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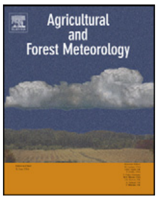

# Long- and short-term precipitation effects on soil $CO_2$ efflux and total belowground carbon allocation

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ABSTRACT

Soil $CO_2$ efflux ($E_{soil}$), the main pathway of C movement from the biosphere to the atmosphere, is critical to the terrestrial C cycle but how precipitation and soil moisture influence $E_{soil}$ remains poorly understood. Here, we irrigated a longleaf pine wiregrass savanna for six years; this increased soil moisture by 41.2%. We tested how an altered precipitation regime affected total belowground carbon allocation (TBCA), root growth, soil carbon, and $E_{soil}$. We used two methods to quantify $E_{soil}$: daytime biweekly manual measurements and automated continuous measurements for one year. We hypothesized that the low-frequency manual method would miss both short- and long-term (i.e., subdaily to annual, respectively) effects of soil moisture on $E_{soil}$ while the high-frequency data from the automated method would allow the effects of soil moisture to be discerned. Root growth was significantly higher in irrigated plots, particularly at 0–20 cm depth. Irrigated annual $E_{soil}$ was significantly greater than that of the control when estimated with the continuous measurements but not when estimated from biweekly measurements. The difference in annual $E_{soil}$ estimates is likely due to (1) the delayed increase in $E_{soil}$ following irrigation pulses of soil moisture (i.e., variation that the biweekly manual measurements missed) and (2) the diel timing of biweekly manual measurements (they were completed early to mid-day before peak efflux). With irrigation, estimates of TBCA increased almost two-fold with automated measurements but only 36% with intermittent measurements. Relative to controls, irrigated treatments stored almost 2 Mg C $ha^{-1}$ $year^{-1}$ more in soils and 0.26 Mg C $ha^{-1}$ $year^{-1}$ more in roots. High-frequency measurements of $E_{soil}$ were essential to estimate total belowground carbon allocation. With irrigation, soil carbon pools were not at steady-state, so shifts in soil carbon storage must be considered in TBCA estimates.

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## 1. Introduction

Atmospheric $CO_2$ has risen 40% since the industrial revolution. This increase is likely to influence both the terrestrial carbon (C) cycle and the complex environmental feedbacks that regulate it (Nemani et al., 2003). Soil $CO_2$ efflux ($E_{soil}$) is the main natural pathway for C movement from the biosphere to the atmosphere, and accordingly is a critical flux in the terrestrial C cycle (Ryan and Law, 2005). Notwithstanding the eight decades of research attention to $E_{soil}$, important questions remain unresolved (Vargas et al., 2010). The insufficient understanding is due in part to the complex nature of $E_{soil}$—a process comprised of both autotrophic and heterotrophic respiratory sources (Bond-Lamberty and Thomson, 2010; Högberg et al., 2002; Tang et al., 2003) which are differentially controlled by environmental factors. The physical and ecological mechanisms that regulate both components also operate at multiple scales in time and space. Soil moisture has been postulated as a critical environmental control (Ryan and Law, 2005) in that it affects $E_{soil}$ directly (Birch, 1964; Liu et al., 2002). However, increased soil moisture also affects $E_{soil}$ indirectly through increasing the temperature sensitivity of respiration (Flanagan and Johnson, 2005; Li et al., 2008; McCulley et al., 2007). Since both temperature and precipitation patterns are predicted to change in future climates, understanding salient environmental controls on soil respiration is critical.

Climate change during the 21st century is predicted to include novel climates—combinations of seasonal temperature and precipitation that have no historical or modern counterpart (Williams et al., 2007). In the US, the southeastern region is predicted to be the most susceptible to novel climates (Williams and Jackson, 2007; Williams et al., 2007). Forecasting ecosystem response to development of novel climates is complicated in several ways. First, correlation-based approaches to prediction are likely to fail

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because novel climates have no existing counterparts; thus, we cannot examine ecosystems in locales with those climate realizations (Jackson et al., 2009; Williams and Jackson, 2007). Second, although all climate models predict substantial temperature increase in the southeastern US, they vary widely in their predictions of future precipitation. Even under the wettest scenarios, however, the climate of the southeastern US may become effectively drier owing to increased evapotranspiration driven by the temperature increase. Furthermore, most simulations suggest greater variability in precipitation patterns, with more high intensity rainfall events and greater drought (O'Gorman and Schneider, 2009) suggesting that pulses of rainfall on dry soils may become more common. However, pulsed events are often not detected by coarse sampling of $E_{soil}$ and may be a critical component of the annual C balance (Vargas et al., 2010)—especially in droughty soils where the impact of soil moisture tends to be greatest (Davidson et al., 2006).

Soil moisture has been shown to affect $E_{soil}$ in complex ways both directly and indirectly. Direct impact of soil moisture on respiration of roots (Burton et al., 2004) and microbes (Birch, 1964) has been reported, and soil moisture affects respiration indirectly through physical changes in the soil environment that influence diffusion rates (Daly et al., 2008; Livingston and Hutchinson, 1995). Furthermore, soil moisture can influence $E_{soil}$ indirectly through attenuation of biological processes such as altering patterns in aboveground C assimilation, and its role in regulating autotrophic respiration (Högberg et al., 2001; Ryan and Law, 2005; Tang et al., 2005a). Lastly, soil moisture indirectly influences $E_{soil}$ through its interaction with the temperature sensitivity of $E_{soil}$ (i.e., $Q_{10}$) (Flanagan and Johnson, 2005; Li et al., 2008; McCulley et al., 2007). Specifically, as soil moisture increases on droughty soils, the rate at which respiration increases as temperature increases is accelerated. These cumulative impacts (i.e., the sum of all direct and indirect impacts) result in both strong patterns of control globally and seasonally (Raich and Potter, 1995; Tang et al., 2005a). However, the cumulative impacts of soil moisture on $E_{soil}$, particularly for subtropical and temperate forests, have been questioned as many studies show very little to poor correlations with soil moisture (Samuelson et al., 2009). The discrepancy between the strong impact of soil moisture at seasonal and global trends reported above—and the lack of impact found in several studies of temperate forests—may be due to methodology.

Accurate measurements of $E_{soil}$ at appropriate and variable temporal and spatial scales, in concert with physical and ecological variables that are likely to regulate variation, are essential to elucidate patterns and controls of belowground metabolic activity (Janssens et al., 2001). Two common methods of measuring $E_{soil}$ are intermittently with a portable soil chamber (LI-6400, Licor Biosciences, Lincoln, NE) and continuously with *in situ* solid-state $CO_2$ sensors (GMM220, Vaisala Inc., Finland); both methods have advantages and disadvantages. The advantages of the intermittent manual method include: mobility, ease of operation, and $E_{soil}$ values that are directly calculated by the machine. Disadvantages of the soil chamber method include: concerns that the chamber can alter the diffusion gradient and have unequal pressure inside and outside the chamber (Davidson et al., 2002), soil disturbance while placing the chamber which can cause errors ($CO_2$ release (Janssens et al., 2000)), coarse temporal sampling, low spatial resolution within the soil column (i.e., surface measurements cannot provide information about the concentration in the soil profile, Tang et al., 2003) and the need for field personnel to conduct measurements. In contrast, advantages of the automated continuous method using *in situ* solid-state $CO_2$ sensors include the ability to take fine-scale, high-density temporal $E_{soil}$ measurements, and collecting data on the spatial variation in $CO_2$ concentration in the soil profile. Disadvantages of the *in situ* solid-state $CO_2$ sensor method include: non-mobile sensor arrays (i.e., limited spatial scale across the site or landscape), requirement of a datalogger with a continuous power source, and $E_{soil}$ calculations based on models which are driven by high density measurements of soil moisture and temperature which can inject error in the estimation of $E_{soil}$.

