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REGULAR ARTICLE

Plant community composition and phenological stage drive soil carbon cycling along a tree-meadow ecotone

Andrew B. Moyes · David R. Bowling

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Abstract
Aims We tested the hypothesis that vegetation composition and phenology drive *both* rhizospheric and heterotrophic soil processes, as an alternative to experimental approaches to partition these soil respiration sources.
Methods We compared surface CO_2 efflux, depth profiles of CO_2 production, extractable SOC and MBC, and soil temperature and moisture along transects between contrasting vegetation types (deciduous riparian trees and adjacent meadow) over the snow-free growing seasons of 2005 and 2006.
Results A dense flush of the nitrogen-fixing forb *Melilotus officinalis* dominated the meadow in 2005, corresponding with very high rates of CO_2 efflux (56 % higher than under trees and 82 % higher than in the diverse meadow community present in 2006). In 2006, proximity to trees was associated with greater surface CO_2 efflux and CO_2 production to 50 cm depth. SOC was higher under trees than in the meadow ($p<0.0001$). MBC was not consistently affected by position relative to trees, but seasonality of MBC was altered by trees as an interactive effect of transect position and sample date ($p=0.01$).
Conclusion Community and phenology effects on soil carbon cycling demonstrate the interactions between plant traits and rhizospheric and heterotrophic soil respiration sources. This study highlights a unique case of a highly productive, nitrogen-fixing monoculture exhibiting vastly higher soil respiration rates than a diverse grass-forb community within a single, unmanaged site.

Keywords Soil respiration · CO2 production · Organic carbon extraction · Microbial biomass · Vegetation type · Nitrogen-fixing forb

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Introduction

Respiratory release of carbon from soil remains a portentous feedback to global climate change, because soils contain two to three times as much carbon as the atmosphere, soils already release about ten times as much CO_2 as fossil fuel combustion, and soil decomposition rates are sensitive to interactive effects of climate, biota, and disturbance (Ciais et al. 2013; Le Quéré et al. 2013). Meta-analysis suggests that recent warming has coincided with greater soil respiration around the world (Bond-Lamberty and Thomson 2010), and forward simulations suggest an increasing efflux from decomposition with continued increases in atmospheric CO_2 (van Groenigen et al. 2014). However, our understanding of soil respiration feedbacks to climate change is greatly

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limited by the complexity of interactions that occur between environment, biota, and diverse soil CO_2 sources (Chapin et al. 2009).

As a first step towards making the challenge of understanding soil respiration more tractable, a functional distinction is often made between two carbon sources: (1) CO_2 arising from roots and root-associated microbial organisms consuming recently fixed photosynthates ("rhizospheric respiration") and (2) CO_2 arising from microbial mineralization of soil organic carbon (e.g., "heterotrophic respiration"). This partitioning is useful because these two categories represent fundamentally different sources with very different implications for exchange of carbon between ecosystems and the atmosphere. However, in real soils there is no division between these categories. Due to factors such as root symbioses, exudation, and turnover, there is a continuum of relative dependence on recently fixed photosynthates in soil, with opportunistic switching between recent and older carbon sources (Högberg and Read 2006).

Additionally, methods to partition rhizospheric and heterotrophic sources have encountered many challenges (Hanson et al. 2000; Kuzyakov 2006; Subke et al. 2006; Trumbore 2006; Hopkins et al. 2013). Perhaps the simplest and most commonly used approach is root exclusion via trenching to a depth below roots and placing a diffusive barrier in the trench, creating soil compartments with and without live roots. However, this approach is hampered by a variety of artifacts that impact the actual or attributed strengths of these sources: the decomposition of roots severed by trenching, differences in soil moisture due to absence of transpiration, priming effects of live root exudation, and lateral diffusion of CO_2 beneath trench barriers (Cheng et al. 2003; Jassal and Black 2006; Subke et al. 2006; Comstedt et al. 2011; Heinemeyer et al. 2012). Thus, while trenching and similar partitioning approaches help us examine how rhizospheric and heterotrophic sources function and respond to environmental change, they often rely heavily on an artificial (and *artifactual*) root-free soil.

An alternative to partitioning approaches is to compare soil carbon cycling between adjacent vegetation types as intact plant-soil systems. Similar to the trenching method, this assumes that climatic and edaphic conditions are largely maintained across short distances (Raich and Tufekcioglu 2000), but this approach provides a way to assess the importance of vegetation in mediating soil carbon dynamics without imposing problematic experimental treatments. Rather than separating rhizospheric and heterotrophic categories, soil processes can be compared more holistically for each type of vegetation, illuminating important interactions (Bell et al. 2015). This inclusive consideration of the plant-soil continuum allows us to evaluate the role of vegetation in soil carbon cycling and its sensitivity to environmental change.

Differences in vegetation type lead to spatial and temporal variability in rates of assimilation and transport of carbon belowground, litter production, soil chemistry and soil microclimate (temperature and moisture), and thus can impact variability in both rhizospheric and heterotrophic soil respiration (De Deyn et al. 2008; Metcalfe et al. 2011; Bell et al. 2015). Fast-growing species like grasses and forbs metabolize greater amounts of carbon for growth, and typically produce large inputs of readily-decomposable plant material, while slower-growing plants like trees generally allocate more carbon to defense and structural tissues, and produce smaller inputs of longer-lasting, nutrient-poor litter (Raich and Tufekcioglu 2000; Chapin 2003). A few existing studies of soil respiration with adjacent grasslands and trees have shown decreasing (Tang et al. 2005) and increasing (Raich and Tufekcioglu 2000) soil respiration rates with distance from trees, depending on interactive effects of vegetation, season, and regional climate (e.g., Mediterranean vs. temperate trees and grasslands). However, these studies did not investigate the different ways that vegetation impacted surface CO_2 efflux, by comparing of depth of CO_2 production, soil available carbon substrates (dissolved organic carbon), or microbial biomass during phenological transitions such as germination, leaf emergence, or senescence.

