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Rapid and transient response of soil respiration to rain

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Abstract

The influence of rainstorm on soil respiration of a mixed forest in southern New England, USA was investigated with eddy covariance, rain simulation and laboratory incubation. Soil respiration is shown to respond rapidly and instantaneously to the onset of rain and return to the prerain rate shortly after the rain stops. The pulse-like flux, most likely caused by the decomposition of active carbon compounds in the litter layer, can amount to a loss of 0.18 t C ha^{-1} to the atmosphere in a single intensive storm, or 5–10% of the annual net ecosystem production of midlatitude forests. If precipitation becomes more variable in a future warmer world, the rain pulse should play an important part in the transient response of the ecosystem carbon balance to climate, particularly for ecosystems on ridge-tops with rapid water drainage.

Keywords: eddy covariance, microbial activity, rainstorm, soil respiration, soil water potential

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Introduction

The need for a precise understanding of the terrestrial carbon sink and climate feedback has motivated extensive studies on environmental influences on soil respiration. At a given site, the daily and seasonal variations of soil CO_2 flux is controlled primarily by temperature. The influence of soil moisture at these short timescales is secondary in normal soil moisture conditions (e.g., Edwards, 1975; Kim & Verma, 1992; Hanson *et al.*, 1993) and becomes more important in severe drought when microbial activities are curbed by physiological stress (Keith *et al.*, 1997; Davidson *et al.*, 1998) and at times of near-saturation, a condition that can exist in rainstorms, when oxygen is thought to be limiting (Bunnel & Tait, 1974, imunek & Suarez, 1993; Moncrieff & Fang, 1999). However, such knowledge is based in large part on field research in fair weather conditions, and the process during rainstorms and its role in the ecosystem carbon balance are not well-understood.

Currently, micrometeorological methods are deployed at hundreds of sites within the global carbon flux network (FluxNet) to understand the dynamics of annual carbon and water balances in various ecosystems (Valentini *et al.*, 2000; Baldocchi *et al.*, 2001). Eddy covariance (EC), the FluxNet core methodology, is more likely to malfunction in bad weather than in good weather, creating data gaps that must be filled in postfield data analysis. It is often assumed that, for the purpose of quantifying the annual net ecosystem production (NEP), the response function established in fair weather can be extended to rainy periods (e.g., Falge *et al.*, 2001). The validity of this assumption is unknown given the difficulty of flux measurement in rain.

The response of soil respiration to wetting has been a subject of numerous studies. Most of them were conducted in a synthetic, laboratory environment (Griffiths & Birch, 1961; Orchard & Cook, 1983; Schnüer *et al.*, 1986; Kieft *et al.*, 1987; Clein & Schimel, 1994; Borken *et al.*, 2003). Few plot-scale studies were reported for field conditions (Rochette *et al.*, 1991; Kelliher *et al.*, 1999; Schimel *et al.*, 1999; Liu *et al.*, 2002). According to these studies, a short wetting event can cause an instantaneous excitation of microbes (e.g., Borken *et al.*, 2003) or a delayed respiration pulse (e. g., Griffiths & Birch, 1961). Wetting of longer duration can promote microbial biomass growth, causing an increase in basal respiration (e.g., Schnürer *et al.*, 1986). If rain continues for long enough time, oxygen may become a limiting factor, although this has not been confirmed experimentally for forest soils because to date, there are no published studies on direct observations of soil respiration *during* rain. The relative role of the three impacts likely depends on soil moisture before the wetting event, soil drainage condition, substrate type, and storm intensity and duration.

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In this study, we investigated the controls on soil respiration of a mixed species temperate forest during rainstorms. The *in situ* EC measurement, initiated in 1999, indicated large pulses of CO_2 efflux in several rain events. However, such measurement itself is not conclusive because of possible advection associated with the nonflat topography of the site and interference of rain with the sonic anemometer. Additionally, it is very difficult to discern the relevant biological and physical mechanisms because controlling variables, such as soil moisture, were highly heterogeneous on rolling topography and thus point measurement of these variables near the EC tower does not offer good representation of the condition in the EC flux footprint. To circumvent these problems, we conducted field manipulative and laboratory incubation experiments to simulate the effect of rain on soil respiration. Each of the three experimental strategies offers its unique advantages, and taken together, they provide an opportunity for us to establish the validity of the rain pulses and identify mechanisms responsible for their occurrence.

Experimental methods

Site

The experimental site was a mixed species forest (red maple, eastern white pine, and hemlock) near a ridge-top in moderately hilly terrain in Great Mountain, Norfolk, Connecticut (41°58′N, 73°14′W, Lee & Hu, 2002). The soil was a Hollis series spodosol, common around this part of New England. The soil, developed in ground moraine till derived from schist and gneiss bedrock, was acid and generally stony sandy loam or loamy sand. Till thickness varied from relatively thick ($>$1–2 m) to absent on exposed ledges. The forest floor (Oie + Oa) was 6.8 ± 0.5 cm thick. A total of fifteen $0.5\,m^2$ soil pits were excavated within the tower footprint in June 2001. Analysis of the soil samples gave a total soil organic carbon content of $16.7\,kg\,C\,m^{-2}$ (litter included), a rock ($>$2 mm) fraction of 34%, and a bulk density of $0.16\,g\,cm^{-3}$ in the O horizon and $1.3\,g\,cm^{-3}$ below the depth of 30 cm. Over 70% of the root biomass was found in the top 20 cm soil layer (including the O horizon). The average (1942–2001) annual temperature was 7.0 °C and total precipitation was 133 cm.