Here, we use both intermittent manual and continuous automated profile methods to measure $E_{soil}$ and test their ability to discern the effects of soil moisture changes on soil $CO_2$ efflux and total belowground carbon allocation (TBCA). We hypothesized that the former measurements fail to capture both the short- and long-term effects of soil moisture on $E_{soil}$ and the resulting TBCA estimates, while the latter measurements allow these effects to be discerned. We tested our hypothesis in a longleaf pine wiregrass savanna in which an irrigation treatment was imposed for almost a decade. Productivity in this system is more constrained by water availability than by temperature or nitrogen availability (Ford et al., 2008; Mitchell et al., 1999). Although a common assumption of the TBCA approach is that soil C stores are nearly at steady state (Giardina and Ryan, 2002), this may not be true in rapidly aggrading ecosystems or in systems with externally imposed treatments or disturbances. Accordingly, we also assessed whether soil C differentially accumulated in irrigated plots or in control plots over the treatment period.

## 2. Methods

### 2.1. Site description and experimental design

The site is located at the Joseph W. Jones Ecological Research Center in SW Georgia, USA (N 31.27, W 84.48, 158 m asl). The site is 115 km$^2$ in area with the dominant vegetation type of 85–95 year-old fire-maintained longleaf pine savanna with a wiregrass-dominated understory that is species-rich (Kirkman et al., 2001; Mitchell et al., 1999). This system is evergreen and experiences year-round physiological activity (Ford et al., 2008). Fire-return intervals are *ca.* every 2 years, and burns typically occur in winter and spring (February–April). The climate is humid subtropical with a mean of 140 cm of precipitation evenly distributed throughout the year. Mean daily temperatures range from 21 to 34 °C in the summer and 5 to 17 °C in the winter.

We selected eight sites with excessively drained xeric soils located on upland sand ridges of undulating slopes of 3–4%. These soils are deep and coarse textured with no argillic horizon for 300 cm or deeper. Soils are classified as Typic Quartzipsamments and have a water holding capacity of 18 cm per meter of soil. We established eight 50 m × 50 m plots in each site and randomly selected four replicate plots ($n = 4$) to receive an irrigation treatment at a rate of 18 mm every eight days. The remaining four replicate plots served as controls and received no treatment. Irrigation water was treated with reverse osmosis due to the high concentration of $Ca^{2+}$. The eight days between irrigation was needed to complete the four replications given the capacity for delivering 18 mm of water. This irrigation regime has been ongoing since 2003. The irrigation treatment increased precipitation by more than 50% of the average rainfall. Aboveground dominant vegetation characteristics before and after irrigation treatment can be found in Table 1.

### 2.2. Soil collections

Soils were collected at both time zero (March 2, 2001) and at the final harvest in February 2010. Samples were collected using a 2 cm diameter core in 2001 and subdivided into 0–10 cm, 10–20 cm, and 20–30 cm depths. In 2010, five replicates of soil samples were collected at each of the plots using a 3.8 cm diameter core. Each sample was stratified into two different depths, one from 0 to 20 cm and a

**Table 1**
Mean (SE) leaf area index (LAI, $m^2\ m^{-2}$), basal area ($m^2\ ha^{-1}$) and aboveground biomass ($Mg\ ha^{-1}$, sum of pine, oak and wiregrass biomass) of study plots before treatments were applied (treatments began in 2003) and at the end of the current study (in December 2009).

| Year | Treatment | Pine LAI | Oak LAI | Wiregrass LAI | Pine Basal Area | Oak Basal Area | Total Biomass |
|---|---|---|---|---|---|---|---|
| 2001 | Control | 1.12 (0.20) | 0.36 (0.12) | 0.51 (0.11) | 7.62 (1.37) | 1.92 (0.67) | 81.59 (11.44) |
| 2001 | Irrigated | 1.51 (0.13) | 0.17 (0.09) | 0.48 (0.12) | 10.28 (0.89) | 0.92 (0.51) | 104.05 (11.50) |
| 2009 | Control | 1.22 (0.23) a | 0.44 (0.15) a | 0.14 (0.02) a | 8.32 (1.54) a | 2.35 (0.81) a | 89.44 (12.31) a |
| 2009 | Irrigated | 1.73 (0.11) b | 0.25 (0.10) a | 0.28 (0.07) a | 11.78 (0.75) b | 1.34 (0.52) a | 120.48 (9.81) b |

Different letters within the same column denote significant treatment differences in 2009 ($\alpha = 0.05$, one-way ANOVA).

second from 20 to 40 cm. Samples were shipped overnight on ice to the University of New Hampshire. After arrival, samples were cleaned of roots and coarse debris and freeze-dried overnight. Single replicates from each plot were then pooled together so that one sample for each plot (eight samples in total) was analyzed for %C on a CHN analyzer interfaced to a ThermoFinnigan isotope ratio mass spectrometer (Delta-Plus). To analyze annual patterns in soil C change, we first assumed a constant rate of change over all years between the initial samples and the 2010 samples. We then multiplied the annual change in %C by the soil bulk density ($1.56\ g\ cm^{-3}$), integrated across the 40 cm sampling depth, and scaled to the plot.

### 2.3. *In-growth core and collar installation*

We installed five experimental in-growth cores per plot in the soil. Experimental in-growth cores were installed specifically for continuous $E_{soil}$ measurements to take place in. Each core was constructed of a cylindrical PVC frame with open windows between the frame supports (open surface area was 77% of the total surface area). Soil media in the cores was the sieved bulk soil that was extracted from the core location. Cores were 40 cm deep—coinciding with most of the root surface area in this system (Addington et al., 2006)—and 20 cm in diameter, with a perforated PVC bottom to allow drainage. All cores were installed in July 2008; thus, at least five months of biomass in-growth was allowed prior to measurements. While the area containing the plots has long been burned on a 2 year interval, during the experiment, plots were burned in January to February of 2005, 2007, and 2009.

PVC collars were placed within the area of each of the in-growth cores, and an additional five were placed in nearby areas without in-growth cores for manual $E_{soil}$ measurements. The five collars outside the in-growth cores were used to assess spatial variability in the plot. Collars were 10.16 cm in diameter and 5 cm in length, 3 cm of which was inserted into the ground and 2 cm left above the ground. Collars were installed concurrently with in-growth cores.

### 2.4. *Root production estimates*

An additional set ($n = 10$) of in-growth cores was established in each plot to characterize root production. The initial soil volume (12.7 cm diameter × 50 cm) was excavated, sieved (2 mm) to remove all root biomass, and replaced in the volume. Soil was tamped to approximate the original bulk density, and a pin-flag was placed in the center. Roots were allowed to colonize the volume for a two month period. After two months, a smaller volume (10.16 cm × 40 cm) was sampled from the center of the initial volume, using the pin-flag as a guide. Sampling a smaller volume ensured that only roots that had grown into the core during the two month time interval would be sampled. Each sample volume was separated by depth (0–20 cm and 20–40 cm) and sieved twice (2 mm followed by 1 mm). Root biomass was then washed, sorted by functional group (i.e., pine, wiregrass, oak and other), dried to a constant mass at 70 °C, and weighed. Root biomass estimates from the smaller sampled volume inside the core were adjusted to account for the unsampled volume inside the core. To convert biomass to carbon, a subsample ($n = 197$) of roots across all treatments, plots, sampling times, plant functional types and diameter classes was analyzed for %C.

In addition to the above cores, one experimental in-growth core (described above) in each plot was destructively harvested every six months to assess root biomass in the core. The core selected for harvest was the core containing the automated probes (described below). The samples were collected and processed in the same way as the two-month in-growth cores described above, with the exception that the entire core was sampled, not just a smaller volume in the center of the core.