In a previous study, we used a high frequency, automated soil gas sampling system located in the center of a Rocky Mountain meadow to evaluate temperature and moisture controls on soil respiration over four growing seasons (Moyes and Bowling 2013). We characterized the interactive effects of interannual differences in moisture, temperature, meadow phenology, and seasonal soil respiration. However, that study was limited to a single location and vegetation type and did not evaluate interactions between vegetation and soil carbon or microbial activity. In the present study, we compared spatial patterns of soil respiration, in addition to soil organic carbon and microbial biomass carbon, along replicated transects running from within the meadow to

underneath surrounding deciduous trees. We examined the influences of contrasting vegetation types and phenologies between deciduous trees and an herbaceous meadow, and a dramatic interannual shift in meadow community composition, on soil microclimate, extractable soil organic carbon and microbial biomass carbon, and soil CO_2 efflux and production with depth. We tested the hypothesis that vegetation composition and phenology drive *both* rhizospheric and heterotrophic soil processes, as an alternative to experimental approaches to partition these soil respiration sources. We expected that soil respiration in the meadow would be coupled to growth of herbaceous annual vegetation, peaking in midsummer, but that respiration under trees would begin earlier in the season and extend through leaf drop in late fall. We also expected that soil organic carbon would be higher under trees than in the meadow and seasonally highest following autumn senescence. In addition, we were interested to observe how microbial biomass would vary in relation to soil respiration and seasonally contrasting vegetation types.

Methods

Site description

We conducted the study around the perimeter of a meadow within Red Butte Canyon (111°47′47″W, 40°47′21″N, 1760 m elevation) near Salt Lake City, Utah, USA, in the snow-free periods of 2005 and 2006. A perennial stream flowed between the trees growing along the western side, but the 4.3 ha meadow was surrounded on all sides by boxelder (*Acer negundo*) and bigtooth maple (*Acer grandidentatum*) trees, with water birch (*Betula occidentalis*), red osier dogwood (*Cornus sericea*), and false Solomon's seal (*Smilacina stellata*) in the understory of the riparian zone. In 2005, the meadow and the understories of several trees were dominated by a dense growth of yellow sweetclover (*Melilotus officinalis*), a nitrogen-fixing legume (Schubert and Evans 1976). The flush of this species in 2005 exceeded 90 % cover (by visual estimation) and 1 m height (Fig. 1), compared to its presence of <5 % cover observed by the authors over the summers of 2006–2009. In 2006 the meadow vegetation contained a variety of native and introduced grasses and forbs< 1 m tall, including orchard grass (*Dactylis glomerata*), blue wildrye (*Elymus glaucus*), rye brome (*Bromus secalinus*), milfoil yarrow (*Achillea millefolium*), dalmation toadflax (*Linaria dalmatica*), and houndstongue (*Cynoglossum officinale*). The site receives about 500 mm of precipitation annually, which primarily arrives as snow in winter. Soils are derived from Holocene flood-plain alluvium extending several meters deep (Ehleringer et al. 1992), are well-drained, calcareous, and are loamy to 20 cm depth (41/41/18 % sand/silt/clay), and sandy loam (55/28/17 %) from 20 to 50 cm depth. Additional site details are available in Moyes and Bowling (2013) and Hultine et al. (2007).

We established transects running 9 m towards the center of the meadow from the bases of eight *A. negundo* (dioecious, 4 male and 4 female) and two *A. grandidentatum* (monecious) trees positioned around the perimeter of the meadow (Fig. 2). Crown radii ranged from 1.6 to 5.0 m (mean, 3.8±0.3 m (SEM)). In 2005, we sampled at 3, 6, and 9 m from tree trunks (Fig. 2). In 2006, we moved one of the sampling locations closer to the trees, and collected measurements at 1.5, 3, and 9 m.

Soil surface CO_2 efflux

We installed 30 soil respiration collars (10-cm diameter polyvinylchloride, 3 per transect) in spring of both years at least 2 days before measurements began, and kept them free of live plant stems for the duration of the summer. We measured surface CO_2 efflux within the collars between 09:00 and 17:00 h using a portable gas exchange system connected to a closed soil chamber (Li-6400 and 6400–09, Licor Biosciences, Lincoln NE, USA). Sampling was conducted along transects in alternating sequences, so that time of day of collar measurements did not bias results by transect number or transect position. Surface CO_2 efflux measurements were conducted every 1–2 two weeks between May 23 (day of year 143) and August 27 (239) in 2005, and from April 27 (117) to November 3 (307) in 2006. During surface CO_2 efflux measurements, we concurrently measured soil temperature at 10 cm using the instrument temperature probe and volumetric water content (θ) of the top 20 cm with a soil moisture probe (Hydrosense, Campbell Scientific, Logan UT, USA).