EC measurement

Details of the micrometeorological measurement have been documented by Lee & Hu (2002). Briefly, the whole-ecosystem flux was measured with a closed-path EC system (model 6262 CO_2/H_2O analyzer, Licor, Inc., Lincohn, NE, USA; model 1012R2A sonic anemometer/thermometer, Gill Instruments Limited, Lymington, UK) at a height of 30.4 m above the ground (roughly 10 m above the canopy). Turbulence time series were recorded at 10 Hz and fluxes were computed over 30 min intervals following the standard procedure. Correction for air storage below the EC sensor was made with CO_2 concentration measurements at five levels (1.5, 7.4, 13.6, 21.7 and 30.7 m above the ground) using a profile system that consisted of a CO_2/H_2O gas analyzer and a manifold.

Rain simulation

Rain simulation was carried out over seven 1 m radius plots, located on a gentle slope with well-drained soil, which is typical within the EC flux footprint. One plot (plot A) was established in May 2001 for a pilot experiment and the other six plots were established in April 2002, forming three pairs, labeled as B/b, C/c and D/d, respectively, with upper-case labels denoting plots with an intact litter layer. Paired plots were located adjacent to each other. Placement of the plots was not entirely random because they must be free of large coarse woody debris and thick understory in order to be accessible for irrigation. Litter (Oie horizon) was removed from one randomly selected plot within each pair (labeled as b, c and d) prior to rain simulation. A PVC collar was inserted in the center of each plot for CO_2 flux measurement. Also inserted in the plot was an access sleeve for soil moisture measurement.

Irrigation was performed four times at plot A in August–December 2001 and once every 7–14 days at all the plots from May to October, 2002. This was achieved by spraying a known amount of water (alternating between 6 and 12 mm) evenly over each plot for 30 min. Soil CO_2 flux and moisture profile were measured with a chamber system (Model 6200, Licor, Inc.) and a portable soil moisture probe (model PR1/4, Dynamax, Inc., Houston, TX, USA), respectively, once prior to, and at set time steps during and after spraying. The irrigation was kept short enough to avoid the confounding effect of diurnal variations in soil temperature and intensive enough to produce a measurable response. In each irrigation run, soil and litter samples were collected outside the plots and were analyzed for their water potential with a water potentiometer (model WP4, Degacon Devices, Inc., Pullman, WA, USA).

The soil chamber system was calibrated for span and zero offset at the beginning of each measurement day. Soil moisture was measured at 10 cm increments down to the depth of 40 cm in plots C, D and d and to the depth of 30 cm in all other plots. Factory-supplied calibration factors for organic and mineral soils were applied to the moisture measurement of the top 10 cm soil layer and the deeper layers below, respectively. In the following, we use the 0–10 cm measurement as an approximation for the moisture content of the litter layer, recognizing that the actual content might be lower than the 0–10 cm average value.

Laboratory incubation

Laboratory incubation was conducted using a continuous flow incubator that consisted of a 300 mL Teflon flask, a micro-pump and a gas analyzer (Model 6262, Licor, Inc.) at a temperature of 21 °C. A soil sample in a small dish was placed in the flask and was flushed with ambient air for 30–60 s at a flow rate of $2.5\,\mathrm{L\,min^{-1}}$. After that, the system was switched to a closed loop at the same flow rate, and CO_2 concentration was recorded every second for 60 s. CO_2 evolution rate (in $\mu\mathrm{mol\,CO_2\,g^{-1}}$ of dry weight per s or $\mu\mathrm{mol\,g^{-1}\,s^{-1}}$) was computed from the rate of change of the concentration with time. The procedure was repeated two to three times for each measurement. Correction for blank, which was measured with the flask being empty, was applied to the measurement.

In the determination of the dependence of CO_2 evolution on soil moisture and water potential, four samples, roughly 1 g each, were wetted to saturation and kept in a sealed container for 8–12 h prior to the actual measurement. CO_2 evolution was measured by placing one sample a time in the flask. After they were all analyzed, the samples were exposed to room air and were dried for ~30 min by a fan. The measurement/drying cycle was repeated until their water potential was approximately −50 MPa, usually within 24 h. The moisture response curve presented below is the average of the four measurements.

Water content of the incubation samples was determined gravimetrically. Conversion of water content to water potential was made from water retention curves established with a separate set of four samples. In the determination of the retention curves, the samples were first wetted to saturation. Next, measurements of water potential (with the WP4 water potentiometer) and drying of the samples were alternated, in a fashion similar to the one described above, until a water potential of approximately −70 MPa was reached. The retention curves based on the average of the four measurements are given by $\psi = -0.033\ \theta_g^{-2.69}$ for mineral soil and $\psi = -1.33\ \theta_g^{-2.22}$ for forest floor litter, where ψ is water potential in MPa and θ_g is water content in $\mathrm{g\,g^{-1}}$. Subsequent sets of measurements with additional samples from the site gave almost identical retention curves.