### 2.5. *Automated soil $CO_2$ flux measurements*

We used automated measurements of soil $CO_2$ concentration, soil temperature, and soil moisture content, along with soil physical models to estimate $E_{soil}$ in each plot from January to December 2009. Soil $CO_2$ concentration measurements were made at two depths (10 and 24 cm) in one in-growth core per plot using solid-state $CO_2$ infrared gas analyzers (GMM220, Vaisala Inc., Finland). Only one core per plot was measured at a time due to cost limitations. Probe pairs had 0–5000 ppm and 0–10,000 ppm measurement ranges, with the higher ranging probe measuring $CO_2$ in the deeper location. The raw output ($V$, mV) from each probe was recorded hourly (CR10X, Campbell Scientific Inc., Logan UT USA) and converted to $CO_2$ concentration ($\mu mol\ CO_2\ mol^{-1}$) at a fixed temperature and pressure with a linear calibration equation and coefficients.

$$C_{mv} = \beta \cdot V \tag{1}$$

Probes arrived from the manufacturer calibrated to NIST standards with each $\beta$ parameter specified. Based on the probe specifications, the manufacturer of the sensor (personal communication with Penny Hickey, Vaisala Inc. in California) provided the following empirical formulas for correcting the $CO_2$ concentration readings (volume fraction, $\mu mol\ CO_2\ mol^{-1}$) for temperature and pressure applicable to GMT222 sensors using:

$$C_{cv} = C_{mv} - C_T - C_P, \tag{2}$$

where $C_{mv}$ is the concentration reading from the probes (%$CO_2$), and is corrected ($C_{cv}$, $\mu mol\ CO_2\ mol^{-1}$) for temperature ($C_T$, $\mu mol\ CO_2\ mol^{-1}$) and pressure ($C_P$, $\mu mol\ CO_2\ mol^{-1}$) dependent fluctuations using

$$C_T = 14,000(K_T - K_T{}^2)\left[\frac{25 - T_c}{25}\right], \tag{3}$$

$$K_T = 0.003 + 0.12 \cdot C_{mv} - 0.125 \cdot C_{mv}^2 + 0.06 \cdot C_{mv}^3, \tag{4}$$

$$C_P = 13800 \cdot C_{mv}\left[\frac{P - 101.3}{101.3}\right]. \tag{5}$$

where $T$ is measured soil temperature in Kelvin, and $P$ is barometric air pressure (kPa). Probe $CO_2$ concentration ($C_{cv}$, $\mu mol\ CO_2\ mol^{-1}$) was converted to mole concentration ($C_{cm}$, $\mu mol\ CO_2\ m^{-3}$) using the ideal gas law as

$$C_{cm} = \frac{C_{cv} \cdot P}{R \cdot T}, \tag{6}$$

where $R$ is the ideal gas law constant ($0.00821\,\text{m}^3\,\text{kPa}\,\text{mol}^{-1}\,\text{K}^{-1}$). Soil $CO_2$ efflux ($E_{\text{soil}}$, $\mu\text{mol}\,CO_2\,\text{m}^{-2}\,\text{s}^{-1}$) that is diffused vertically in the soil over a depth ($z$, $\text{m}^2$) was calculated according to Fick's first law of diffusion:

$$E_{\text{soil}} = -D_{\text{s}}\ \frac{\delta C_{\text{cm}}}{\delta z}, \tag{7}$$

where $D_{\text{s}}$ is the coefficient describing the diffusion of $CO_2$ in soil ($\text{m}^2\,\text{s}^{-1}$), $\delta C_{\text{cm}}/\delta z$ is the change in $CO_2$ concentration over the measured depth. $D_{\text{s}}$ was estimated using the Moldrup model (Moldrup et al., 1999) as

$$D_{\text{s}} = D_{\text{a}} \cdot \phi^2 \left(\frac{\varepsilon}{\phi}\right)^{\beta S}, \tag{8}$$

where $S$ is the percentage of mineral soil with size >2 μm (i.e., silt + sand content). The Moldrup model has been widely adopted (Baldocchi et al., 2006; Barron-Gafford et al., 2011; Tang et al., 2005b; Vargas and Allen, 2008); and because of the better fit between measurement techniques it produced in these studies, we chose to use this model in our study. At our site, $S = 0.96$. $\beta$ is a constant ($\beta = 2.9$). We used the $CO_2$ diffusion coefficient ($D_{\text{a0}}$, $\text{m}^2\,\text{s}^{-1}$) in free air for a certain temperature ($T_0$, K) and pressure ($P_0$, kPa) to estimate the $CO_2$ diffusion coefficient ($D_{\text{a}}$, $\text{m}^2\,\text{s}^{-1}$) in free air at another temperature ($T$) and pressure ($P$):

$$D_{\text{a}} = D_{\text{a0}}\left(\frac{T}{T_0}\right)^{1.75}\left(\frac{P}{P_0}\right). \tag{9}$$

The total volumetric soil porosity ($\phi$)—the sum of the soil volumetric water content ($\theta$) and the soil volumetric air content ($\varepsilon$)—was estimated using

$$\phi = 1 - \frac{\rho_{\text{b}}}{\rho_{\text{m}}} = \varepsilon + \theta, \tag{10}$$

where $\rho_{\text{b}}/\rho_{\text{m}}$ is the ratio of soil bulk density to particle density (Lal and Shukla, 2004). We assumed $\rho_{\text{m}} = 2.65\,\text{g}\,\text{cm}^{-3}$ and we determined $\rho_{\text{b}}$ on two mineral soil samples from the depth the probes were measuring $\delta C_{\text{cm}}$ over in each plot (10 and 24 cm).

### 2.6. Manual soil $CO_2$ efflux measurements

In each plot, we manually measured $E_{\text{soil}}$ on each collar ($n = 10$) biweekly (LI-6400-09, LI-COR, Lincoln, NE, USA) and concurrently measured soil $T$ (6000-09TC, LI-COR) and $\theta$ (CS620, Campbell Scientific Inc.) from January to December 2009. Insertion depth at each collar was also measured each time and used to correct soil chamber volume and the resulting $E_{\text{soil}}$. Manual $E_{\text{soil}}$ measurements were not taken during periods of precipitation or irrigation, but resumed as soon as moisture conditions allowed. Two consecutive measurements were made on each collar at a target of 380 ppm. If the plot mean $E_{\text{soil}}$ was greater than $2\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ and consecutive readings disagreed by >15%, measurements were retaken. If the plot mean $E_{\text{soil}}$ was $2\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ or less and consecutive readings disagreed by ≥25%, measurements were retaken.

### 2.7. Climatic and soil abiotic measurements

An open-field weather station measured (TE525, Campbell Scientific Inc.) and recorded (CR10X, Campbell Scientific Inc.) precipitation totals every 15 min. Every 1 min, we measured photosynthetically active radiation (PAR, LI-190SA, LICOR Inc., Lincoln, NE) 6 m above the canopy on a 34.5 m eddy covariance tower, and logged 30 min means (CR3000, Campbell Scientific, Logan, UT). Barometric air pressure, measured *ca.* 1 m above the soil surface, was recorded hourly in one plot. In all plots, automated soil $T$ and $\theta$ measurements were recorded hourly from probes placed adjacent to the in-growth cores. Soil $T$ was measured at two depths (10 and 24 cm) with a type-T thermocouple junction. Soil moisture content was estimated using time domain reflectometry (CS616, Campbell Scientific Inc., USA). In each plot, one probe was inserted at an angle to estimate shallow $\theta$ (10–24 cm depth), two were inserted horizontally to estimate intermediate $\theta$ (30 cm), and one was inserted horizontally to estimate deep $\theta$ (90 cm). Output from each probe ($\tau_{\text{m}}$, μs) was corrected for $T$-dependency ($\tau_{\text{c}}$, μs) using:

$$\tau_{\text{c}} = \tau_{\text{m}} + (20 - T) \cdot (0.526 - 0.052 \cdot \tau_{\text{m}} + 0.00136 \cdot \tau_{\text{m}}^2), \tag{11}$$

where $T$ is in °C (Campbell Scientific Inc., 2002–2006). Soil-specific calibrations that related $\tau_{\text{m}}$ to $\theta$ were made in the laboratory.