Soil CO_2 production with depth

To characterize depth patterns of soil CO_2 production under each vegetation type, and their variation with season and plant phenology, we modeled diffusion and

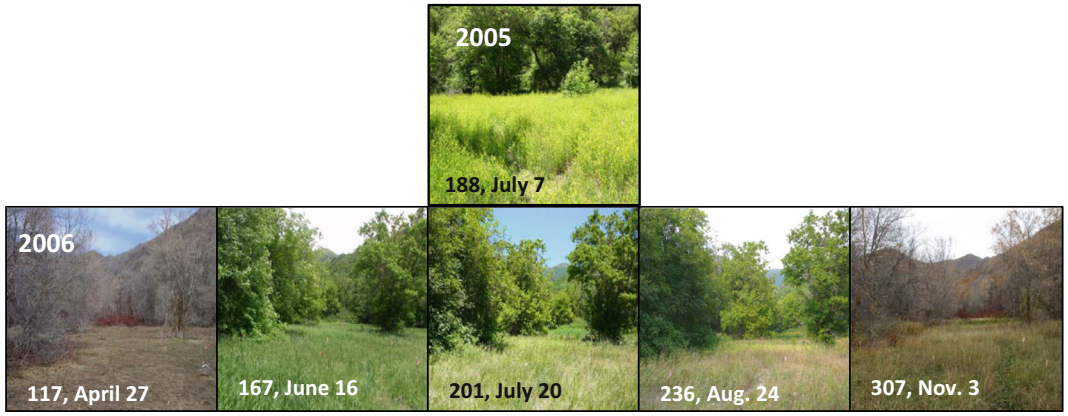

Fig. 1 Upper image shows 2005 flush of *Melilotus officinalis* in the meadow in midsummer. Lower photographs were taken in 2006 looking northwest from a central position in the meadow, showing phenological status of trees and meadow vegetation on the five intensive sampling dates (numbers are day of year)

production with depth using measured depth profiles of CO_2 and diffusive gas transport parameters. We selected five time periods to represent phenological transitions of the meadow and trees during the 2006 growing season. These were centered on tree bud break, before meadow germination (day of year 117, April 27); tree leaf expansion and meadow post germination (DOY 167, June 16); initiation of meadow senescence (DOY 201, July 20); initiation of autumn leaf color and abscission in trees (DOY 236, August 24); and post tree leaf drop and meadow senescence (DOY 307, Nov. 3) (Fig. 1).

To measure CO_2 depth profiles, we installed gas well arrays at 1.5, 3, and 9 m transect positions of six replicate transects (108 wells total). These six transects included five *A. negundo* (3 male, 2 female) and one *A. grandidentatum*, and were selected to have equal spacing around the meadow, near and opposite the stream side. Gas wells consisted of 6.35 mm OD stainless steel tubing attached to tube unions (SS-400-6, Swagelok, Solon, OH) at the top, sealed with septa (Microsep F-138, Alltech, Deerfield, IL, USA), and with buried, open ends inserted to 5, 10, 20, 23.5, 38.5, and 48.5 cm soil depths. Gas wells were tapped into the ground vertically from the surface (without digging) using a rubber mallet, with a steel rod temporarily placed within each tube during installation to

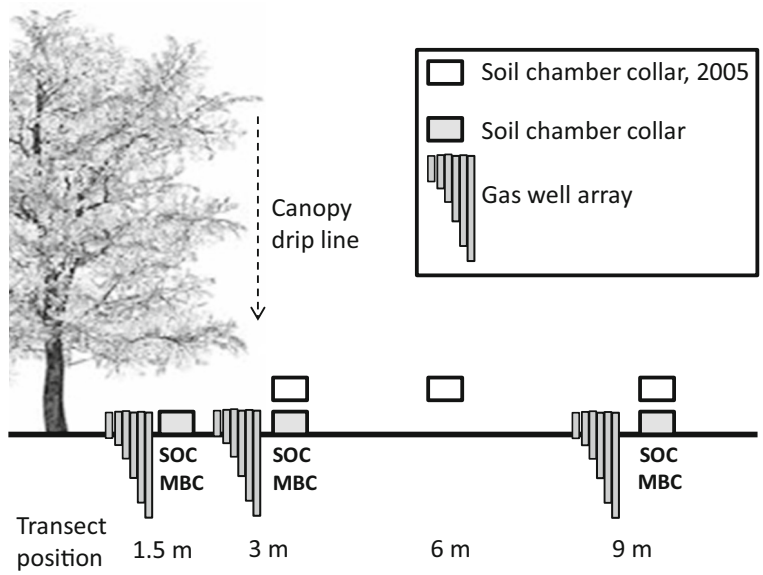

Fig. 2 Schematic showing one of 10 tree-meadow transects used in this study, showing transect positions used for soil chamber, gas well, soil organic carbon (SOC), and microbial biomass carbon (MBC) measurements. Open rectangles represent soil chamber measurement positions in 2005. All other measurements occurred exclusively in 2006. The canopy drip line is also shown, as some data are presented relative to this position to account for differences in tree size and 2005–2006 measurement positions

prevent clogging with soil or roots. Gas wells were left in place throughout the 2006 snow-free season. We measured mole fraction of CO_2 from each well by sampling gas via the septum with a gas-tight syringe (050035 (A-2), Pressure-Lok, VICI, Baton Rouge, LA) and injecting 0.5 mL at ambient pressure into a circulating, CO_2-free air loop, just upstream of an infrared gas analyzer (LI-7000, Licor Biosciences, Lincoln NE, USA), as described by Davidson and Trumbore (1995). We calibrated injection peak areas by measuring injection standards prepared from volumetric combinations of CO_2-free air and pure CO_2, as described by Moyes et al. (2010b).

We measured depth profiles of soil moisture by collecting soil cores to 50 cm in 10 cm increments using a bucket auger and determining soil water content of each increment gravimetrically. We measured initial mass of cores in the field with a digital scale and then dried samples in an oven at 60 °C before measuring dry mass on the same scale. We calculated volumetric water content (θ, $m^3\ m^{-3}$) by assuming a soil particle density of 2.65 g/cm^3.

