our study, both ST and soil moisture varied by plant community type (Fig. 1, Table 2), with grasslands being generally warmer during the summer months than adjacent woody plant communities in both control and irrigated treatments. Microclimatic differences between grasslands and woodlands are well known (e.g., Vetaas, 1992), and in more temperate locations, higher soil temperatures in grasslands are thought to drive the enhanced SR rates in these communities compared with adjacent woodlands (Smith and Johnson, 2004).

Sensitivity of SR to temperature (measured as Q_{10}) increased with water additions at this site, a result in agreement with work from semiarid Arizona ecosystems (Conant et al., 2004) and Oklahoma grasslands (Zhou et al., 2006). Soil respiration temperature sensitivities, however, did not differ between plant community types at this site under either control or irrigated conditions (Table 2). The Q_{10} values in our irrigated subtropical grassland and *Prosopis*–mixed shrub communities were similar to those reported by Smith and Johnson (2004) for temperate grassland and *Juniperus* communities, but the control Q_{10} for all plant community types (1.6) is significantly lower than the global average (Schlesinger, 1997), suggesting that water limitations severely limit the ability of respiration to respond to changing temperature (Conant et al., 2004; Harper et al., 2005). Overall, our results suggest that ST and biotic characteristics play a secondary role to precipitation in governing SR at this semiarid, subtropical site.

CONCLUSIONS

Irrigation increased SR rates in all plant community types, suggesting that SR at this site is strongly limited by water availability. Soil respiration rates in woody communities were higher and more responsive than grasslands to water supplementation, suggesting that conversion of grassland to woodland in this bioclimatic region has resulted in a net increase in CO_2 efflux from soils and that this trend will be magnified if precipitation increases in the future. Moisture enhancements also appeared to increase the sensitivity of SR to soil temperature and to biotic influences.

Our water supplementation experiment represented a two- to fourfold increase over mean annual rainfall, meted out (30–50-mm pulses) at a high frequency (weekly). Even so, the SR response to irrigation showed no sign of diminishing during the 1-yr study. Indeed, all plant communities had at least 1 mo during the second growing season (1997) where increases in SR resulting from irrigation were comparable to or greater than those measured after the first water application in July 1996. Thus, there was no suggestion that the elevated SR response to increased water availability was transient or short term. From this study, we conclude that conversion of grassland to woodland at this South Texas site has enhanced the ability of ecosystem C fluxes to respond to increases in water availability.

ACKNOWLEDGMENTS

This research was supported by the USDA/CSRS Rangelands Research Program (94-38300-0286), USDA/NRICGP Ecosystems Program (96-35101-3210), the NASA-EOS program (NAGW–2662), and the Texas Agricultural Experiment Station (H-6945 and H-6717). We thank Andy Hubbard, Chris Stokes, Virginia Capelle, Muzhi He, Chad McMurtry, and Jim Nelson for technical assistance in the lab and in the field. We are also grateful to Dave McKown, Manager of the La Copita Research Area, for his assistance with on-site logistics and housing.

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