### 2.8. Estimating total belowground carbon allocation

To estimate TBCA, we used the approach of Giardina and Ryan (2002). This approach is based on a mass balance approach that relies on conservation of mass (Raich and Nadelhoffer, 1989), but also accounts for changes in the C content of the soil and the C content of roots. Total annual C allocation to roots may be calculated by subtracting the C added to the soil via above-ground litter from the C removed from the soil via $E_{\text{soil}}$ (Raich and Nadelhoffer, 1989) and adding in the annual change in soil and root C content. For the latter estimate, we used our estimates of annual root production (described above) and added in an estimate of the change in coarse root C.

To estimate the change in coarse root C content, we assumed that the coarse root biomass was approximately 17% of aboveground biomass, which was estimated from allometric equations (Mitchell et al., 1999; Mitchell et al. unpublished data) (Table 1). We chose this percentage based on a range of published coarse woody root measurements for southern pine species (Johnsen et al., 2001; Miller et al., 2006; Samuelson et al., 2008, 2010), as no data were available for longleaf pine. Our approach is similar to that of Hendricks et al. (2006a).

The contribution of aboveground litter to soil C flux estimates was considered to be negligible as: (i) there was not a persistent organic horizon on the forest floor due in part to frequent surface fires that consume litter every two years; (ii) the substrate quality of above-ground litter in these systems is low, resulting in slow biological decomposition rates prior to thermal mineralization (Hendricks et al., 2002); (iii) much of the recalcitrant foliar litter was trapped in wiregrass crowns above the soil surface, which further reduces the litter decomposition rates and the potential C input to the soil system (see Hendricks et al., 2002); and (iv) much of the C lost through decomposition is respired directly to the atmosphere (i.e., not via the soil system) or immobilized in the tissues of decomposer organisms. Thus, the annual estimate of $E_{\text{soil}}$ plus the change in soil and root C content was considered to be the estimate of annual TBCA.

We used two separate $E_{\text{soil}}$ series to calculate TBCA: the intermittent manual series, and a modeled continuous $E_{\text{soil}}$ series (Fig. 1). Intermittent manual measurements were spatially averaged in the plot, then scaled to the plot linearly, and integrated in time. The modeled continuous $E_{\text{soil}}$ series was constructed using individual plot multiple linear regression models predicting $E_{\text{soil}}$ manual flux measurements from the automated continuous measurements, root biomass, and soil abiotic conditions. This was necessary since the continuous measurements only captured soil $CO_2$ efflux between 10 and 24 cm depths (i.e., we did not have soil surface $CO_2$ concentration measurements), while the biweekly measurements captured soil $CO_2$ efflux from the entire soil column. All regression models were significant ($P < 0.001$). Independent variables for all regression models included the following: an intercept, total root biomass (g, 0–40 cm), $E_{\text{soil}}$ from automated continuous measurements ($\mu\text{mol}\,CO_2\,\text{m}^{-2}\,\text{s}^{-1}$), soil $T$ (°C, 10 cm), and $\theta$ (% (v/v), 10–24 cm). The number of observations in each plot ranged from 7

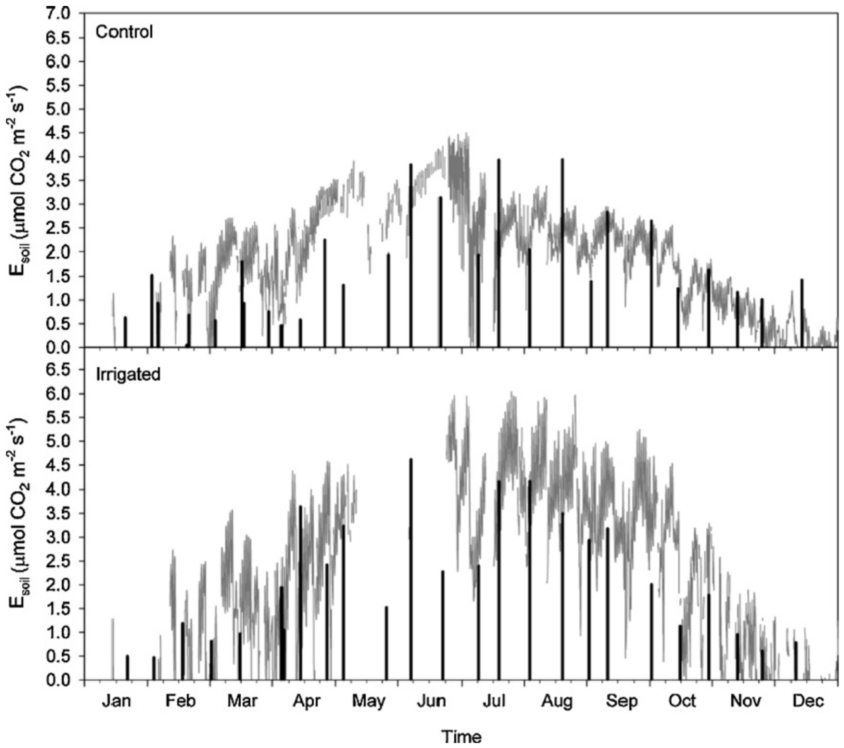

**Fig. 1.** Soil $CO_2$ efflux measured biweekly (vertical bars) and hourly (grey line) in one replicate control (top panel) and one replicate irrigated (bottom panel) plot. Gaps in grey line indicate missing data due to power outages (May), time needed to move systems during experimental in-growth core harvests (January and July), and system downtime during prescribed burns (January and February).

to 10 (i.e., the number of times chamber and profile measurements were available at the same time), and the coefficient of determination (i.e., $R^2$) ranged from 0.53 to 0.99. Equations derived from individual plot data were used with all independent variables to forecast a continuous $E_{soil}$ series. Using the manual biweekly measurement variability and ratios, we incorporated an estimate of plot spatial error in the modeled continuous measurements. We then scaled these estimates to the plot level, and integrated in time.

### 2.9. Statistical models

We tested for treatment and depth effects in soil $T$, $\theta$, cumulative root in-growth, and change in soil C using a mixed linear model with repeated measures (PROC MIXED, SAS). We used the covariance structure that produced the smallest value for the Akaike's Information Criterion (AIC) (Little et al., 1996). For all variables, we evaluated the main effects of depth, treatment, and depth by treatment interactions, and for root in-growth we tested the main effects of functional group, treatment, depth and their interactions. If overall $F$-tests were significant ($P \leq 0.05$) then least squares means tests were used to evaluate significance among treatments and depths. We transformed variables to meet normality assumptions if necessary. Because our hypotheses were stated to expect increases in $\theta$, total root biomass, and soil C in the irrigated treatment these particular post hoc tests were one-tailed.

We tested whether annual TBCA was higher in the irrigated treatment (1-tailed, PROC GLM) compared to the control plots. We used two ANOVA models for these data. In the first model, we tested the effects of method (continuous automated vs. intermittent manual) and treatment, with method within plot considered a repeated measure (PROC MIXED). In this test, we could evaluate whether using both data sets singularly or in combination were valuable in detecting treatment effects. In the second test, we used two separate models to test if the two estimates that differed in frequency could separately discern treatment effects (PROC GLM).

We tested for the short-term effect of irrigation-driven increases in $\theta$ on soil $CO_2$ efflux. Only the modeled continuous series of $E_{soil}$ could be used for this analysis, as the biweekly measurements could not capture the variation among the eight days following irrigation treatments. For this analysis, we used daytime integrated $E_{soil}$ during July 18–August 21. This period represented three complete eight-day irrigation cycles for all four replicate irrigated plots (Fig. 2). We chose this period due to the completion of the dataset (very few missing data), and the fact that this period represented 10–15% of the annual flux. Each day in the irrigation cycle was transformed to a "days after irrigation" series, and $E_{soil}$ for each day was normalized by dividing by the flux on day 0 (the day of irrigation). Within each plot, we averaged fluxes by "days since irrigation" for the three cycles. Then, we tested for the increase in normalized flux among "days since irrigation" (1-tailed) using a mixed linear model with repeated measures (PROC MIXED, SAS). Covariance structure, normality, and post hoc test procedures followed those described above.