To model a soil temperature profile for each sample date and transect position, we utilized concurrent soil temperature data obtained from type T thermocouples buried at 3, 10, 22, and 48 cm in the center of the meadow and measured automatically several times a day (Moyes and Bowling 2013). We adjusted this temperature profile to match soil probe temperature data collected at 10 cm during soil respiration measurements at each transect position.

Our model results of CO_2 production and flux densities were calculated according to soil porosity-diffusivity relationships developed for this site and additional diffusive transport equations described by Moyes and Bowling (2013). We modeled vertical fluxes of CO_2 at each 5 cm depth interval (and the soil surface) using Fick's first law of diffusion, as the CO_2 molar density gradient times a diffusion coefficient. We then calculated CO_2 production ($\mu mol\ m^{-3}\ s^{-1}$) within depth intervals as the difference in CO_2 flux density between the upper and lower depth limits of each interval, divided by the difference in depth.

Soil organic and microbial biomass carbon

To compare effects of vegetation on potential soil organic matter mineralization, we measured extractable soil organic carbon (SOC) and microbial biomass carbon (MBC). We collected 5 cm diameter soil cores to 10 cm depth at 1.5, 3, and 9 m transect positions of all 10 transects (n=30 per sample date) during each of the five intensive sampling periods. We sieved soil samples to particles<2 mm at field moisture, and then placed two 5 g samples into separate 25 ml sample tubes. We collected an additional soil sample, which was subsequently dried and weighed to correct measurements to dry soil mass. We extracted SOC from one 5 g sample using 20 ml 0.5 M potassium sulfate (K_2SO_4) solution. We incubated the second samples with cotton doused with 2 ml chloroform for 2 days to lyse microbial cells, after which we removed the cotton and extracted the sample with 20 ml 0.5 M K_2SO_4 solution. Sample solutions were filtered (No. 4, Whatman International LTD, Maidstone, UK) and stored at −18 °C until measurement with a total organic carbon analyzer (TOC 3201, Shimadzu, Columbia MD, USA), against blanks prepared using the same procedure, but omitting soil. Carbon amounts in un-fumigated samples were assumed to represent K_2SO_4-extractable SOC, and K_2SO_4-extractable MBC was calculated by subtracting SOC from paired fumigated samples (Vance et al. 1987; Needelman et al. 2001).

Statistical analysis

We used analysis of variance (ANOVA) to test for differences in soil respiration chamber measurements associated with year (2005 and 2006), position of collar under canopy vs. in open meadow, time of sampling, and their interactive effects. We compared equal sample sizes from 2005 to 2006. Sampling dates were matched and separated into periods classified as either during the growing season (between days 100 and 213 (Moyes and Bowling 2013)), or after senescence (days 214 to 271). We evaluated effects of tree canopy on soil moisture and temperature by comparing average temperature and soil moisture under the canopy and outside the canopy for each sample date in 2005 and 2006 using a t-test. We used ANOVA to test for effects of transect position and sampling date on modeled CO_2 efflux, soil organic carbon, and microbial biomass carbon. Soil CO_2 production was compared across depths of 0–10, 10–20, and 20–50 cm (as the sum of modeled 5 cm depth intervals within each larger interval) by day of sampling, and by transect position, using ANOVA. We identified significant differences (p<0.05) using Tukey's honestly significant difference criteria for pairwise comparisons,

with Bonferroni corrections. We used linear regression to test for correlations of SOC and MBC with modeled CO_2 production in the top 10 cm of soil.

To compare soil respiration in 2005 and 2006 we utilized soil chamber data because the same chamber measurement method was used in both years. However, to evaluate soil respiration patterns in 2006, we emphasized CO_2 diffusion model results for two reasons. First, the diffusion model provided additional information about depths of CO_2 production, which we expected to differ between tree and meadow locations. Second, we previously found that for this site, our modeling approach gave reliable estimates of daily average CO_2 flux densities (Moyes and Bowling 2013), which we deemed more informative than instantaneous chamber data, which are subject to seasonally-variable diel fluctuations.

Results

Soil moisture and soil temperature were negatively correlated, following a similar relationship across all transects and over the measurement periods in both 2005 and 2006 (Fig. 3e), though the meadow vegetation contrasted strongly between the 2 years (Fig. 2). Soil moisture and temperature varied more with season ($p<0.001$) than with transect position ($p<0.006$, Fig. 3). However during the warmest months, soil moisture was slightly higher ($p<0.01$ between days 147–239) and soil temperature slightly lower ($p<0.01$ between days 147 and 209) under tree canopies than in the open meadow (Fig. 4). Dense growth of the nitrogen-fixing, Eurasian legume *Melilotus officinalis* in 2005 was associated with greater soil CO_2 efflux in the meadow during growing season of 2005 (10.36± 4.32 μmol m^{-2} s^{-1}, $n=300$) than 2006 (6.53± 1.97 μmol m^{-2} s^{-1}, $n=155$, $p<0.0001$, Fig. 3). This difference in soil respiration between years was larger than differences associated with transect positions from tree to meadow in the 2006 growing season (6.88± 0.22 μmol m^{-2} s^{-1}, $n=87$ under trees and 5.89± 0.17 μmol m^{-2} s^{-1}, $n=50$ in the meadow), though the impact of trees on soil chamber measurements was significant across 2005–2006 ($p<0.001$, Figs. 4 and 5).

