

Short-term effects of rain on soil respiration in two New England forests

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Abstract To gain new insights into the underlying mechanisms responsible for wetting-induced soil respiration, rain simulation field experiments were carried out in two temperate mixed-hardwood forests in New England (Great Mountain Forest and Harvard Forest). The rain-induced CO₂ pulses were observed in both xeric and mesic soils. The pulse intensity was negatively correlated with the site moisture level and the pre-rain soil CO₂ flux. At both forests, plots without O horizon responded to wetting with limited or even negative enhancement, confirming previous finding that the rain pulse was likely due to enhanced microbial consumption on substrates mainly of microbial origin. Our results show that the flux rain pulse was a reproducible phenomenon not limited to dry soils.

Keywords Birch effect · Carbon cycling · Precipitation · Pulse dynamics · Simulated wetting · Soil moisture · Soil respiration · Great Mountain Forest · Harvard Forest

Introduction

Soil CO₂ emission is the second largest carbon flux in most terrestrial ecosystems (Law et al. 1999; Longdoz et al. 2000), and represents 40–80% of forest ecosystem respiration (Goulden et al. 1997; Law et al. 1999; Janssens et al. 2001; Yuste et al. 2005; Davidson et al. 2006a). Variations in seasonal and annual soil respiration due to weather and climatic factors can contribute to interannual variations in ecosystem carbon balance, and thus affect short-term and long-term carbon sequestration (Barford et al. 2001). A precise estimate of respired carbon from soils relies on effective measurements and empirical models, as well as on in-depth knowledge of the response dynamics of soil respiration to biotic and abiotic factors.

Rain-induced soil CO₂ pulses, now a widely recognized phenomenon for forests and grassland, play an important role in ecosystem carbon balance. Enhanced soil CO₂ emissions following wetting were first characterized by H.F. Birch through laboratory observations in 1950s and 1960s (Birch 1958a, b; Griffiths and Birch 1961). Since then, this phenomenon, also known as the “Birch effect” (Jarvis et al. 2007), has been reported by numerous studies (e.g., Hanson et al. 1993; Davidson et al. 1993; Kelliher et al. 1999; Schimel et al. 1999; Boroken et al. 2002; Rey et al. 2002; Liu et al. 2002; Yuste et al. 2003; Xu et al. 2004; Huxman et al. 2004; Palmroth et al. 2005;

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Jarvis et al. 2007). Wetting has been reported to trigger an instant soil CO₂ pulse (Borken et al. 2003; Xu et al. 2004; Sponseller 2007), a delayed response (Griffiths and Birch 1961), or an initial pulse followed by a second peak hours later (Orchard and Cook 1983). Wetting-induced soil CO₂ emissions could contribute to substantial annual soil carbon loss and impact ecosystem carbon balance (Lee et al. 2002; Lee et al. 2004).

Despite available laboratory and field observations, the effects of rainfall on soil respiration via altered soil moisture regime or other routes have not been fully elucidated. The occurrence and scale of immediate, transient CO₂ pulses are not effectively addressed within existing temperature-moisture models of soil respiration, which often fall short in explaining short-term variations, and do not tackle the underlying physiological processes affected by temperature and moisture (Davidson and Janssens 2006; Davidson et al. 2006b). Most existing empirical models predict soil respiration during rain events based on the changes in soil moisture content (e.g., Howard and Howard 1993; Davidson et al. 2000; Reth et al. 2005), which may not always be a valid and sufficient predictor. Elevated soil respiration driven by rain often deviates from the normal temperature function (e.g., Lee et al. 2002; Savage et al. 2009), and coincides with increase in soil moisture. However, increase in respiration does not necessarily correlate to changes in soil moisture (Savage and Davidson 2001; Borken et al. 2002). The magnitude of enhanced respiration is site-specific, and often quite variable both temporally and spatially. The likely factors that determine enhancement magnitude include pre-rain soil moisture (Lee et al. 2002; Borken et al. 2002; Xu et al. 2004; Sponseller 2007), soil organic layer (Borken et al. 1999; Savage and Davidson 2001), organic carbon pool (Franzluebbers et al. 2000), nutrient input through precipitation, wetting intensity (Orchard and Cook 1983; Liu et al. 2002; Borken et al. 2003), and stress history (Taylor and Parkinson 1988; Clein and Schimel 1994; Schimel et al. 1999).

Constrained by the technical difficulties to measure in rain and the unpredictable nature of rainy weather, most studies trying to quantify soil respiration through in-situ measurements have been unable to cover periods during and immediately following rain events. While soil respiration may be inferred from

measurements of eddy covariance, optimal meteorological and environmental conditions rarely exist to allow and facilitate accurate estimates of soil CO₂ emissions. Alternatively, soil respiration is measured with portable chambers on some fixed time schedule, but the site visits are usually done in fair-weather conditions. Even fully automatic chambers can easily miss the rain pulse if sampling frequency is not high. For these reasons, there are few published studies on the rain pulse *during* rain events (e.g., Lee et al. 2004; Xu et al. 2004).

In this study, we investigated in-situ, short-term response of soil respiration during and immediately following rain through rain simulation experiments. Rain simulation was carried out at two temperate, mixed-hardwood New England forests — Great Mountain Forest, Connecticut, for one growing season in 2002 (referred to hereafter GM02), and at Harvard Forest, Massachusetts, for two growing seasons in 2004 and 2005 (HF04 and HF05). The 2002 observation, made at xeric plots and reported by Lee et al. (2004), was compared with the new data obtained in 2004 and 2005 at mesic plots in Harvard Forest. Soil CO₂ flux measurements were made with a portable soil chamber system. Field manipulative experiments allowed more control than in-situ observations over environmental variables while reflecting on-site field conditions, and could provide complementary information to measurements made in undisturbed conditions. Rain simulation avoided the difficulties and unpredictability of measuring in natural rain events, and the use of the portable chamber system allowed swift data collection. The standardized experiment protocol, such as identical site preparation and irrigation methods, known amount of water addition, and consistent measurement intervals, made it possible to quantify and compare rain-induced CO₂ pulses within and across sites. This approach provided a starting point for assessment of annual carbon loss in natural rain events, and yielded rich information on the likely mechanisms of the CO₂ flux pulses. The same field method was also applied in an agricultural ecosystem in Nebraska in 2006 (Wu and Lee 2010).