## 3. Results

### 3.1. Short- and long-term irrigation effects on soil abiotic conditions

Irrigation treatments increased soil moisture content on short and long time scales. Immediate increases in soil moisture were evident after irrigation treatments (Fig. 2). Following an irrigation event, soil moisture increased by *ca.* 1.2 fold and declined slowly to pre-irrigation six days after the irrigation event (Fig. 3). Over longer time scales, irrigation treatments effectively increased soil moisture in all depths (treatment effect $F_{1,14} = 11.99$, 1-tailed $P < 0.01$) and did so independently of depth (i.e., no treatment by

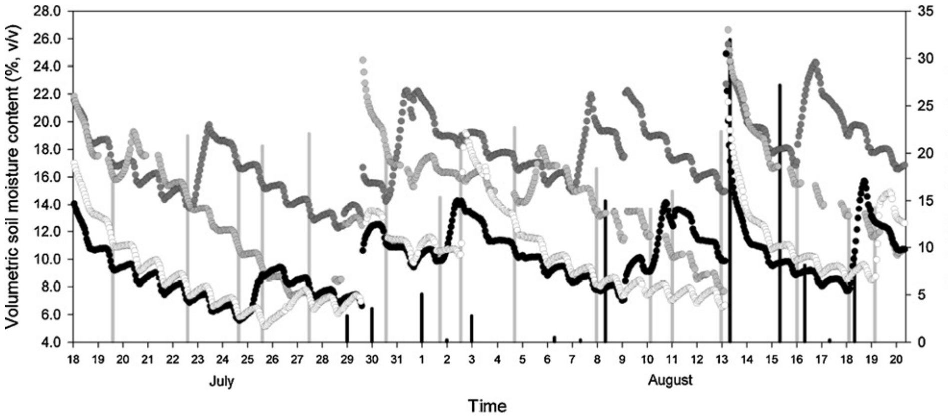

**Fig. 2.** Hourly volumetric soil moisture content from four replicate irrigated plots (lines and symbols), and total daily precipitation (black vertical bars) and irrigation (grey vertical bars) during July 18 to August 21, 2009. Plots were irrigated every eight days on a rotating schedule. Time frame shown represents three complete irrigation cycles for each plot.

depth interaction, $F_{1,14} = 0.61$, $P = 0.28$). From shallowest to deepest soil depth, the mean annual increase was 41.2%, 86.5% and 32.6% (Fig. 4). Soil moisture was higher in the shallowest depth (depth effect $F_{2,14} = 5.43$, $P = 0.01$) compared to the two deeper soil layers (Fig. 4). Across all depths, mean annual soil moisture in the control plots was 7.8%, while in the irrigated plots it was 11.8%. While this substantial increase in soil moisture could possibly reduce surface soil temperature through evaporative cooling, soil temperature measured at 10 and 24 cm did not differ between treatments (treatment effect $F_{1,12} = 0.09$, $P = 0.77$; depth effect $F_{1,12} = 0.20$, $P = 0.66$; interaction $F_{1,12} = 0.47$, $P = 0.51$), and averaged 22.6 and 22.4 °C at 10 and 24 cm, respectively.

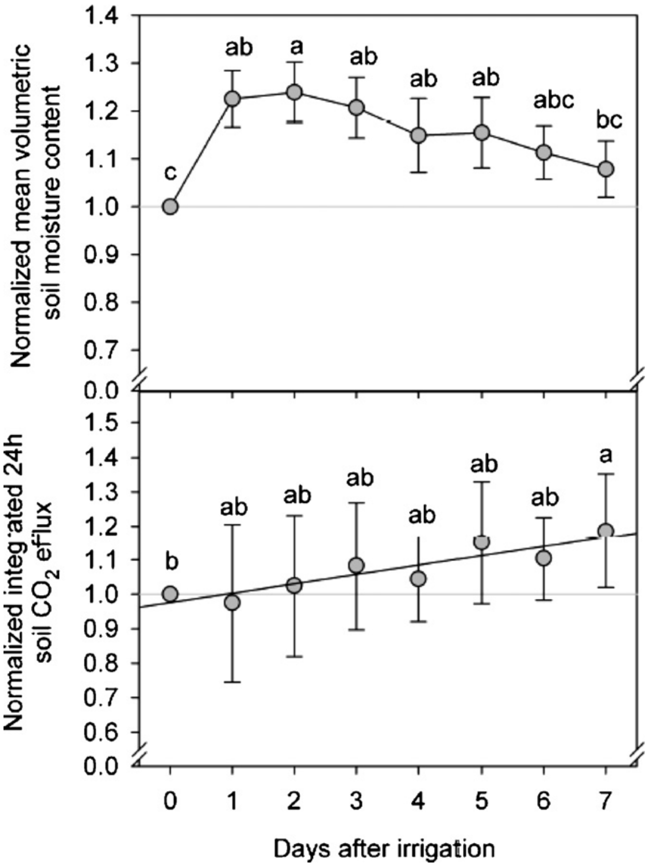

**Fig. 3.** Mean ($n = 4$) normalized daily soil moisture (top panel) measured at 10–24 cm depth and soil $CO_2$ efflux ($\mu$mol $CO_2$ $m^{-2}$ $d^{-1}$, bottom panel) as a function of days since irrigation treatment during July 18 to August 21. Values were normalized by dividing each observation by the observed value on the day of irrigation (day 0). Bars denote standard error. Different letters denote statistically significant differences among days ($\alpha = 0.05$). Line at unity shown for reference. Regression line in bottom panel is $y = 0.97 + 0.027x$, $R^2 = 0.82$, ($P < 0.001$).

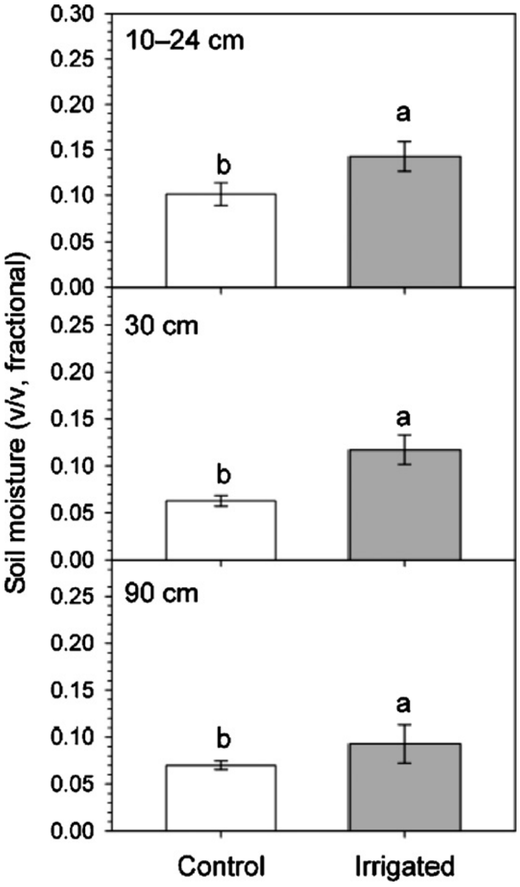

**Fig. 4.** Mean ($n = 4$) annual soil volumetric moisture content in 10–24 cm, 30 cm and 90 cm depths in control (white) and irrigated (grey) plots. Bars denote standard error. Different letters denote statistically significant differences between treatment plots (1-tailed $\alpha = 0.05$).