We also simulated the rain response in the laboratory. We first determined the CO_2 evolution rate of air-dried litter samples, wetted the samples to a desired water content, measured the evolution rate within 1 min after the wetting, and tracked the rate for 68 h. We did not control the sample water loss since we were mainly interested in the initial respiration pulse.

Results

From 1999 to 2002, the EC measurement showed 1–3 events per year of unusually large CO_2 flux associated with rainstorms in the later part of the growing season when the soil was drier. This was demonstrated by the occurrence of Hurricane Floyd on September 16, 1999 (Fig. 1). The storm, which produced 170 mm of rain in 26 h and had sustained high wind (average friction velocity $u_* = 1.0\,\mathrm{m\,s^{-1}}$), was chosen for a detailed analysis for several reasons. First, the storm was long enough so that turbulence was sufficiently stationary. Second, the rain intensity was high enough to overcome canopy interception and produce a clearly detectable flux pulse. Third, the above-canopy eddy flux was dominated by the soil flux because of the very low photosynthetically active photon flux density ($<150\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) and hence small canopy CO_2 uptake. Fourth, air was well-mixed throughout the whole event, with air stability varying from slightly unstable in daylight hours to neutral at night, thus minimizing the influence of advection (Lee, 1998).

During the storm event, a large whole-ecosystem flux from the forest to the atmosphere was observed, its magnitude and direction being consistent with an

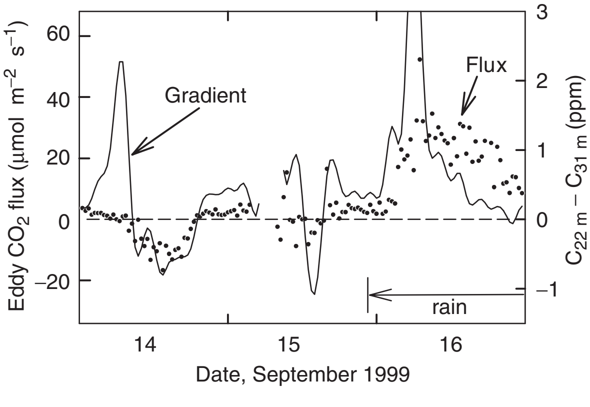

Fig. 1 The whole-ecosystem CO_2 flux measured with an EC system before and during Hurricane Floyd. Also plotted was an independent measurement of the vertical gradient of CO_2 volume mixing ratio over the forest. Positive flux denotes CO_2 loss from the forest to the atmosphere. The delay between the respiration pulse and onset of rain was probably caused by canopy interception of rainwater. The data was terminated by a power outage.

independent observation of the vertical CO_2 concentration gradient over the forest. The average flux during the storm was 21.9 μmol m^{-2} s^{-1}, equivalent to a loss of roughly 0.18 t C ha^{-1} to the atmosphere over 20 h, or 5–10% of the annual NEP of mid-latitude forests of similar structure and age (Black *et al.*, 1996; Lee *et al.*, 1999; Barford *et al.*, 2001; Aubinet *et al.*, 2002). For comparison, a soil temperature-dependent function, established with soil chamber measurements in fine weather (Lee & Hu, 2002), would predict a soil efflux of 3.9 μmol m^{-2} s^{-1}, giving a flux enhancement ratio of about 5. The actual enhancement should be lower than this because of respiration of the above-ground biomass.

Analysis of the EC diagnostics did not suggest degraded performance in rain. Inspection of the raw turbulence time series and their spectra and cospectra shows that the highly positive correlation between the 10 Hz CO_2 concentration and the vertical velocity data was genuine. The mean turbulence statistics also behaved in an expected manner. For example, the ratio of the vertical velocity standard deviation to u_* was 1.15 (Fig. 2), falling within the range of observations in neutral air (e.g., Aylor & Ducharme, 1995). Other researchers also found that the type of anemometer deployed in this study gave reliable measurements in rain (Malhi *et al.*, 1998; Gash *et al.*, 1999). Thus, the flux rain pulse was not caused by instrument errors. However, because the flux was observed in rainy weather on rolling topography, conditions that were not ideal for EC experiments, a measurement artifact due to meteorological causes cannot be ruled out completely. This emphasizes the importance of independent data from rain simulation and incubation for cross validation (section on flux rain pulse intensity and duration).

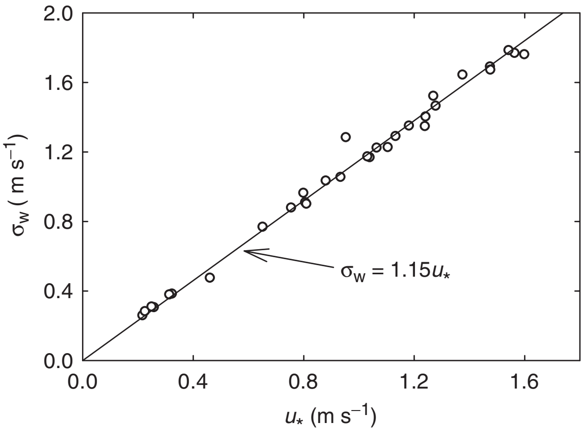

Fig. 2 Scatter plot of the vertical velocity standard deviation against friction velocity, September 16, 1999.