In this paper, we aim to identify the response patterns and magnitudes of rain-induced soil respiration, and to gain new insights into the underlying mechanisms responsible for the enhanced soil respiration. The question of interest concerns the variation

of the pulse intensity across soil moisture gradient, that is, how wet is a forest soil wet enough to suppress the rain pulse. The two forests were similar in species composition and climate, but the plots chosen for the study varied over a wide range of soil moisture regime.

Methods

Site description

The Great Mountain Forest is located in Norfolk, Connecticut (41°58'N, 73°14'W). The mean temperature at Great Mountain Forest site is 19.9°C in July and -6.5°C in January. Annual precipitation at the area is 1,310 mm and is more or less evenly distributed throughout the year. Within the research area, vegetation composition includes red maple (*Acer rubrum*), oaks (*Quercus* spp.), beech (*Fagus grandifolia*), eastern white pine (*Pinus strobus* L.) and understory mountain laurel (*Kalmia latifolia*). The soil is well-drained Charlton series inceptisol. The mean forest floor thickness was 6.7 cm, and the forest floor soil bulk density was 0.16 gcm⁻³. The soil organic matter stored in O horizon was 6.7 kgm⁻². Seven plots, each with a radius of 1 m were set up on a gentle slope near a meteorological tower and within its eddy covariance flux footprint. One plot was set up in 2001 for a pilot study, and the other three pairs, consisting of six plots, were established in April 2002. Paired plots were adjacent to each other with 1–2 m in between. Placement of plots was not entirely random because of the need to avoid large coarse woody debris and thick understory in order to access the plots for irrigation. Forest floor organic horizon (O horizon) was removed from a randomly chosen plot of each pair prior to the commencement of the experiment. Both the intact plots and bare plots were treated with rain simulation.

Harvard Forest is located in Petersham, MA (42°53'N, 72°17'W). Our experimental site was located on an east-facing, lower slope on the Prospect Hill Tract of the forest, and was about 1.5 km SE of the eddy covariance tower for long-term flux measurement (Wofsy et al. 1993). The mean temperature at Harvard Forest is 20.0°C in July and -7.0°C in January. The annual precipitation is 1,100 mm. The forest stand at the site is at mid- to late-successional

stage, and species composition includes red oak (*Quercus rubra*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and Eastern hemlock (*Tsuga canadensis*). Soil texture is characterized as fine sandy loam. Forest floor thickness at the site was 6.3–6.7 cm, and the soil organic matter stored in O horizon was 7.0 kgm⁻² (Savage and Davidson 2001; Boroken et al. 2003). A total of 12 plots were set up with a block design. Three blocks were created in May 2004. In 2005, one extra block was established to increase sample size. These blocks were laid out along an elevation gradient and within 100 m of one another. Each block consisted of three plots of radius of 1 m with similar soil moisture and litter layer thickness, and different treatments were randomly assigned to the plots. Control plots were not treated with rain simulation or removal of O horizon. The other plots were treated with rain simulation, including plots with intact O horizon, and plots with O horizon removed.

The two forest sites were quite similar in terms of climate, species composition, forest floor thickness and soil organic matter content. However, soil moisture at the Harvard Forest site, which is close to a beaver pond, was consistently higher than that at Great Mountain Forest. The seasonal mean soil moisture at the depths of 5, 15 and 25 cm was 10.6, 12.9, and 27.8, respectively, during GM02, 30.1, 43.8 and 61.7, respectively, during HF04, and 33.7, 44.3 and 59.6% by volume, respectively, during HF05.

Rain simulation

The experimental protocol was described by Lee et al. (2004). Briefly, rain simulation experiments were carried out by spraying 6 mm or 12 mm of water in 30 min with a watering can on the treatment plots every 1 to 2 weeks during the growing season. The simulated rain was short enough to avoid the confounding effect of the diurnal change in soil temperature and intense enough to produce a measurable response. For comparison, the average rain intensity at Great Mountain was 8 mm per storm, falling in the range of the simulated amounts, although the average storm duration was longer than 30 min. No experiment was done on rainy days or right after rain in order to avoid confounding effects of wetting caused by natural rain. Simulated rain

lasted for 30 min. Soil CO₂ flux, soil moisture profile, and soil temperature were measured prior to, and at set time steps during and after irrigation. The total experiment time was 2 h. Measurements were made at 7 time steps at 0, 10, 20, 30, 45, 60, and 120 min into the experiment, denoted with subscript 0 through 6 respectively. Soil temperature was measured at 10 cm depth; temperature change from the beginning to the end of the 2-h experiment was normally within 1°C, and the maximum difference, in rare cases, was 1.8°C. Water used was groundwater near the sites.

Rain simulation was performed at Great Mountain Forest from May to October, 2002 and at Harvard Forest from May to October in 2004 and 2005. The total water added during the experiment season was roughly 20% of the summertime precipitation and 5% of the annual precipitation.

The manipulative field approach allowed us to better control environmental variables and to capture the immediate response. The irrigation time was short enough to minimize the complexity and confounding effects from diurnal variations that could otherwise occur in regular field observation. The standardized experimental protocols also allowed meaningful quantification of rain-induced soil respiration, as well as cross-site and within-site comparison.

Soil CO₂ flux was measured with portable photosynthesis systems (models 6200 and 6400, LI-COR, Inc., Lincoln, Nebraska, USA) coupled to soil CO₂ flux chambers (models 6000–09 and 6400–09, LI-COR, Inc.). Field comparison showed that measurements taken with the two systems were in excellent agreement, with the linear relationship between the two systems of $y = 1.0494x - 0.0006$ ($R^2=0.99$, $n=24$, variables in $\mu\text{molm}^{-2}\text{s}^{-1}$). Soil moisture content was measured with a portable soil moisture probe (model PR1/4, Dynamax, Inc., Houston, TX, USA). The access tubes of the probe were inserted into soils on each plot weeks prior to the commencement of experiments. The access tubes were carefully positioned so that the sensor rings of the probe could detect soil moisture at the depths of 5, 15, 25, and 35 cm. In addition, soil samples from Great Mountain Forest were collected near all plots for water potential measurement in the laboratory.