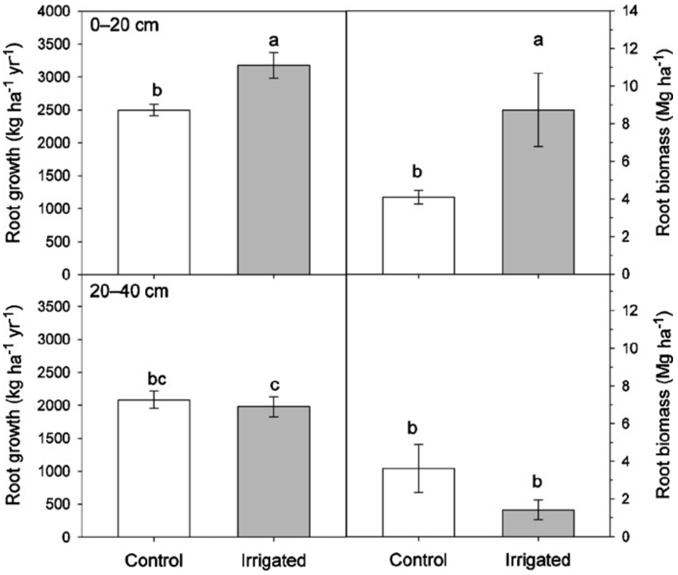

**Fig. 5.** Mean ($n = 4$) cumulative root in-growth for study period (January 2009–September 2010) in 0–20 cm (top panel) and 20–40 cm (bottom panel) soil depths. Bars denote standard error. Different letters denote statistically significant differences between treatments and depths ($\alpha = 0.05$). Mean ($n = 4$) root biomass measured at end of study in January 2010 in 0–20 cm (top panel) and 20–40 cm (bottom panel) soil depths. Bars denote standard error. Different letters denote statistically significant differences between treatments and depths ($\alpha = 0.05$).

### 3.2. *Long-term effects of altered precipitation regimes on soil C*

From 2001 to 2010, irrigation promoted the accumulation of soil C while soils without irrigation had no accumulation of soil C (treatment effect $F_{1,12} = 9.61$, $P < 0.01$). Irrigated soils gained on average 0.45% C over the 9 years (2001–2010). Control plots lost 0.09% C, but this was not statistically different from zero. Soils accumulated or lost C similarly in both soil depths (depth effect $F_{1,12} = 3.34$, $P = 0.09$; interaction $F_{1,12} = 1.22$, $P = 0.29$). At the stand scale, nonirrigated soils lost 0.32 Mg C ha$^{-1}$ year$^{-1}$, while irrigated soils accumulated 1.55 Mg C ha$^{-1}$ year$^{-1}$.

### 3.3. *Long-term effects of altered precipitation regimes on root growth*

Over relatively long time scales, irrigation stimulated root growth 11% in the 0–40 cm soil layer. Cumulative root in-growth mass during the study was significantly greater in the irrigated plots, and the increased mass was distributed with depth in differing ways (treatment by depth interaction, $F_{1,12} = 7.01$, $P = 0.02$). The increased root growth in the irrigated plots was largely concentrated in the 0–20 cm depth, while the root growth in the control plots was more evenly distributed with depth (Fig. 5). In the 0–20 cm soil layer, all plant functional groups increased in root growth; the effect was not dominated by one plant functional group (treatment effect $F_{1,24} = 6.83$, 1-tailed $P < 0.01$; type effect $F_{3,24} = 5.98$, $P = 0.003$; no treatment by type interaction $F_{3,24} = 2.72$, $P = 0.06$).

### 3.4. *Effect of precipitation regime and $E_{soil}$ measurement method on total belowground carbon allocation*

With each irrigation event, the increase in $E_{soil}$ was gradual (*ca.* 3% d$^{-1}$ rate of increase). The day of, and the day after the irrigation event marked the lowest values of $E_{soil}$ for the irrigation cycle (Fig. 3). The seventh day following an irrigation event, $E_{soil}$ was *ca.* 1.2 fold greater than on the day of, or the day following irrigation. Further, it was only after seven days that $E_{soil}$ had increased sufficiently to detect a treatment effect (Fig. 3).

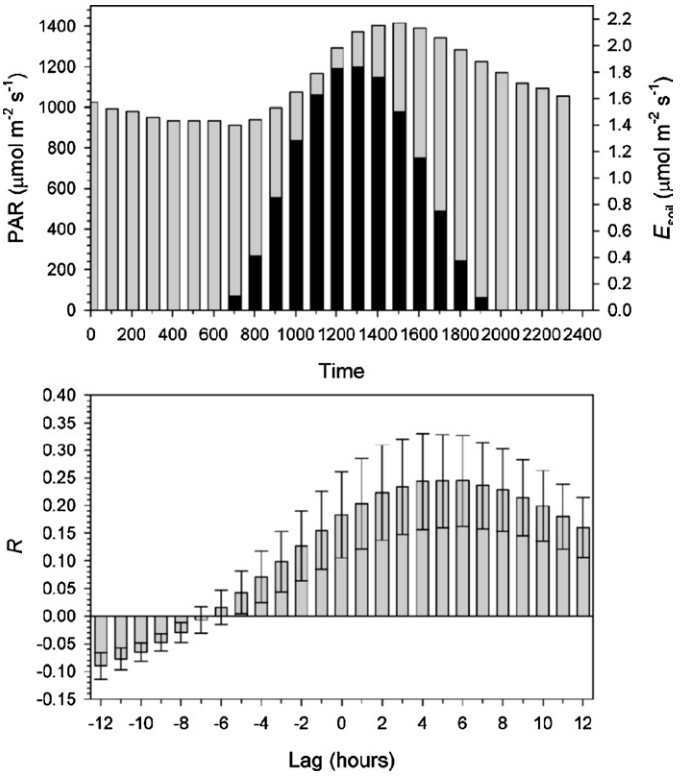

**Fig. 6.** Mean ($n = 4$) annual diel course of soil $CO_2$ efflux ($E_{soil}$, grey bars, top panel) and photosynthetically active radiation (PAR, black bars, top panel). Mean ($n = 4$) Pearson's simple correlation coefficient ($R$) between $E_{soil}$ and PAR for various hourly time lags (bottom panel). Bars are standard error. All $R$ data shown are statistically significant ($n \sim 14{,}000$, $\alpha = 0.05$).

We found a pronounced diel pattern in soil $CO_2$ efflux, with higher efflux in the daylight hours and lower efflux at night (Fig. 6, upper panel). Soil $CO_2$ efflux peaked approximately 4–5 h after maximum PAR (Fig. 6, lower panel).

Total belowground C allocation was dominated by the $E_{soil}$ signal (Figs. 7 and 8). Had we assumed steady state soil C conditions and only used $E_{soil}$ as the variable to estimate TBCA, the $E_{soil}$ measurement method used (i.e., the frequency of measurements) and whether each method was used singularly or in combination to estimate TBCA would have influenced our ability to detect irrigation treatment effects (*cf.* Figs. 7 and 8). Annual $E_{soil}$ intermittent manual measurements estimated were 13.7% higher in the irrigated plots compared to the control plots, but not significantly different ($F_{1,6} = 1.37$,1-tailed $P = 0.14$). However, using continuous automated measurements, annual $E_{soil}$ was significantly higher (82.5%) in the irrigated plots compared to the control plots ($F_{1,6} = 8.27$,1-tailed $P = 0.01$). When both methods were used together, the treatment effect was significant (treatment effect $F_{1,12} = 9.42$,1-tailed $P < 0.01$), and consistent among methods (method effect $F_{1,12} = 0.78$, $P = 0.39$; no treatment by method interaction, $F_{1,12} = 3.49$, $P = 0.08$).

Because soil C was not in steady-state, and C allocation to root biomass increased significantly with irrigation (Fig. 5), increases in TBCA were detected with either $E_{soil}$ method used singularly (automated treatment effect $F_{1,12} = 12.94$, $P = 0.01$; intermittent treatment effect $F_{1,12} = 7.08$, $P = 0.04$) or in combination (type effect $F_{1,12} = 0.45$, $P = 0.51$; treatment effect $F_{1,12} = 20.00$, $P < 0.01$; no treatment by method interaction, $F_{1,12} = 2.05$, $P = 0.18$).