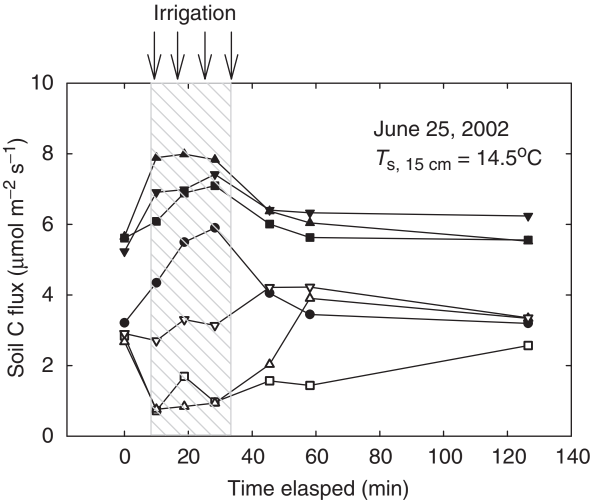

Fig. 3 An example of soil CO_2 flux response to rain simulation in the early part of the growing season. Solid symbols denote observations from plot A (bullet), B (square), C (triangle) and D (upside down triangle), and open symbols denote observations from plots where the litter layer had been removed prior to the experiment (square, plot b; triangle, plot c; upside down triangle, plot d).

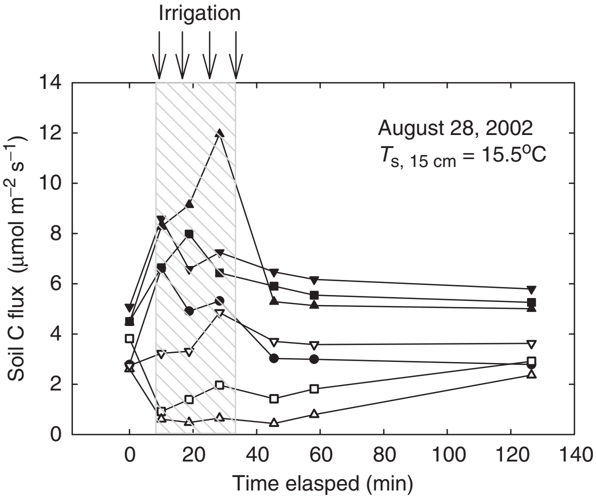

Fig. 4 As in Fig. 3 except in the later part of the growing season (August 28).

Figures 3 and 4 give two examples of soil CO_2 flux response to rain simulation. The flux increased immediately after water was sprayed over the forest floor and returned to the preirrigation value in <1 h after the irrigation, and showed no sign of a postwetting respiration pulse (Bottner, 1985; Clein & Schimel, 1994). These flux values often exceeded the maximum obtained in dry weather, suggesting that, contrary to some studies (Bunnel & Tait, 1974, Kelliher *et al.*, 1999), fine-weather observations cannot define the realizable respiration potential of a soil. The pattern of flux response resembled the *in situ* EC measurement in rain, although a direction comparison was not desirable because of their different footprints and rain intensities. The behavior of plots b, c and d (plots without a litter layer) was quantitatively different from those with an intact litter layer, showing a reduced respiration rate in response to irrigation.

The instantaneous response to wetting was also confirmed by a laboratory incubation of litter samples collected from the site (Fig. 5). CO_2 evolution increased by as much as 10-fold within 1 min, the shortest measurement interval allowed by our incubation system, after water was added to dry litter samples. The water contents of the samples immediately after wetting were 1.02, 2.52, 3.59, 4.58 $g\,g^{-1}$. Using a water retention curve established for maple litter, these correspond to water potentials of -2.2, -0.44, -0.23, and -0.15 MPa. The slow decline of the evolution rate with time following the wetting event was attributed mostly to sample water loss (0.3 $g\,g^{-1}$ over the initial 6 h of incubation), which could reduce the evolution rate by up to 0.0015 $\mu mol\,g^{-1}\,s^{-1}$ according to a separate experiment on the effect of water content, and to a lesser extent to the decline in substrate supply.

The relative contribution of the litter layer to the total soil C flux depends strongly on the litter layer soil moisture, as shown in Fig. 6. Here the data was obtained from the paired plots right before the irrigation began. To calculate the relative contribution, we first computed the average flux, F_1, of plots B, C and D (plots with an intact litter layer) and the average flux, F_2, of plots b, c and d (plots without a litter layer), and then divided the difference between the two averaged fluxes, F_1-F_2, by F_1. The ratio was about 0.5 at a litter layer water content of 12–14% by volume (May and October) and decreased linearly with water content to a low value of 0.35 (August). Strictly, litter removal could alter the biophysical conditions so that the observations at plots b, c, and d did not represent the true flux contribution from the undisturbed Oa horizon and the deeper soil layer. The extent of this artifact was not known, although soil moisture in these plots did not appear to be a limiting factor for most observations.