Data analysis

The soil flux data are presented in three ways: plot mean over the season — to get spatial variation, site

mean for daily site visit — to get temporal variation through the season, and ensemble mean over the 2 h duration — to suppress experimental noise and bring rapid response into a sharp focus. Plot mean values are averages of all valid 15–20 observations over one season for each of the replicated plots; there are 4 plot mean values during GM02, 3 during HF04 and 4 during HF05. Site mean values are computed for each field day by averaging the observations of the replicated plots; the number of site mean values varies between 15 and 20 among the three site-years. The ensemble mean values are computed for every time step (0, 10, 20, 30, 45, 60, and 120 min) of all 2-h irrigation experiments and replicates during a given site-year. Each ensemble mean is the average of replicated samples taken throughout one-site year (total number of samples = 72 for GM02, 36 for HF04 and 72 for HF05). So for each site-year, there is one ensemble curve for the plots with intact O horizon and one for the plots with O horizon removed, with no distinction made between the simulated rain intensities of 6 and 12 mm.

Results

Short-term flux response to wetting

Soil CO₂ flux on plots with O horizon increased immediately after the onset of wetting, and dropped back to values slightly higher than the pre-wetting rate usually within 90 min after irrigation had stopped (Fig. 1). For each 2-h experiment, baseline CO₂ flux was measured at the given plot right before the commencement of irrigation (F_0). To avoid the confounding effects of variation in soil temperature, moisture and inherent plot variability, CO₂ flux measured at different time steps since the commencement of irrigation (F_i) is normalized by the pre-rain baseline flux (F_0). The ratio obtained by the normalization is flux enhancement ratio (F_i/F_0). A ratio greater than 1 indicates occurrence of flux enhancement and a ratio less than 1 flux suppression due to wetting. Corresponding to the enhancement pattern was a rise in the 5-cm soil moisture by an average absolute change of 8% by volume at the end of the 30 min irrigation. In comparison, little change in the 15-cm soil moisture was evident (Wu 2010). On plots with intact O horizon, the average maximum

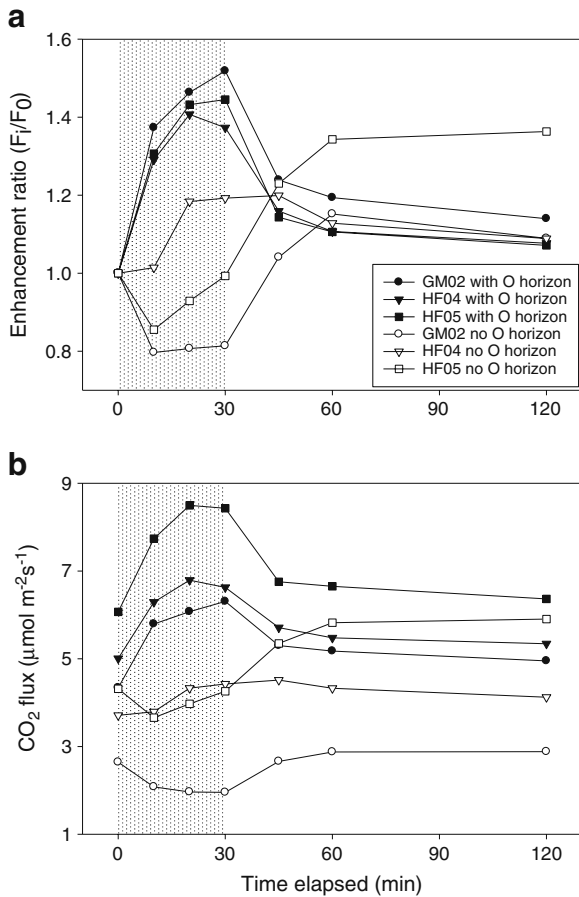


Fig. 1 Ensemble plots of flux enhancement ratio (a) and soil CO₂ flux (b) during and following rain simulation at GM02, HF04, and HF05. The shaded area represents the 30-min rain simulation. Data of GM02, HF04 and HF05 are denoted as circle, triangle, and square respectively. Solid symbols represent plots with intact O horizon, and open symbols plots without O horizon. Each data point represents the ensemble mean of replicate plots over the season. A typical standard deviation of the flux of the samples for the ensemble mean calculations was 2.7 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for plots with O horizon and 2.1 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for plots without O horizon

enhancement ratios were 1.52, 1.41 and 1.45 for GM02, HF04 and HF05, respectively (Fig. 1a). At GM02 and HF05, average enhancement ratio peaked right after 30 min of rain simulation, whereas at HF04, it occurred at 20 min into rain simulation. The average enhancement at 2 h was 1.14 ± 0.20 for GM02 (mean \pm one standard deviation; number of samples $n=72$), 1.09 ± 0.12 for HF 04 ($n=36$) and 1.07 ± 0.19 for HF05 ($n=52$), all significantly different from unity ($p < 0.01$). While the average enhancement ratios at the three site-seasons appeared comparable, CO₂ flux in general

was lowest at GM02 and highest at HF05, likely due to the difference in soil moisture (Fig. 1b).