Over the 2006 growing season, modeled surface CO_2 efflux was higher under trees (1.5 m, 4.38± 0.39 μmol m^{-2} s^{-1}, $n=30$) than at the 3 (2.51± 0.17 μmol m^{-2} s^{-1}, $n=30$) and 9 m (2.47± 0.22 μmol m^{-2} s^{-1}, $n=30$) transect positions ($p<0.0001$). Model results for surface CO_2 efflux were similar for the 3 and 9 m positions throughout the year. Day of year affected modeled surface CO_2 efflux across all transect positions ($p<0.001$), with a significant increase from day 117 to day 201, and then a decrease to lowest observed values at day 307. Interactive effects between transect position and day of year were suggested, but not significant for modeled surface CO_2 efflux ($p=0.057$). Production of CO_2 within the soil was generally greatest near the surface (Fig. 5d), decreased to 10–20 cm and continued to decrease to 20–50 cm ($p<0.0001$). CO_2 production throughout the profile was greater at the 1.5 m transect position at all depth intervals ($p<0.0001$). Interactive effects of transect position x sample date were also found for CO_2 production at all three depth increments ($p<0.0001$).

Seasonal comparisons of modeled surface CO_2 flux density vs. soil temperature and soil moisture during the intensive study periods of 2006 reflected seasonal patterns under trees and in the meadow (Fig. 6). At day 117 (April 27) the meadow vegetation had just recently begun to germinate or re-sprout and trees were just about to flower (trees of the two tree species flower just before leaf expansion). However, by this time average surface flux density at the 1.5 m transect positions was already 4.4±0.5 μmol m^{-2} s^{-1}, 77 % of the seasonal maximum of 5.7±0.5 μmol m^{-2} s^{-1} (measured on day 201), whereas flux density at the 9 m (meadow) position increased from 2.1±0.3 at this date to a seasonal maximum of 3.2±0.5 μmol m^{-2} s^{-1} on day 236. Surface CO_2 flux density remained at the seasonal maximum between days 201 and 236 under trees and in the meadow ($p<0.0001$), despite senescence of meadow between these dates (Fig. 1). By day 307, the coldest and wettest sample date after senescence of both vegetation types (Fig. 1), surface CO_2 flux density was similarly low under trees and in the meadow.

Extractable soil organic carbon (SOC) in the upper 10 cm of soil was greater at the end of the growing season than in spring for all transect positions ($P=0.004$), and was higher under trees than at the 3 and 9 m positions ($P<0.0001$, Fig. 5b). In contrast, extractable microbial biomass carbon (MBC) was highest in spring when the majority of extracted soil carbon was found as microbial biomass (Fig. 5a, $p<0.0001$). MBC was not consistently related to vegetation type (transect position), but was interactively affected by transect position x sample date ($p=0.014$). Consistent relationships were not found between CO_2 production rate found for

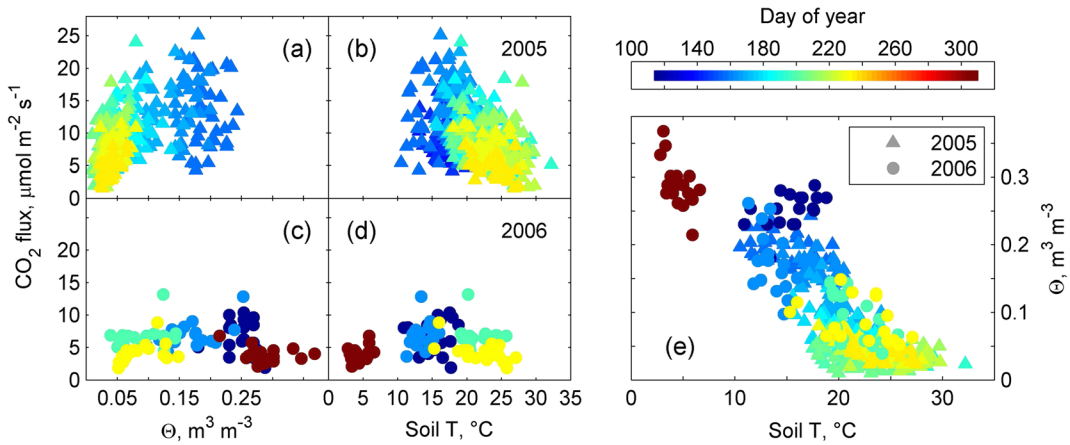

Fig. 3 Point measurements of surface CO_2 flux density made with the soil chamber vs. volumetric soil moisture at 0–20 cm (θ, **a**, **c**) and soil temperature at 10 cm (**b**, **d**) for growing seasons of 2005 and 2006. (**e**) Volumetric soil moisture plotted against soil temperature during soil chamber measurements. Symbol color in all panels corresponds with day of year, shown in the color bar above (**e**)

the 0–10 cm interval of soil and MBC (p=0.76) or SOC (p=0.30) from 0 to 10 cm (Fig. 7).

Discussion

To evaluate the role of vegetation traits on soil carbon cycling, we capitalized on vegetation gradients between a meadow and surrounding trees, and compared intact plant and soil processes, thus avoiding experimental artifacts often imposed in partitioning studies. Our study benefitted from an ideal natural experiment that occurred when the vegetation within the meadow drastically changed between years without accompanying changes in seasonal microclimate or other environmental conditions. Effects of contrasting vegetation traits and phenology were apparent in seasonal patterns of surface efflux, depth profiles of CO_2 production, soil organic carbon, and microbial biomass carbon.