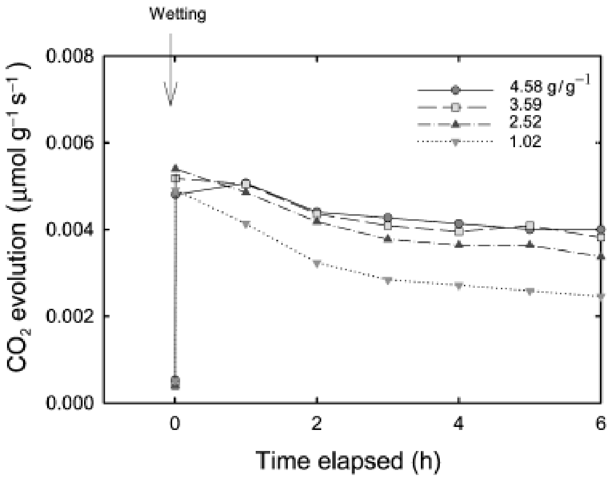

Fig. 5 Response to wetting of four air dry red maple litter samples. Water content ($g\,g^{-1}$) was measured immediately after wetting.

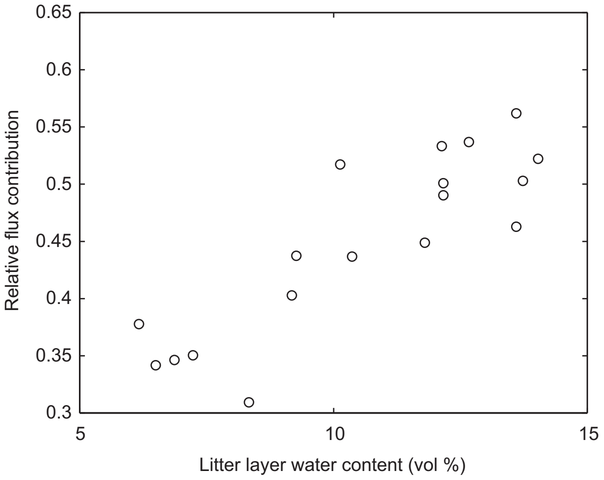

Fig. 6 Relative contribution of the litter layer to the total soil CO_2 flux as a function of the litter layer soil moisture from May to October, 2002.

Figure 7 compares soil CO_2 fluxes before and 30 min into the rain simulation at plot A over a range of soil temperature conditions. Flux enhancement due to wetting was observed in all irrigation runs. The degree of enhancement varied considerably, from less than 10% in early May when soil moisture was abundant to 170% in late August when the soil was driest of the year.

To reduce the confounding effects of seasonal variations in soil moisture and temperature, we computed a flux enhancement ratio by dividing the observed flux, F, by the flux prior to the rain simulation, F_0, and a soil moisture increment by subtracting the initial moisture, θ_0, from the moisture observed during and after the simulation, θ. We found that moisture increment of the litter layer was a robust predictor of the flux enhancement ratio for most observations (Fig. 8, $R^2 = 0.42$, $n = 92$ excluding outliers). A notable exception was a group of outliers (open symbols, Fig. 8) from two irrigation runs in late August, which is further discussed in the section on mechanisms responsible for the flux rain pulse. A similar data graph was presented by Borken *et al.* (2002).

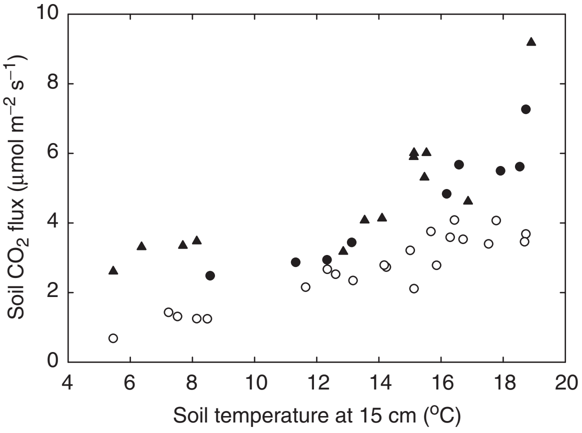

Fig. 7 Soil CO_2 flux as a function of 15 cm soil temperature for plot A: circles, flux before rain simulation; filled symbols, flux at 30 min into rain simulation (bullets, rain intensity 6 mm; triangles, rain intensity 12 mm).

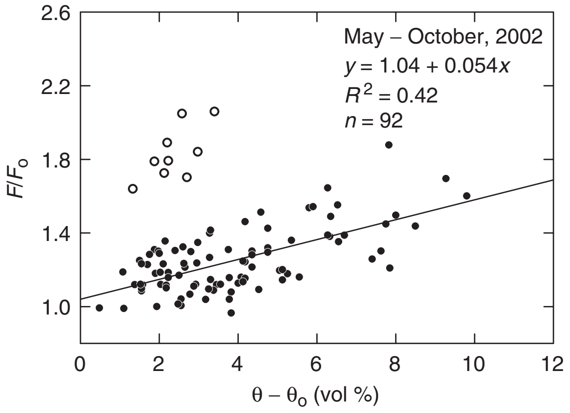

Fig. 8 Flux enhancement ratio plotted against litter layer soil moisture increment from the rain simulation experiment. Data were average of four plots (A, B, C, D) with intact litter layer. Outliers (circles) were observations in late August following a moderate drought.