Variations in flux enhancement

Figure 2 shows the seasonal variations in CO₂ flux, flux enhancement and 15-cm soil moisture. CO₂ flux peaked in July, coinciding with the occurrence of the highest soil temperature. In comparison, flux enhancement followed the opposite seasonal pattern, with lowest values in July. Soil moisture regime was

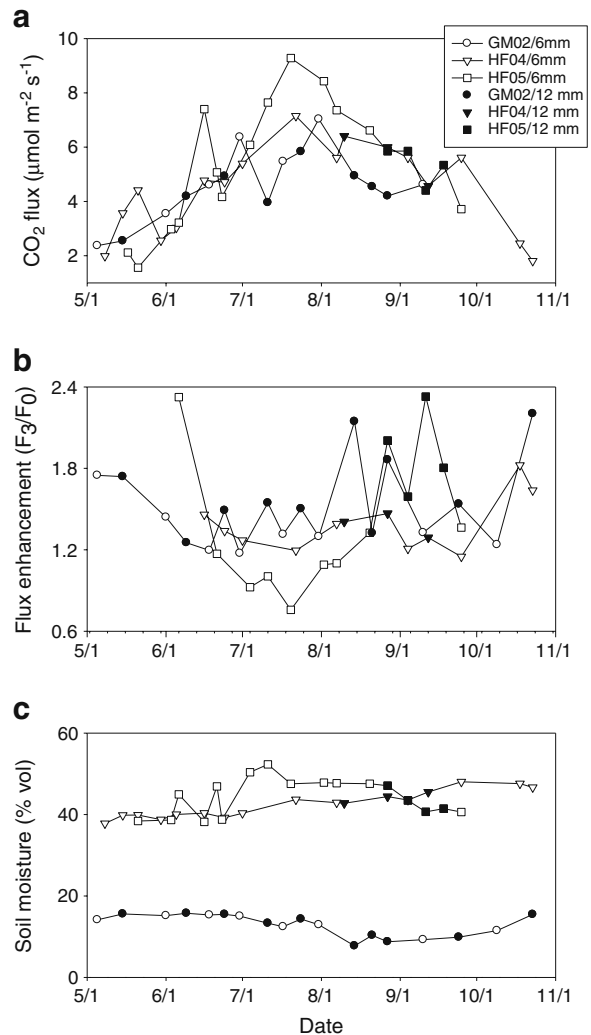


Fig. 2 CO₂ flux (a), enhancement (F_3/F_0) (b), and soil moisture at 15 cm depth (c) over the growing season for GM02, HF04, and HF05, denoted as circle, triangle, and square respectively. Each data point represents the average value of replicate plots on a filed day

distinctly different at Great Mountain Forest and Harvard Forest. During the growing season, especially from mid June to late August, flux enhancement at HF05 was clearly lower than GM02 and HF04. Note that some of the high values at GM02 were contributed by 12-mm irrigation, while all the enhancement ratios at HF04 and HF05 during this period of time were results of 6-mm irrigation (12-mm irrigation at HF04 and HF05 only took place after late August).

To further explore the temporal variation in flux enhancement, we plot the site average flux enhancement ratio of replicate plots immediately following 30-min rain simulation (F_3/F_0) against the average baseline CO_2 flux (Fig. 3). When the data from all the three site-years were pooled together, the flux enhancement was negatively correlated with pre-rain baseline CO_2 flux (linear correlation $R = -0.59$, significant at $p < 0.001$). This negative correlation was mostly driven by the 6 mm irrigation data. If separated by irrigation intensity, the 6 mm subgroup of data retained a significant correlation between the baseline flux and the flux enhancement ($p < 0.001$) whereas the 12 mm subgroup did not ($p > 0.20$). Some of the scatter in this graph was caused by irrigation intensity. Flux enhancement was higher with the addition of 12 mm water than with 6 mm: the average enhancement of the three

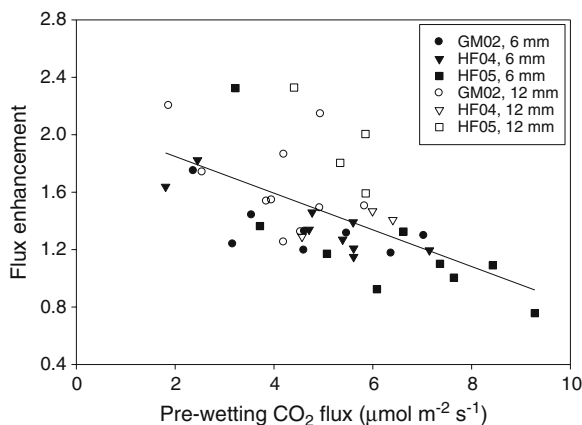


Fig. 3 Flux enhancement (F_3/F_0) vs. pre-wetting CO_2 flux for GM02, HF04, and HF05, denoted as circle, triangle, and square respectively. Solid symbols represent data from 6-mm irrigation, and open symbols those from 12-mm irrigation. Each data point represents the average value of replicate plots on a field visit. The linear regression of the combined data of 6-mm and 12-mm irrigation showed a negative correlation between enhancement and pre-wetting flux [$y = -0.13(\pm 0.05)x + 2.10(\pm 0.29)$, $R = -0.59$, $n = 43$, parameter uncertainty at 95% confidence]

site-years was 1.66 and 1.32 for 12 and 6 mm irrigation, respectively. Xu et al. (2004) also found a positive correlation between the total amount of respired carbon and the amount of precipitation in a grassland and an oak/grass savanna ecosystem.

Previous research has shown that larger flux rain pulses should occur in the drier part of the season, implicating the pre-rain soil moisture as a key variable controlling in the variations in the pulse intensity within the growing season (Rey et al. 2005; Lee et al. 2002; Xu et al. 2004; Jarvis et al. 2007; Sponseller 2007; Inglisma et al. 2009). In the present study, the pre-rain soil moisture was a good indicator of rain-induced flux enhancement magnitude (Fig. 4). The linear correlation between flux enhancement and the 15-cm soil moisture was -0.65 ($p < 0.05$) if all the data from the three site-years were pooled together.

Moisture dependence of flux enhancement was also manifested at a finer temporal scale. Figure 5 shows the ensemble mean flux enhancement over the 2-h rain simulation on the four replicate plots with O horizon at Harvard Forest in 2005. Seasonal average soil moisture of each plot ranged from 26 to 71% by volume. Plots with lower pre-rain soil moisture showed greater enhancement, while plots with higher soil moisture showed less enhancement or even suppression of CO_2 flux.