The meadow vegetation during 2005 was unique because yellow sweet clover (*Melilotus officinalis*) emerged and created a dense canopy greater than 1 m tall (Fig. 2). This biennial legume was introduced to Rocky Mountain grasslands in the mid 1800's to stabilize soils against erosion, and is known to occasionally develop dense patches up to 3 m tall (Wolf et al. 2003). Despite its typical biennial habit and ability to dominate a site, this species was a relatively small fraction of percent cover in the five other growing seasons between 2004 and 2009, (authors estimate<5 % from regular site visits). The dense flush of *M. officinalis* in 2005 may have been promoted by selective effects of preceding rainfall patterns against more competitive grasses (Pitt and Heady 1978), although these "clover year" conditions were previously only shown to favor up to 20 % cover. The extent of grassland replacement by *M. officinalis* observed in the current study was similar to grass-forb shifts described in other grasslands after disturbances such as a fire (Moyes et al. 2005; Gucker 2009).

Although we do not know why *M. officinalis* grew so dramatically in 2005 to form a near monoculture, the rapid and dense growth of *M. officinalis* in 2005 corresponded with unusually high soil respiration during afternoon chamber measurements, including flux densities exceeding 20 μmol m^{-2} s^{-1} (Fig. 3). Remarkably, the interannual difference in meadow community composition corresponded with a larger effect on afternoon surface CO_2 efflux than position relative to lush, mature trees of several meters height in 2006 (Figs. 3 and 4; *M. officinalis* extended under several tree canopies in 2005, where high flux densities appear under trees in Fig. 4). One possible explanation could be high tissue nitrogen content, which in addition to facilitating high productivity and therefore substrate supply, has been shown to boost respiration rates from root biomass (Wang et al. 2010). Greater rhizosphere priming by *M. officinalis* is also possible, based on comparisons of priming with root respiration (Zhu et al. 2014) and between wheat and soybean (Cheng et al. 2003).

The relative synchronization of rhizosphere activity and phenological events of bud break and leaf drop in

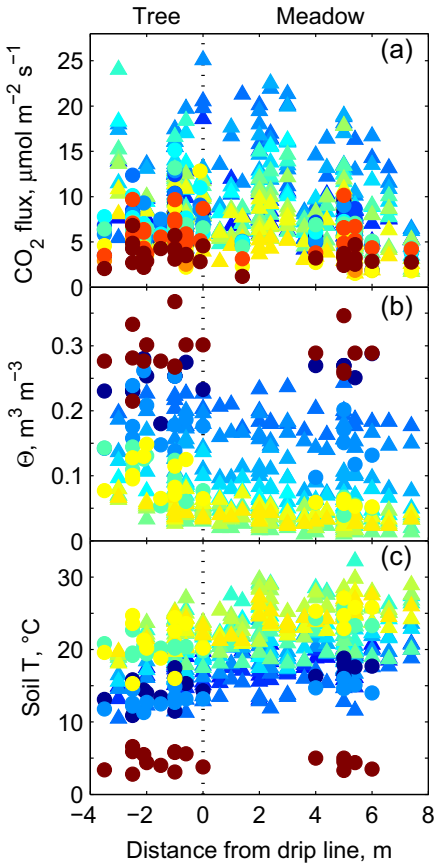

Fig. 4 Soil chamber measurements of surface CO_2 flux density (**a**) volumetric soil moisture (θ, **b**), and soil temperature (**c**), against transect position relative to the canopy drip line (see Fig. 2 for depiction of drip line). Transect positions are normalized to the drip line location to account for differences in tree size and to highlight the boundary between tree and meadow (abscissa values <0 are under tree and values>0 are in the meadow). Triangles are data from 2005 and circles are from 2006, and color represents the day of year (shown in Fig. 3)

deciduous trees has been shown to vary across several studies. Here, we found high soil respiration under trees apparent early in the growing season, before leaves had begun to emerge, and then low rates similar to the meadow once leaves had fallen (Fig. 5). In a previous study, conducted with boxelder trees grown from cuttings collected at this site and transplanted into an experimental garden, we found that respiration from tree roots coincided with bud break and continued well beyond leaf drop (Moyes et al. 2010a). A trenching study in a mixed maple-oak stand in Harvard Forest USA found rhizosphere respiration began with bud break and quickly tapered off at leaf drop (Savage et al. 2013). Congeneric sugar maple (*Acer saccharum*) in northeastern USA was shown to produce shallow fine roots maximally in spring (April/May) before leaf expansion (Hendrick and Pregitzer 1996). Although spring priming of microbial activity under trees has been associated with root release of sucrose in a subalpine forest (Scott-Denton et al. 2005), at the time of our first measurements, MBC was at a seasonal high value while SOC was seasonally low (Fig. 5). At this time, MBC was similarly high in the meadow and under trees despite differences in soil respiration between these locations. Thus, we did not find support for a localized pulse of exudation by tree roots in the upper 10 cm of soil leading to increased soil respiration rates in spring. However, we cannot exclude the possibility that tree roots extended 9 m into the meadow (though this more than twice the radius of the largest tree canopy) or of differences in microbial activity per unit biomass. Thus, we conclude that root activity was a direct source of soil respiration before leaves appeared. This is consistent with results of Misson et al. (2006), in which a large spring increase in soil respiration was associated with initiation of growth of ponderosa pine roots before the growth of new needles.