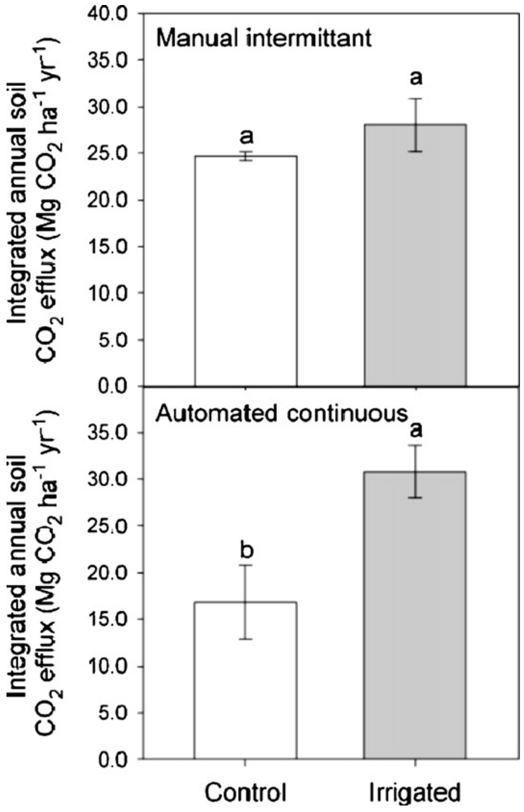

**Fig. 7.** Mean ($n = 4$) integrated annual $E_{soil}$ estimated with intermittent manual measurements (top panel) and modeled from automated continuous measurements (bottom panel) in control (white) and irrigated (grey) plots. Bars denote standard error. Different letters denote statistically significant differences between treatment plots for each estimate type (1-tailed $\alpha = 0.05$).

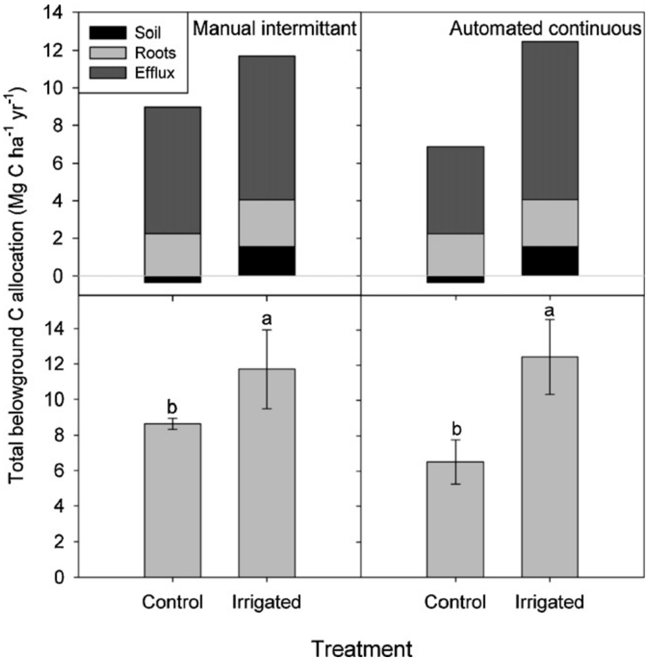

**Fig. 8.** Individual components of total belowground carbon allocation (top panels), and the sum of the components (bottom panels) in irrigated and control plots. Left panels use annual $E_{soil}$ estimated from automated continuous measurements. Right panels use $E_{soil}$ estimated from intermittent manual measurements. Bars denote standard error. Different letters denote statistically significant differences between treatment plots for each estimate type (1-tailed $\alpha = 0.05$).

## 4. Discussion

The irrigation treatment increased soil moisture on short (daily to weekly) and long (annual) time scales, which in turn affected $E_{soil}$, both directly and indirectly, resulting in complex but discernable effects. Moreover, the method of assessment (intermittent manual vs. continuous automated, or both methods used in concert) influenced the ability to resolve these relationships. The intermittent measurements alone failed to capture the short- and long-term effects of soil moisture on $E_{soil}$, while the continuous measurements, alone or in concert with the intermittent measurements, allowed these effects to be discerned, supporting our hypothesis in-part. Once $E_{soil}$ estimates were corrected for the change in soil and root carbon, total belowground allocation increases were evident regardless of the $E_{soil}$ method used.

### 4.1. *Effects of temporal scale*

Soil moisture pulses increased $E_{soil}$ indirectly over short time scales. The effect of the irrigation pulse resulted in soil moisture and $E_{soil}$ patterns that were negatively correlated in time. At short time scales, soil moisture increased by approximately 20% immediately after irrigation; but decreased over time such that seven days after irrigation no treatment effects were observed. In contrast, soil CO$_2$ efflux was affected in a similar magnitude but with contrasting temporal variation. Soil CO$_2$ efflux increased linearly over the eight-day irrigation schedule. This is likely due to several separate processes such as diffusion of CO$_2$ in water coupled with low soil organic matter, and short-term root demographic patterns.

The reduced $E_{soil}$ in the days following irrigation may be due to changes in gas diffusivity in the soil rather than to a direct impact on respiration. The rate of diffusion of CO$_2$ is strongly influenced by soil moisture (Hirano et al., 2003; Tang et al., 2003). The rate of diffusion of CO$_2$ in air is 16 mm$^2$ s$^{-1}$, while it declines by a factor of 10,000 in water (Hillel, 1998). The increased soil moisture from the irrigation events likely lowered CO$_2$ gas diffusion in the pore spaces, increasing CO$_2$ concentration but decreasing flux. This effect can persist for several days (Hirano et al., 2003). For example, Liu et al. (2002) showed that soil moisture peaked in the first 24 h following irrigation pulses, with exponential decreases thereafter; while soil CO$_2$ efflux could increase more gradually, peaking 2–5 days after the event, depending on the amount of the irrigation pulse. This pattern is consistent with our data: the soil moisture peak was followed by the peak in $E_{soil}$ after several days.

Many studies using daily or sub-daily measurements of the response of $E_{soil}$ to soil moisture have reported an immediate increase in $E_{soil}$ in the 24–48 h following a pulse of moisture that declines exponentially with time (Jarvis et al., 2007; Shi et al., 2011; Xu and Qi, 2001). This immediate release of CO$_2$ is most commonly attributed to the rapid availability of labile soil organic matter associated with soil microbial biomass, i.e., the Birch effect (Jarvis et al., 2007). Soils at our sites are defined by little soil organic matter and microbial biomass, characteristic of the Typic Quartzipsamments soils. For example, in the top 20 cm, DeBusk et al. (2005) report approximately one tenth of total soil C (10.1 kg ha$^{-1}$) and dissolved organic carbon (39.4 mg kg$^{-1}$) in this soil series, compared to that found in the more organic lowland soils in the region. They also report *ca.* 145 mg kg$^{-1}$ of soil microbial biomass in this soil series, which is less than 10% of that found in the more organic lowland soils in the region. Similarly, in the top 50 cm of soil, Ike (2010) reports that among the seven soil taxonomic great groups at this site, Quartzipsamments had the lowest carbon concentration at 2.3% and content at 37.3 Mg ha$^{-1}$, or an average of 29% lower and 42% lower than the other groups, respectively. Given the low soil organic matter and microbial biomass in this system, it is not surprising that the immediate pulse of $CO_2$ 24–48 h after an irrigation event was not detected.

Soil moisture pulses can also affect short-term root demographic patterns, which in turn affect soil $CO_2$ efflux. For example, in this system, root demography changes significantly following rainfall events. Root production increases significantly in the 14 days following a pulse of rainfall; and 14 days following pulses of production, mortality increases (Stevens, 2001). A similar pattern has been documented in temperate hardwood systems where low root growth during dry periods was followed by higher growth during higher soil moisture periods (Joslin et al., 2000). Moreover, increased production was also typically followed by significantly increased mortality rates of fine roots in this system (Joslin et al., 2000). The gradual increase in $E_{\text{soil}}$ in the 7 days following an irrigation event is likely the direct result of growth respiration of new roots.

The capacity for intermittent measurements to characterize the complex soil moisture controls on soil $CO_2$ efflux may be affected by these short-term indirect and direct relationships. The degree that irrigation impacts are seen depends on when in the irrigation cycle soil respiration is measured. In our system, bi-weekly measures made 7 days following an irrigation event would have large differences while those made after 1 day would not. In tallgrass prairie, depending on the size of the irrigation event, bi-weekly measures made 2–5 days following an irrigation event showed large differences, while those made after 7–10 days showed very little difference (Liu et al., 2002).