Soil moisture also contributed to the difference in enhancement between three site-years (Fig. 2). The

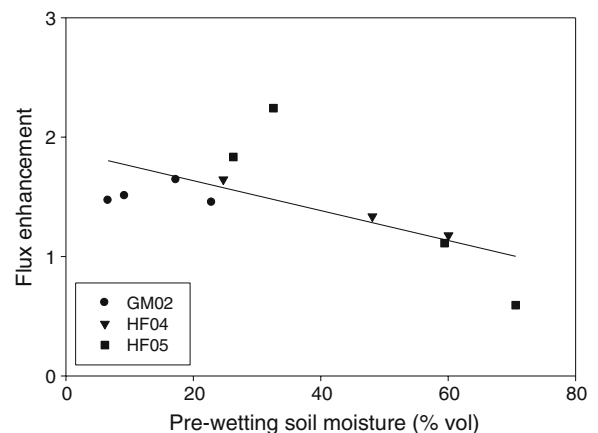


Fig. 4 Flux enhancement (F_3/F_0) of individual plots vs. pre-wetting soil moisture at 15 cm depth. Each data point represents the plot mean over the season. Spatial variation in flux enhancement across the plots of the three site-years showed a negative relationship to site moisture condition [$y = -0.013(\pm 0.011)x + 1.89(\pm 0.45)$, $R = -0.65$, $n = 11$, parameter uncertainty at 95% confidence]

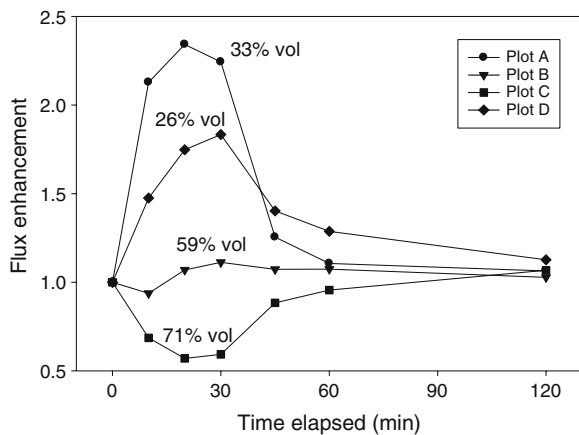


Fig. 5 Plot mean flux enhancement (F/F_0) of the four replicate plots over 2-h rain simulation at HF05. Each data point represents the plot mean over the season at each time step. Average soil moisture of each plot is also marked. At Harvard Forest, xeric plots appeared to show greater enhancement than mesic plots

July–August flux enhancement was highest at GM02 and lowest at HF05. During the same period, soil moisture content at GM02 was much lower than that at HF04 and HF05. In general, plots at Harvard Forest were wetter in 2005 than in 2004. In fact, all of the existing replicate plots created in 2004 showed increased soil moisture in 2005. (The increase in soil moisture at Harvard Forest was likely caused by an elevated water table, a consequence of beaver damming activities in a nearby pond).

The spatial variation in flux enhancement across the two New England forests showed a negative linear correlation to pre-rain soil moisture ($R=-0.65$) (Fig. 4). Soil moisture here was measured in the mineral layer at the 15 cm depth and was a good indicator of the drainage condition at individual plots. Not surprisingly, flux enhancement was higher on xeric plots and lower on mesic plots. Our results indicate that averaged over the season, wetting can enhance CO_2 flux at locations in a wide moisture range. Only at locations with seasonal mean moisture greater than 60% by volume did we see suppression of the CO_2 flux by wetting. This threshold is very close to the porosity of 69 and 87% in the mineral soil at Great Mountain and Harvard Forest, respectively.

The role of O horizon

CO_2 flux from the plots without O horizon was consistently smaller than that from the plots with O

horizon, and showed much weakened enhancement or even suppression during rain simulation (Fig. 1). While the response pattern and magnitude on the plots with O horizon were very similar and consistent at all three site-years, the plots without O horizon showed rather variable response patterns. At GM02, CO_2 flux on the plots without O horizon kept decreasing throughout the 30-min wetting and only started to recover back to the pre-rain level when rain simulation stopped. At HF04, flux enhancement was negligible in the first 10 min of wetting, and then flux increased as rain simulation went on, and dropped back to the pre-rain value after rain had stopped. At HF05, there was an initial decrease in CO_2 flux during the first 10 min of rain simulation, and then flux started to increase even after rain simulation stopped. The distinct difference in response patterns and magnitude between the plots with and without O horizon indicates that organic forest floor litter was the major contributor to increase in CO_2 flux during rain.

To quantify the relative contribution of O horizon to the total soil respiration, we first compared the pre-wetting CO_2 flux at the plot with O horizon (F_O) and the plot without O horizon (F_B) in a given block/pair. The difference of the two was divided by the flux of intact plot (F_O), and the ratio obtained was flux contribution of O horizon, as

$$\text{Flux contribution of O horizon} = \frac{F_O - F_B}{F_O}$$

This method is based on the assumption that soil respiration on the plots in a given block/pair was identical before one of them was treated with O horizon removal. It also ignores the fact that by removing the O horizon, the bare soil would dry faster than normal.

Figure 6 shows the site mean flux contribution of O horizon as function of soil moisture. In this figure, each data point of flux contribution was the average of the replicate plots measured on a given field day. Flux contribution was highest at GM02 (averaged 0.44), and was similar at HF04 and HF05 (averaged 0.26 and 0.29). Over the season, flux contribution of O horizon at GM02 increased with increasing pre-wetting soil moisture ($R=0.87$); however, an opposite trend was observed at HF04 ($R=-0.67$) with the highest values of flux contribution (>0.3) all occurred at the beginning of the growing season (May and June). No clear trend was found for HF05.