Contrasting seasonal patterns of CO_2 production with depth between trees and meadow emphasize the interactive effects of rhizospheric, heterotrophic, and abiotic processes. Typical patterns of decreasing root density and carbon content with depth (Jobbagy and Jackson 2000) were generally reflected in decreasing production of CO_2 from the surface (Fig. 5d), with the exception of deeper autumn CO_2 production under trees. Production profiles in the meadow transect positions agreed with estimates from multi-year study of CO_2 production in the center of the meadow using an unreplicated, automated, soil gas profile sampling system (Moyes and Bowling 2013). Interestingly, we found that soil respiration decreased under trees immediately after leaf drop, despite a late season increase in soil organic carbon (Fig. 5c and b). However, soil CO_2 production remained higher at 10–20 cm depth under trees at this time (Fig. 5d). This suggests that the presence of deep tree roots continued to promote CO_2 production at depth (either by root or microbial activity), while production near the soil surface may have been limited due to moisture saturation and colder temperature (Davidson et al. 2014). At depths below 10 cm, respiratory CO_2 production was greater under trees than at the other transect positions throughout the study (Fig. 5d). Although we lacked root distribution data, this result is

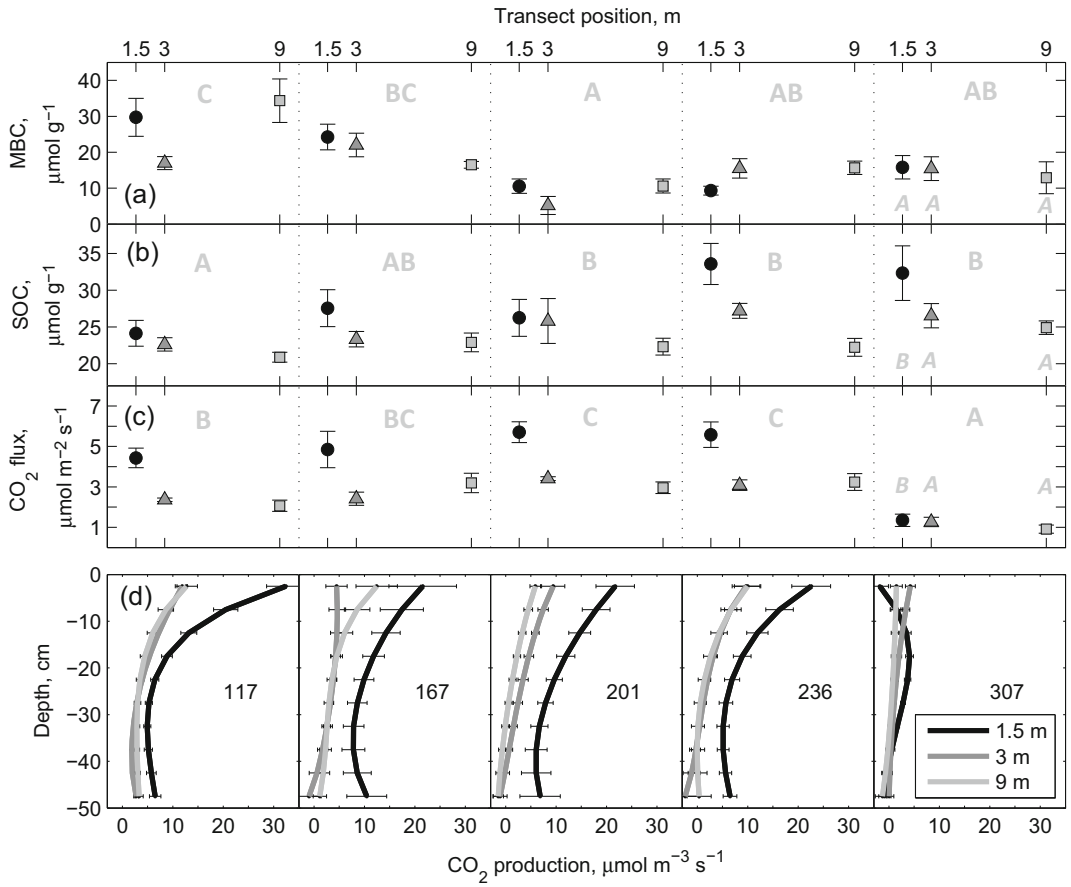

Fig. 5 Extractable microbial biomass carbon (MBC, (**a**)), extractable soil organic carbon (SOC, (**b**)), and modeled surface CO_2 efflux (**c**) vs. transect position for each of the five intensive sampling periods (separated by vertical dotted lines). (**d**), model results of CO_2 production with depth for each transect position for each sampling date (numbers are day of year). Error bars are ±1 SEM, $n=6$ for modeled surface CO_2 efflux and production, and $n=10$ for MBC and SOC. Letters near the top of (**a**–**c**) denote statistically different sampling dates ($p<0.05$), and italicized letters in the far right column show significant differences between transect positions (across all dates). Transect position x date interaction was found only for MBC ($p=0.014$)

not surprising because boxelder trees are known to root to at least 4 m depth (Canadell et al. 1996) and have been shown to rely on deep soil moisture at this site (Dawson and Ehleringer 1991), while grassland plants typically have 83 % of roots in the uppermost 30 cm (Jackson et al. 1996).

Soil organic carbon and microbial biomass carbon did not correspond consistently with variability in soil respiration in our site, even when considering only the top 10 cm of soil where soil was collected for SOC and MBC extractions (Fig. 7). Our soil carbon extractions made no distinction of SOC lability, which may have varied between tree and meadow sources (Van Miegroet et al. 2005; Olsen and Van Miegroet 2009). We also did not distinguish microbial identity or function, and considered only total microbial biomass. However, we expected some variability in soil respiration to be explained by SOC and MBC, as indicators of heterotrophic activity (Scott-Denton et al. 2005; Zhu et al. 2014). In a study of paired riparian and meadow vegetation zones along streams in Oregon, USA, higher soil respiration rates were associated with greater organic carbon, phosphorus, and mineralizable nitrogen in soils under riparian trees (Griffiths et al. 1997). Microbial biomass was also found to correspond strongly with soil respiration in a ponderosa pine plantation, although other potential respiration drivers were found to covary with MBC and could not be excluded (Xu and Qi 2001). In this study, we found a change in soil carbon between seasonally high MBC/low SOC in spring and seasonally low MBC/high SOC in fall, which suggests that winter decomposition at the site may lead to metabolism of