Many studies in temperate systems such as ours that conduct intermittent measurements (weekly, bi-weekly, monthly) also report little to no soil moisture effect on $E_{\text{soil}}$. For example, Maier and Kress (2000) conducted monthly sampling and report that after four years of irrigation a significant irrigation effect was only observed during August sampling (when soil moisture was below 4%). It is worth noting that while our study shares the same soil type (Lakeland sand) the species differed in our study (*Pinus palustris*) from the *Pinus taeda* in Maier and Kress (2000). Similarly, soil moisture increased in 22-year-old thinned compared to unthinned loblolly pine stands, but soil $CO_2$ efflux was only higher in the former stands during two monthly sampling periods; when normalized for temperature, soil $CO_2$ efflux was actually lower in thinned than in unthinned stands (Selig et al., 2008). After six years of irrigation treatments, Samuelson et al. (2009) showed that $E_{\text{soil}}$ was only marginally higher than non-irrigated stands. They also showed that the component of $E_{\text{soil}}$ that most often increases in the first 24–48 h following moisture pulses—the heterotrophic component—showed no increases with irrigation. They also suggested that the apparent lack of soil moisture controls on southeastern temperate systems is a product of soil moisture not falling below critical thresholds that would influence heterotrophic and autotrophic respiration rates. However, each of these studies used intermittent, coarse temporal sampling. Since soil moisture impacts are variable at fine temporal scales, intermittent sampling might have affected the ability to discern soil moisture impacts on $E_{\text{soil}}$. For example, if rainfall or irrigation events delivered periodic pulses of soil moisture, then intermittent sampling may miss these episodes. Likewise, if periodic, systematic intermittent sampling was done relative to the irrigation cycle then bias could result depending when in the cycle sampling occurred.

In addition to short temporal scales, irrigation influenced smaller scale spatial patterns of $E_{\text{soil}}$ (e.g., within the soil profile). While soil moisture increased throughout the first 1 m of soil in response to irrigation, root in-growth only increased in the top 20 cm. This increase in root production was associated with increased soil $CO_2$ concentration and $E_{\text{soil}}$ with irrigation at 0–20 cm depth. The increase in root growth is likely to result in longer-term impacts on $E_{\text{soil}}$ through increasing root standing crop (Fang et al., 1998). Using *in situ* $CO_2$ sensors at various depths can supply additional information into ecosystems function, particularly in savannas and woodlands that continuous chambers at soil surface and periodic sampling cannot (Baldocchi et al., 2006; Carbone and Vargas, 2007).

### 4.2. Precipitation effects on $E_{\text{soil}}$ and total belowground carbon allocation

The capacity to measure fine temporal scale pulses in soil $CO_2$ efflux may be critical to accurately integrating longer term patterns (Vargas et al., 2010). While $E_{\text{soil}}$ differed significantly with treatment over the long term (integrated annual cycle), continuous measures increased the estimate from a 14% increase over the controls to an 83% increase over the controls compared to the intermittent measures. Although there was no significant method by treatment interaction, for the irrigated plots the estimated annual $E_{\text{soil}}$ was slightly higher (10%) when using the continuous automated method compared to the intermittent manual method, and slightly lower (−31%) for the control plots. Two separate effects are influencing these patterns: bias due to measurement timing during the diel cycle, and failure of the intermittent measurements to capture increases in soil $CO_2$ efflux as a result of irrigation pulses. We showed that over a 24 h period, soil $CO_2$ efflux peaked during 1200–1800 h, and this likely biased both of the intermittent manual estimates of TBCA upward. When the daytime upward bias was removed with the automated continuous measurements, the estimate of TBCA was lowered. This effect influenced both treatments. However, the increases in soil $CO_2$ efflux as a result of irrigation pulses likely only affected the automated continuous measurements and not the intermittent manual measurements. This is because the irrigation pulse events significantly increased $E_{\text{soil}}$ in the days following these events, and this was variation that the intermittent manual measurements could not capture. This suggests that cumulative effect of irrigation pulses on $E_{\text{soil}}$ was considerably more important than the cumulative diel bias.

Finer-scale patterns of belowground carbon allocation to root production, mortality, and respiration have emerged primarily from experiments on seedlings in which environmental conditions are tightly controlled. Root elongation starts to decline at soil water potential of −0.3 MPa, and virtually ceases at −1.2 MPa (Kuhns et al., 1985; Larson, 1980; Teskey and Hinkley, 1981; Torreano and Morris, 1998), illustrating the importance of soil wetting events on belowground allocation and root demography. Wetting events, or irrigation pulses, increased total belowground carbon allocation significantly in our study. There are few studies to compare our results to, as manipulative studies of soil moisture in the field are not common. Gower et al. (1992) reported that leaf area and aboveground net primary productivity (NPP) of Douglas fir (*Pseudotsuga menziesii* var *glauca*) were significantly increased by irrigation but belowground NPP was not affected. However, the study was only conducted for 2 years. After four years of treatment, irrigation consistently and significantly increased stem volume increment, aboveground NPP and leaf area index by 25%, 23% and 16%, respectively for stands of *P. taeda* L. (Albaugh et al., 1998). However, fine root production was significantly decreased in only one of the four years studied. Both of these studies used coring methods that underestimate root growth compared to methods that separately assess production and mortality (Hendricks et al., 2006b).

Although the prevailing view—that as soil resources increase, belowground allocation decreases (Molles, 2005; Smith and Smith, 2001)—has been generally incorporated into ecosystem models (Gower et al., 1992; Woodward and Osborne, 2000), this conclusion is under increasing scrutiny. The difficulty in drawing generalizations from the literature is due to several confounding factors. First, soil resources differ in how they influence aboveground vs. belowground growth (Coyle and Coleman, 2005; Ledig et al., 1970). Thus, increased nutrient availability in the soil may differ from increased soil water resources. Secondly, treatments that increase growth rates will alter the proportion of above ground vs. below ground allocation (Ledig et al., 1970). However, most studies of irrigation impacts ignore ontongentic shifts (see discussion by Coyle and Coleman, 2005). In other words, increased soil moisture typically accelerates development of trees; but very few studies compare developmentally similar trees, rather they compare chronologically similar ones. Furthermore, the amount of irrigation that is required to adequately supplement precipitation is often not possible (e.g., irrigation amounts that are low relative to precipitation patterns or throughfall studies that supply a constant proportion of rainfall). During drought conditions, reallocation of a proportion of insufficient precipitation is unlikely to elicit a response. For example, Joslin et al. (2000) report results from a five-year study of mixed hardwoods in which 33% of the throughfall precipitation was removed from the dry treatment and applied to the wet treatment. Net root growth was unaffected by treatment. Root growth varied seasonally but less growth during dry periods was followed by significantly higher growth during more favorable periods. Moreover, treatments and time that show increased production also significantly increased mortality rates of fine roots (Joslin et al., 2000). These data provide mounting evidence for a relatively constant allocation across gradients of soil resources (Hendricks et al., 1993). To this effect, Coyle and Coleman (2005) show evidence that increased belowground resources increase belowground carbon allocation; but, that this is primarily an effect of accelerated growth, not shifts in allocation once growth is accounted for. The amount of carbon allocated to similar sized trees in the control stands over time was no different than that allocated belowground in the faster growing (higher resource) stands at similar ontogenetic stages.

Relative to aboveground production, our present understanding of belowground allocation is weak, despite its critical role in ecosystem C storage, belowground C cycling, water relations, and nutrient uptake by roots and mycorrhizal fungi. The best estimates of belowground allocation appear to derive from mass balance calculations, where total belowground allocation is determined from the difference of $E_{soil}$ and C inputs from litterfall, and corrected for any changes in soil and root carbon storage (Giardina and Ryan, 2002). We found that for this approach to estimating total belowground carbon allocation, high-frequency measurements of $E_{soil}$ were essential. In addition, the assumption of steady-state soil carbon pools was not valid when the effects of changing precipitation regimes were of interest.

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