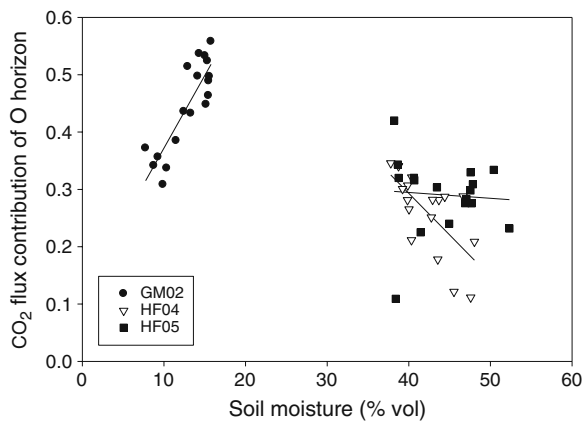


Fig. 6 Flux contribution of O horizon vs. pre-wetting soil moisture at 15 cm depth. Each data point represents the average flux contribution of replicates (site mean) on a field visit. Temporal variation in O horizon flux contribution showed opposite relationships with soil moisture at GM02 and HF04 ($y = 0.03x + 0.12$, $R = 0.87$, $n = 18$; $y = -0.02x + 0.87$, $R = -0.67$, $n = 17$)

Spatial variation in flux contribution of O horizon showed a strong negative correlation with mean pre-rain soil moisture ($R = -0.74$) (Fig. 7). In other words, at wetter sites, O horizon contributed less to total soil respiration. The seasonal mean flux contribution of individual plots at the 3 site-years ranged from 0 to 0.55. Average pre-wetting soil moisture among the plots varied greatly from 6.6 to 70.6% by volume. At the near water-logged plot — the plot with the highest

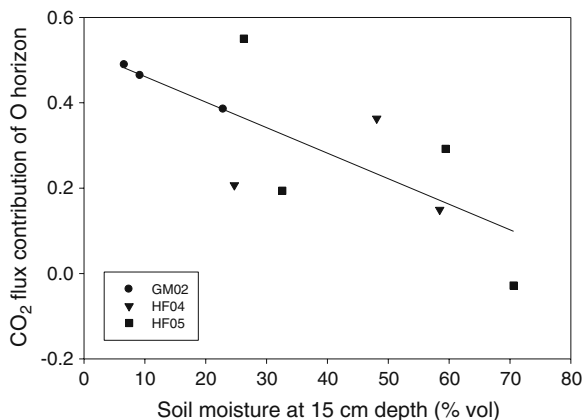


Fig. 7 Flux contribution by O horizon of individual plots vs. pre-wetting soil moisture at 15 cm depth. Each data point represents the plot mean value over the season. Spatial variation in flux contribution across the plots of the three site-years showed strong negative correlation to plot moisture condition [$y = -0.0104 (\pm 0.004) x + 0.52 (\pm 0.18)$, $R = -0.74$, $n = 10$, parameter uncertainty at 95% confidence]

seasonal mean soil moisture of 70.6% — O horizon made virtually no contribution to the total flux. The results demonstrate that spatial variation in flux contribution of O horizon was strongly dependent on inherent site soil moisture conditions.

Effect of repeated wetting

Figure 8 compares the soil CO_2 flux between the treatment plots with intact O horizon and the control plots at HF04 and HF05. No paired comparison was available for GM02. The measurement was made prior to the start of each rain simulation. To retain consistency between HF04 and HF05, we excluded the data from the new block of plots established in 2005. The flux from the treatment plots tracked that from the control at HF04, but was slightly lower than the latter at HF05, suggesting that repeated

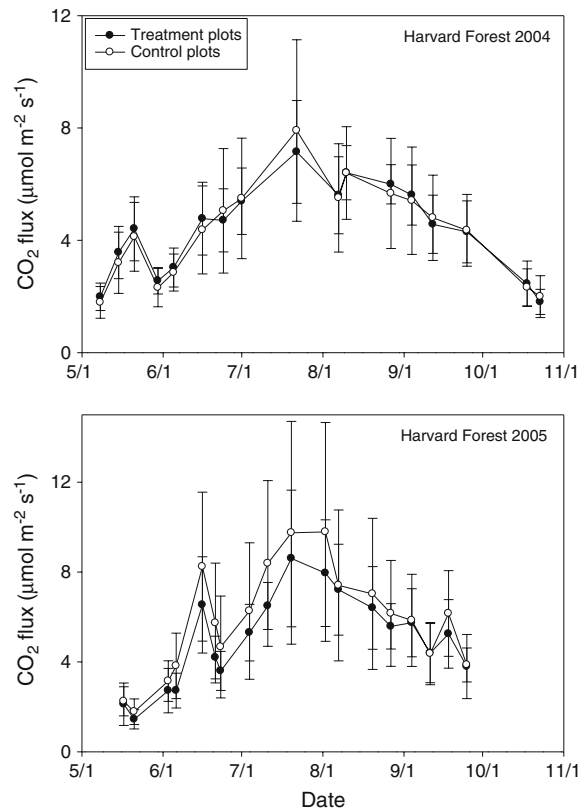


Fig. 8 Soil CO_2 flux of treatment and control plots at Harvard Forest. Each data point represents the average flux of replicate plots (site mean) on a field visit. Rain simulation was carried out on the three treatment plots for two growing seasons, and the flux difference between treatment and control plots was greater in 2005 than 2004

wetting may have suppressed the baseline flux. However, a *t*-test revealed no statistically significant difference between the treatment and the control plots (HF04, $p < 0.95\%$; HF05, $p < 0.59\%$). It is unclear whether this would remain true if rain simulation experiments were to be carried on for additional seasons. The large spatial variability as indicated by the error bars in Fig. 8 also raises the possibility that the difference at HF05 maybe true but the number of replicates (3) was too small to provide a robust statistical assessment.

Discussion

Likely mechanisms of rain-induced CO₂ pulses

The results obtained with our standardized experimental protocol yielded rich information on the mechanisms of the CO₂ flux pulses. The distinct response patterns between plots with and without intact O horizon suggest that rain-induced flux contribution was dominated by heterotrophic respiration. One piece of evidence is that, our laboratory incubation experiment on leaf litter showed immediate CO₂ pulses upon wetting with even greater enhancement magnitude than that observed in the field (Lee et al. 2004). This is further supported by a published field study using isotope tracer (¹⁴C) to trace the source of soil CO₂ flux in a temperate deciduous forest at Oak Ridge, Tennessee. Based on the change in the ¹⁴C-signature of CO₂ during rain events, it was shown that flux contribution of leaf litter decomposition to total soil respiration increased from 5 to 37% after wetting, which was sufficient to account for all rain-induced increase in soil CO₂ flux (Cisneros-Dozal et al. 2007). While fine roots are most abundant in O horizon (for example, 50% of fine root biomass was present in the litter layer at a study site at Harvard Forest as reported by Cisneros-Dozal et al. 2007), autotrophic respiration is usually more controlled by growth-related photosynthetic activities and inherent site productivities than by soil moisture (Högberg et al. 2001; Janssens et al. 2001; Sampson et al. 2007). Moreover, root growth normally does not respond to wetting until several days after rain (Borken et al. 1999; Ivans et al. 2003). Similar conclusion is also reached by Inglima et al. (2009) for a Mediterranean ecosystem. In other words, the

rain pulse was most likely of microbial origin (Fierer and Schimel 2002).