Figure 9 shows the relative CO_2 evolution rate, measured in the laboratory with the incubator, as a function of moisture content. The relative rate was the ratio of the actual to the maximum rate (1.5×10^{-3} and 0.17×10^{-3} µmol g^{-1} s^{-1} for litter sample and mineral soil, respectively). The evolution rate increased monotonically with the sample moisture. Contrary to some other laboratory studies (Flanagan & Veum, 1974; Bowden *et al.*, 1998), we did not observe a reduced rate near the water holding capacity (WHC) for both the mineral soil and the litter samples. Over the relatively narrow range of moisture conditions that occurred in the field in fine weather (5–15% by volume, Fig. 6), the response of the litter sample was approximately linear, in agreement with the rain simulation result (Fig. 8) and litterbag data (Schimel *et al.*, 1999). The CO_2 evolution of the mineral soil sample, on the other hand, was less sensitive to moisture over the range of field conditions (moisture at 20 cm depth varying from 15% to 30% by volume).

When presented as a function of water potential, the litter sample data suggests two regimes separated by a threshold value of approximately −0.1 MPa (Fig. 9). Above this threshold the evolution rate was not sensitive to water potential and below the threshold the evolution rate was log-linear with water potential. A log-linear relationship was also reported by Orchard & Cook (1983) for mineral soils. The measurement uncertainty of the mineral soil samples was relatively large because its evolution rate approached the detection limit of the incubation apparatus. Despite the large

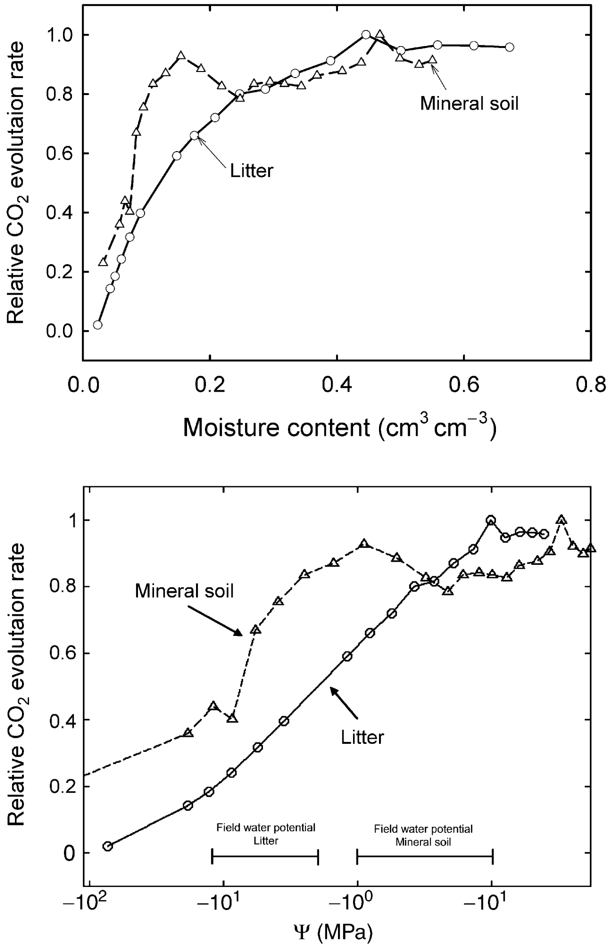

Fig. 9 Relative CO_2 evolution, determined with a laboratory incubator, as functions of water content (top) and water potential (bottom). Horizontal bars indicate ranges (10–90 percentile) of water potential variations in the field. Water holding capacity was 0.64 for mineral soil and 0.51 cm^3 cm^{-3} for forest floor litter.

measurement noise, one could identify a more negative threshold value of -1 MPa for the mineral soil, below which the evolution rate was sensitive to water potential.

Discussion

Mechanisms responsible for the flux rain pulse

One possible explanation for the flux rain pulse may be related to the release of CO_2 dissolved in rain, the displacement of soil air by rainwater, or degassing due to the decrease in barometric pressure with time. At a temperature of 15 °C, 1 m^3 of liquid water could dissolve 0.7 g CO_2 (Yamartino, 1985). Assuming an intensive rain rate of 12–24 mm h^{-1} and that all dissolved CO_2 was released upon contact with the forest floor, the resulting flux would only be 0.05–0.1 μmol m^{-2} s^{-1}. Using a mean concentration of 0.3% found in the top 20 cm soil layer at the well-drained sites (Oishi & Lee, 2002), a rain rate of 12–24 mm h^{-1} would displace 0.4–0.8 μmol m^{-2} s^{-1} out of the soil. Furthermore, theoretical calculations show that pressure change can cause degassing by air convection in and out of the soil column only if the oscillation period is on the order of 1 s (Colbeck, 1989). In comparison, the timescale of the barometric pressure change during the storm was several orders of magnitude longer. Therefore, degassing due to these physical disturbances was too small to explain the observed flux.