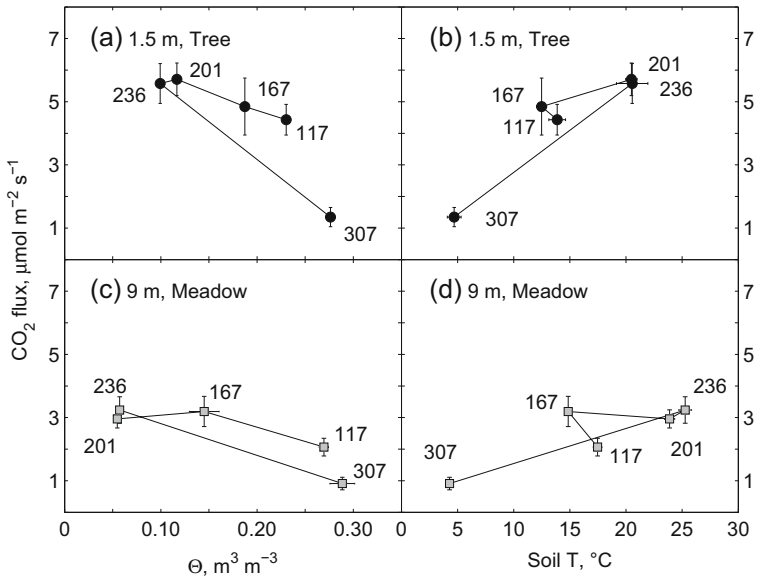

Fig. 6 Modeled surface CO_2 flux for each of the five intensive sampling dates (numbers) vs. measured soil temperature ((**a**), and (**b**)) and volumetric water content (θ, (**c**) and (**d**)) at 10 cm. Plots (*a*) and (*b*) are from 1.5 m transect positions (under tree canopies) and (*c*) and (*d*) are from 9 m positions (in open meadow). Error bars are ±1 SEM and are smaller than symbols in some cases

litter and proliferation of the microbial community, as has been observed in other sites with winter snow (Coxson and Parkinson 1987; Brooks et al. 2005; Kueppers and Harte 2005). This conclusion was also supported by comparing fall and spring relationships between soil respiration and temperature for our meadow location in a previous study (Moyes and Bowling 2013). Microbial biomass then crashed during the most favorable period for plant growth between snowmelt and midsummer. This dramatic decline in soil microbial biomass may have been due to depletion of soil moisture by plants, or competition with roots for soil nutrients, as was shown with four grass species growing in a controlled greenhouse experiment (Bell et al. 2015). Interactive dynamics between rhizospheric and heterotrophic processes such as this are missed by physical partitioning methods like root trenching.

Conclusions

Using transects running from under trees into an adjacent meadow, we capitalized on spatial and interannual variability in traits of plants growing in otherwise similar soil and microclimate conditions. We found strong evidence that soil respiration was influenced by plant

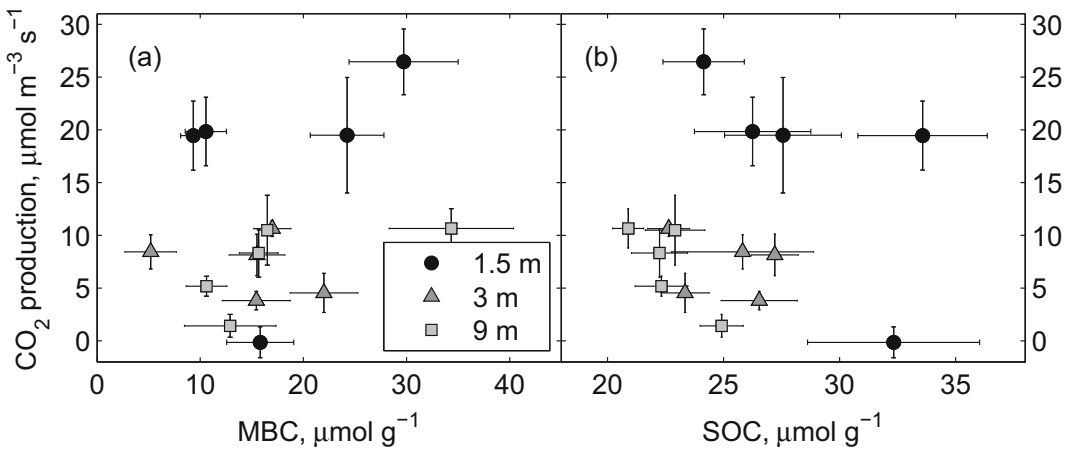

Fig. 7 Calculated rates of production of CO_2 within the top 10 cm of soil for each transect position vs. extractable microbial biomass carbon (MBC, (**a**)) and extractable soil organic carbon (SOC, (**b**)) from 10 cm-deep soil cores. Each point is an average of n=6, ±1 SEM

growth form (deciduous trees vs. meadow grasses and forbs) and interannual variability in meadow plant community composition. Effects of vegetation traits (phenology, rooting depth, growth form, and nitrogen fixation) were apparent as differences in total soil respiration, depth patterns of soil CO_2 production, and extractable soil organic and microbial biomass carbon. This study exemplifies an alternative to partitioning studies, in that we considered the role of vegetation within the context of the entire plant-soil continuum.

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