Substrates of both plant litter and microbial origin were possible sources that fueled the enhanced microbial metabolism in our study. This is because leaf litter and plant detritus provide decomposition substrate rich in labile carbon. Water addition not only enhances microbial activities/populations that have been suppressed by water deficiency on well-aerated forest floor (Birch 1958a; Orchard and Cook 1983), but also facilitates movement of dissolved organic carbon from litter into deeper soils for decomposition (Cleveland et al. 2007; Lee et al. 2004). Increased substrate availability may also result from enhanced access to non-biomass labile organic carbon through physical alternation of soil aggregates (Van Gestel et al. 1991; Van Gestel et al. 1993; Wu and Brooks 2005), lysing microbial cells due to water potential shock from wetting (Kieft et al. 1987), and cytoplasmic solutes released by viable microbes in response to water potential shock (Halverson et al. 2000; Fierer and Schimel 2003; Lovieno and Bååth 2008). In a rain simulation experiment conducted at a Mediterranean oak woodland site, Unger et al. (2010) found that the ¹³C-CO₂ composition of soil respiration changes rapidly, by more than 4‰, in response to wetting in the organic layer. Such an isotopic pulse cannot be explained by the ¹³C composition of the SOM-bound carbon. Rather it is indicative of assimilation of the desiccated microbial biomass, or of microbes feeding on (dead) microbes. The labile carbon pool released by microbes is small (Fierer and Schimel 2003; Saetre and Stark 2005), and can be exhausted soon after wetting. If our rain simulations lasted longer, the main substrate used for soil respiration would eventually shift to plant organic matter.

The rapid increase in respiration and short-lived pulses can be taken as evidence of reactivation of microbial activities by water addition, rather than rapid increase in microbial biomass. Low water potential of the porous, exposed surface litter layer often curbs microbial activity and enzyme movements. Wetting relieves the desiccating stress for dormant microbes in the litter layer, and creates a temporarily favorable environment for them to resume activity (Orchard and Cook 1983). Lovieno and Bååth (2008) found no correlation between soil respiration and microbial growth during the first hours following wetting: while soil respiration leaps

right after wetting, microbial population only shows a linear instead of the normal exponential increase, and exponential growth only takes place 7 h after wetting. Saetre and Stark (2005) also found an initial decoupling between soil respiration and microbial growth following wetting, with respiration increased two orders of magnitude than microbial biomass. Both studies attributed the initial respiration pulses mainly to reactivation of dormant cells upon wetting rather than microbial population growth. The phenomenon of decoupling between soil respiration and microbial growth is referred to as “wasteful metabolism” (Lovieno and Bååth 2008).

One conclusion of our study is that the rain-induced pulses were not limited to dry soils. The pulse intensity was negatively correlated with the plot soil moisture status. Only at plots with seasonal mean moisture approaching field capacity did we see no enhancement or slight suppression of the CO₂ flux by wetting (Fig. 4). In other words, some level of drought stress existed even at the mesic plots in Harvard Forest.

Flux contribution of O horizon

Since O horizon contains organic carbon that is very sensitive to wetting, it is important to understand its contribution to the total soil respiration. Our data show that the fractional contribution was highly variable in space and time. Averaged over the 2004 and 2005 growing season, nearly 30% of soil respiration came from O horizon at the Harvard Forest site, a fraction that is lower than numbers reported in other studies conducted at the same forest. At a well-drained site at Harvard Forest, 63% of annual soil respiration comes from O and A horizons, and 59% is derived from photosynthate carbon residing in the plant and soil for less than 1 year (including root respiration) (Gaudinski et al. 2000). In a decade-long trenching experiment with root exclusion, Melillo et al. (2002) reported that microbial respiration contributes to 80% of annual soil respiration at Harvard Forest. More specifically, Bowden et al. (1993) found that aboveground litter accounts for 37% of annual soil respiration, and belowground soil organic matter and live roots contribute 30% and 33% respectively. Davidson et al. (2006c) reported that based on mean annual sums, O horizon contributes to 40–48% of the total CO₂ efflux at Harvard Forest. However, comparison with these studies maybe

confounded by the difference in experiment methods. Assuming that flux from O horizon was dominated by microbial respiration, then the reason for such differences between our results and other studies' maybe that, instead of calculating the annual flux contribution, our data were only obtained from the growing season when root respiration was most vigorous. Some of the differences may have been a result of different soil moisture between these study sites. Site soil moisture status was negatively correlated with the fractional flux contribution of O horizon (Fig. 7) and our study sites were wetter than those used by Gaudinski et al. (2000), Melillo et al. (2002), and Davidson et al. (2006c).

Previously we showed that flux enhancement was negatively correlated with the plot soil moisture status (Fig. 4). The plot-mean flux enhancement (the y-variable in Fig. 4) was positively correlated with the fractional flux contribution of O horizon (the y-variable in Fig. 7), with a significant but weaker correlation than in Fig. 7 (linear correlation $R=0.74$, $p<0.05$). The role of soil moisture appears to be twofold: flux enhancement was weaker at more mesic soils because of less drought stress and a reduced fractional flux contribution of O horizon.