The markedly different response between the plots with and without a litter layer (Figs 3 and 4) indicates that the most tenable explanation lies in the processes occurring in the litter layer. This layer, being highly porous (porosity 90%) and directly exposed to canopy air with extremely low water potentials (typically < -50 MPa), was almost always at a water potential below -1.5 MPa (Fig. 9), a critical value that essentially deactivates bacterial respiration and also limits the function of the fungal community (Griffin, 1981). Penetration of rainwater quickly made the physical environment favorable to the microbes and at the same time released easily available energy and carbon, perhaps from the microbial biomass that had died from desiccation in the preceding drying cycle (Bottner, 1985; Kieft *et al.*, 1987), resulting an instant increase in CO_2 release. An instant response was also reported by Davidson and colleagues (Davidson *et al.*, 1993; Borken *et al.*, 2003) but not by Griffiths & Birch (1961), Orchard & Cook, 1983, Schnürer *et al.* (1986), Kieft *et al.* (1987), and Clein & Schimel (1994), although some of these authors may have observed and ignored the short-term response.

It is also possible that some substrate was translocated from the litter layer by the wetting front to the microbial sites in the deeper, mineral soil, at a speed much faster than could be achieved by solute diffusion. Obviously, microbes in the plots where the litter layer was removed did not benefit from the translocation mechanism, as evidenced by the lack of enhancement due to wetting (Figs 3 and 4). The translocation mechanism could be particularly important in the later growing season when readily decomposable organic compounds are depleted at the microbial sites in the mineral soil.

The flux enhancement from two irrigation runs in the later part of the growing season (August 15 and 28) had a large deviation from the regression function on the litter layer moisture content (Fig. 8), indicating a large contribution of the deeper, mineral soil to the observed flux (Figs 4 and 6). These observations were made after a moderate drought had reduced the mineral soil water potential (20 cm depth) down to approximately -3 MPa. At this water potential, the microbial community would suffer drought stress according to the incubation data (Fig. 9) and field observations elsewhere (Wildung *et al.*, 1975; Davidson *et al.*, 1998). However, the flux at plots b and c (plots without a litter layer) did not increase in response to wetting, suggesting that relief of physiological stress was not the sole factor and that interactions among various layers of the soil column, possibly through translocation of substrate by the wetting front discussed above, played an important part in producing the flux pulse. (The slightly increased soil flux at plot d during the irrigation run on August 28 was caused by a rapid increase of the soil surface temperature due to a sunfleck passage.)

Flux rain pulse intensity and duration

The intensity of the flux rain pulse differed among the three experiments. The increase was about fivefold for EC (Fig. 1), up to twofold for irrigation (Figs 3, 4, 8), and about 10-fold for incubation (Fig. 5). In addition to footprint sizes being different, this was linked to the level of substrate dryness before the wetting event (Fig. 7) and the amount of substrate moisture change caused by the water injection (Fig. 8).

The persistence of the flux rain pulse appeared to be controlled by the substrate moisture content during and after the wetting event. The substrate remained wet in the incubation experiment and as a result, a high evolution rate was sustained (Fig. 5). For the rain simulation, the litter layer water content displayed a similar pattern of time evolution as the flux time series: It showed an immediate increase (by up to 10% by volume, Fig. 8) in response to irrigation and returned to the prewetting level in less than 1 h (data not shown). No moisture data was available for Hurricane Floyd. Given the high rain intensity (170 mm over 26 h), the litter layer moisture content must have remained high throughout the storm, causing a long flux rain pulse. The transient nature of the flux enhancement is a consequence of the relatively fast drying of the litter layer in the field after the wetting event was over.

The unusually large EC flux (Fig. 1) was a cause for concern. No data on soil moisture was available for 1999. Observation in the subsequent years showed that the litter layer moisture was roughly 5% by volume in early September. Given that the 1999 growing season was relatively dry, with June-August precipitation 30% below normal, we suggest that the litter moisture content could be also on the order of 5% by volume, if not lower, prior to the storm passage. According to the incubation data (Fig. 9), an increase in the litter water content from 5% by volume to WHC would cause a fivefold increase in the CO_2 evolution rate. In this regard, the large eddy flux during the storm seemed reasonable, even though large soil CO_2 fluxes of this magnitude have never been reported for fine weather.

The role of rainstorm in ecosystem carbon balance

According to Fig 8, a model of the form $F = F_0(T_s,\ \theta)(a + b\Delta\theta)$ may be appropriate for filling data gaps in rainstorms, where F is flux in rain, F_0 is a modeled flux based on fair-weather observations that is a function of soil temperature (T_s, °C) and soil moisture (θ), a and b are regression coefficients, and $\Delta\theta$ is soil moisture increment in rain. In this study, F_0 is given by

$$F_0 = \frac{\theta}{0.001 + \theta} \times \frac{3.82}{3.82 + \theta} \times 2.41 \times 3.11^{(T_s - 10)/10},$$

where the parameter values were estimated with a regression procedure using the average soil flux and litter moisture content observed along a 100 m transect in fine weather (Lee & Hu, 2002). Applying this model with the aid of automatic soil moisture and temperature measurements, we estimated that soil flux was on the order of $0.8\,\mathrm{t\,C\,ha^{-1}}$ for rainy periods during the growing seasons in 2002, a year with nearly normal precipitation. The estimate was reduced to $0.6\,\mathrm{t\,C\,ha^{-1}}$ if only the fair weather function F_0 was used. This suggests a bias error of $0.2\,\mathrm{t\,C\,ha^{-1}}$ in NEP had the fair weather response function alone been used for rainy periods.

In this order of magnitude estimate of flux bias, we have ignored the possibility of flux decline with time in actual rainstorms due to substrate decline, as suggested by the trend in Fig. 1, although the trend was also correlated with decreasing litter layer temperature ($R^2 = 0.40$, $n = 39$). On the other hand, the uncertainty due to substrate decline could be offset by the increase in respiration in storms that lasted long enough to allow significant microbial biomass growth (Griffiths & Birch, 1961; Schnürer *et al.*, 1986, Schimel *et al.*, 1999), by the supply of carbon compounds leached from the canopy, and by the fact that the enhancement could have been larger at times of low moisture conditions in the mineral soil (outliers, Fig. 8).

The pulse-like flux was indicative of a rapidly changing soil biophysical environment during rain, and suggests that, even in heavy rainstorms, the soil did not reach an oxygen-limiting condition assumed by the inverse U-shape function of moisture response (Bunnel & Tait, 1974). It is conspicuous that the phenomenon has not been reported for EC observations at other FluxNet sites. FluxNet, by design, is biased toward flat terrain where water drainage is presumably not as fast, and oxygen may become limiting owing to surface ponding during rainstorms. Our site is characterized by shallow glacial till soil and undulating topography. Consequently, water-limiting conditions prevail soon after rain stops. If the difference between our site and other FluxNet sites is indeed caused by the interplay between topography and soil drainage, soil carbon flux in rainy weather may play a disproportionately large role in the carbon budget of ecosystems near ridge-tops, as suggested by the study of Lee *et al.* (2002). In this respect, investigation of the topographic influences, along with ecotype, chronosequence, land use history and management regime (Valentini *et al.*, 2000; Baldocchi *et al.*, 2001; Law *et al.*, 2001), may lead to a more complete understanding of the variability of carbon flux across the landscape.

One critical question regarding the global carbon cycle concerns the transient response of the terrestrial carbon flux as a result of inter-annual climate variability (Trumbore *et al.*, 1996). Because NEP is a small difference between two large fluxes (gross primary production and ecosystem respiration), the flux pulse produced by rain could play an important part in the inter-annual variability in NEP, particularly in view of the projection that precipitation will be more variable in a future climate (Giorgi *et al.*, 2001). It is shown that soil respiration is higher in a wetter year, causing a lower NEP (Barford *et al.*, 2001); the NEP estimate would be further reduced if the rain pulse were considered. Furthermore, timing of storms is also important: a storm following a drought could result in a much more substantial carbon release than that occurring in a wet period. This and other aspects of the rain response represent another dimension of biosphere–atmosphere interactions that can confound the climate feedback via a temperature response. A quantitative understanding of the rain response is, however, necessarily more complex than the simple first-order approach commonly used for the temperature response.

Strengths and weaknesses of the three experiments

The EC, field manipulative and laboratory incubation experiments each had their unique advantages and were also sensitive to different errors. EC was a natural experiment that offered *in situ* observations with minimal disturbance to the forest. However, it could be ambiguous in rough terrain because its assumptions regarding mass conservation may be violated in the atmospheric surface layer. Previously, we reported that nighttime CO_2 flux was problematic and attributed the problem in part to advection caused by the terrain complexity (Lee & Hu, 2002). Since most rainstorms occurred at night with low wind speed, a reliable estimate of the annual sum of the flux in rain cannot be derived from the EC measurement.

In the rain simulation experiment, measurements of dependent and independent variables (rain rate, soil moisture, temperature and presence/absence of litter) were made at the same location, overcoming the problem of footprint mismatch with the tower measurements. However, several drawbacks of the experimental design warrant attention. For logistical reasons (section on rain simulation), the layout of the plots was not entirely random and the number of replicates was small. Therefore, extrapolation of the data to the eddy flux footprint could carry a large uncertainty. Also the repeated artificial wetting cycles may have changed the microbial biomass (Schimel *et al.*, 1999). In another related study, Clein & Schimel (1994) found that over a 60-day incubation period, the respiration rate of rewetted birch litter was significantly lower than moist control litter, possibly due to the loss of critical decomposing organisms. While the current experimental design was adequate for studying short-term (hours) responses to rain, noting that the impact of artificial wetting on the moisture sensitivity was probably negligible (Schimel *et al.*, 1999), measurements prior to (ideally for at least one growing season) irrigation and litter removal that compared the irrigation treatment plots and additional control plots would have shed some light on these longer term changes.

The most obvious drawback to the laboratory incubation was its low physical realism: The experiment was done in a synthetic environment that lacked interactions among environmental parameters (e.g., interactions between various soil layers). On the other hand, it was able to regulate and extend the range of independent variables which otherwise could not be done economically in natural conditions (Diamond, 1986).

Because each of the three experiments was prone to its own uncertainties, it is important that they were implemented together to provide independent data sets for cross validation. In our view, the combined approach produced strong evidence for a previously under-recognized mechanism of carbon exchange between the atmosphere and terrestrial ecosystems.

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