Temporal variation in flux contribution of O horizon showed opposite relationship with soil moisture in the two forests (Fig. 6). At the drier GM02, flux contribution of O horizon increased with soil moisture. However, at HF04, flux contribution decreased with soil moisture. The opposite trends seem to suggest a potential soil moisture between 20 and 40% by volume for an optimal flux contribution. A similar relationship exists between total soil respiration and moisture: soil respiration usually increases with soil moisture until reaching a turning point of maximum respiration, and decreases with increasing soil moisture beyond that point (Linn and Doran 1984; Skopp et al. 1990). At poorly-drained sites at Harvard Forest, such a turning point of soil moisture is 12% by volume. However, the results are confounded by temperature (Davidson et al. 1998). The turning point of maximum is at 20.6% (vol) in soil moisture content in a coniferous forest in the Sierra Nevada Mountains (Qi and Xu 2001).

The site-mean and plot-mean flux contributions represent seasonal and spatial variations, respectively, and responded differently to soil moisture. We suggest that the temporal fluctuations of flux contribution are dominated by newer and more labile

carbon which is more responsive to the changeable environmental factors, such as soil temperature and moisture, whereas spatial variation in flux contribution reflects the activities of both newer and older carbon, which is determined by the long-term, combined effects of inherent site properties, such as site productivity and soil drainage condition.

The above discussion is based on the assumption that that soil respiration on the plots in a given block/pair was identical before one of them was treated with O horizon removal. Although the paired plots had similar biophysical features (soil moisture content, litter thickness, slope), some natural variations were inevitable that could confound the above interpretations.

Enhanced soil carbon release during rain

Models of soil respiration not taking rain-induced CO₂ pulses into account would underestimate soil CO₂ flux; so would studies with coarser time resolution or longer lapse between the time rain stops and the time measurements begin. In our study, the initial enhancement of soil respiration would have been overlooked had the measurements not been made during rain simulation. If the measurements started 90 min after rain had stopped, they would have misleadingly suggested no enhancement for some plots.

The enhanced soil CO₂ release as a result of rain in the growing season can be roughly estimated as

$$F = F_0 \times (F_i/F_0 - 1) \times t$$

where F is the enhanced total soil CO₂ release during rain, F_0 is the seasonal average baseline CO₂ flux of a site, F_i/F_0 is the site-specific average enhancement ratio during the rain simulations, assumed to represent the enhancement ratio during actual rain events, and t is the total time of rainy periods during the growing season (May to October). Based on our results, at GM02, the average baseline CO₂ flux is 4.34 μmol m⁻² s⁻¹, and the average enhancement ratio is 1.34. The total time of rain during the growing season of 2002 is 305 h. Thus, the enhanced soil CO₂ flux triggered by rain is estimated to be 0.19 t C ha⁻¹. Using the same calculation method, the total rain-enhanced soil C release during the growing season at HF04 and HF05 is 0.32 and 0.15 t C ha⁻¹ respectively.

Our calculations of the rain-enhanced soil carbon loss should be considered order-of-magnitude estimates only.

They have ignored the possibility of flux decline with time due to decrease in substrate or oxygen availability. However, the supposed overestimation could be compensated by the greater enhancement ratio due to greater rain intensity, longer duration of rain, or low soil moisture conditions. Indeed the enhancement ratios used for the estimation are low (from 6 mm rain intensity), and our estimation did not include the soil CO₂ flux that remains elevated after rain stops. Therefore, it is likely that the actual rain-induced carbon loss is greater than our estimate.

Since the pulses are usually short-lived, the amount of rain-enhanced carbon release is much smaller than the annual total soil respiration. Take our estimation at HF05 for example; rain effects add only 0.15 t C ha⁻¹ to soil C release during the growing season, while soil respiration at Harvard Forest for the period between 1995 and 1999 was estimated to be 6.4–8.7 t C ha⁻¹ yr⁻¹ (Savage and Davidson 2001). As Borken and Matzner (2009) concluded in a review, cumulative carbon loss from soils undergoing repeated drying and wetting tends to be smaller than from soils with optimum moisture, which also suggests that wetting-induced CO₂ pulses may not offset the low respiration rate during drought periods. However, if the initial enhancement is high and rain lasts long, rain-induced emission can result in considerable carbon loss at some sites. It was estimated that at Great Mountain Forest, with an average flux of 21.9 μmol m⁻² s⁻¹ during rain and a rain duration over 20 h, a single rain storm can lead to a loss of 0.18 t C ha⁻¹, or 5–10% of the annual net ecosystem production of mid-latitude forests (Lee et al. 2004). In some areas, more carbon is released by soils subject to drying-rewetting cycles than by soils maintaining constant moist (Jarvis et al. 2007; Xiang et al. 2008). Laboratory experiments also found that overall bacterial population growth and respiration are greater in rewetted soil than in constantly moist soil (e.g., Lovieno and Bååth 2008). In summary, the impact on annual carbon sequestration due to wetting can be significant or negligible, depending on site-specific conditions.

Conclusions

The results from our rain simulation experiments showed that even without long-lasting drought at the study sites, mild to medium wetting was enough to

trigger immediate increase in soil CO₂ flux. Rain-induced soil CO₂ pulses were not limited to dry soils. Only at plots with seasonal mean soil moisture approaching field capacity did we fail to see wetting-induced flux enhancement. Therefore, some level of drought stress existed even at the mesic sites. Across the three site-years, flux enhancement was moisture dependent: The seasonally averaged enhancement showed strong negative correlation with the mean soil moisture among the treatment plots.

Soil CO₂ flux showed rapid increase within 10 min of the onset of wetting, and started to decline as soon as the 30-min wetting had ended, along with declining soil moisture. Such pulse-like response pattern was shared by Great Mountain Forest and Harvard Forest. Loss of moisture, instead of substrate availability, appears to be the main reason for the observed fast decline in the post-wetting CO₂ flux. The presence or absence of forest floor organic horizon led to marked difference in the response pattern. While the plots with intact O horizon consistently showed rain-induced CO₂ flux enhancement with similar enhancement ratios at the three site-seasons, the plots without O horizon responded with limited or even negative enhancement.

We estimated that the rain-enhanced soil carbon loss was 0.15 to 0.32 t C ha⁻¹ during the growing season, which although much smaller than the annual total soil respiration, is 10–20% of the annual net ecosystem production. The actual carbon loss maybe under-estimated because we used an enhancement ratio from a low rain intensity, and we did not include the continuing loss of carbon after rain had stopped.

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