Abstract

Wetting-Induced Soil Carbon Dioxide (CO_2) Pulses in Temperate Forests and Agricultural Fields

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Enhanced soil respiration due to wetting can contribute to interannual variations in ecosystem carbon balance, and affect short-term and long-term carbon sequestration. Improved knowledge on wetting effects is important particularly because of the projected increased in precipitation variability due to climate change.

This study sought to enhance understanding of short-term effects of wetting on soil respiration and to estimate wetting-induced soil carbon emissions. Simulated wetting experiments were conducted in two New England forests and on Nebraska soybean fields. Laboratory incubation experiments on forest floor litters were performed to provide complementary information for our field experiments.

At the forest sites, in-situ soil CO_2 flux measurements showed immediate and short-lived increase in soil respiration upon wetting. Enhancement magnitude was similar at the two forests. Flux enhancement occurred mainly on plots with intact organic layer, suggesting that O horizon is the main contributor of the enhancement. Flux enhancement increased with wetting intensity and moisture increment. Flux enhancement and flux contribution by O horizon were both negatively correlated with pre-wetting soil moisture, indicating that on drier plots, flux enhancement and O horizon flux contribution is greater. Our results also allowed rough estimates of soil carbon loss during wetting.

At the Nebraska soybean sites, wetting also triggered soil CO_2 pulses, but enhancement magnitude was greater than that at the forest sites. On bare plots, wetting not

only induced enhancement, but also produced extended duration of elevated CO_2 flux, phenomena not observed on bare plots at the forest sites. This indicates that, regardless of the presence or absence of crop residues, upon mild wetting events, the soybean fields have potential to lose more soil carbon than the forest sites. Nonetheless, wetting-induced carbon loss from agricultural soils could be constrained due to anaerobic conditions commonly seen in compact agricultural soils. Flux enhancement was negatively correlated with moisture increment, suggesting that oxygen is the limiting factor for soil respiration at the soybean sites.

The incubation experiments showed that moisture level did not affect temperature sensitivity of decomposition, and that substrate availability was not a limiting factor for litter decomposition as long as moisture was sufficient.

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Chapter 1

Introduction

ABSTRACT

This chapter delineates the role of soil respiration in ecosystem carbon balance, the potential impacts of climate change on soil respiration, and the needs to understand the effects of change in precipitation and soil moisture regimes on soil respiration. All these gave rise to the motivation of the study, and an overview of research problems and objectives is presented. Relationships between soil temperature and moisture and soil respiration are briefly reviewed, with an examination on the effects and uncertainties of drought. A synopsis of current knowledge of wetting-induced soil respiration in this chapter provides general information for later chapters.

1.1. INTRODUCTION

CO_2 efflux from soils is the second largest carbon flux (after gross primary production, GPP) in most terrestrial ecosystems (Law et al. 1999, Longdoz et al. 2000). With precipitation becoming more variable in the future due to global climate change (Intergovernmental Panel on climate Change, IPCC, 2001), and a projected decrease in soil moisture in most regions on earth during this century (Meehl et al. 2007), it is crucial to understand the physical and biological mechanisms of soil respiration in response to rain, and thereby better predict global carbon flow under the changing climate. My research aimed to investigate the short-term responses of soil CO_2 flux during and immediately following rain events at temperate forests and agricultural lands, and to determine the mechanisms responsible for the behavior of soil respiration and the variations in rain-induced soil CO_2 flux.

Soil organic matter is the third largest global carbon pool (second to the oceans and fossil fuel reserves), holding 1500 Pg of organic carbon in the upper 1 meter (Batjes 1996). Estimated global CO_2 flux from soils is 77 Pg C yr^{-1}, and is greater than terrestrial net primary production (NPP) (Raich and Potter 1995). A change of 10% in soil organic carbon may contribute to an equivalent amount of atmospheric CO_2 as anthropogenic emission over 30 years (Kirschbaum 2000). On the other hand, increased sequestration of carbon by soil through reforestation or management of agricultural soils may help control atmospheric CO_2 levels (Schlesinger 1999, Post and Kwon 2000, Lal et al. 2004). Mid-latitude North America has been responsible for major terrestrial uptake of atmospheric carbon (1.7 ± 0.5 Pg C/yr) due to recovery of abandoned farmlands and previously logged forests (Wofsy et al. 1993, Fan et al. 1998). Studies have shown that soil respiration represented 40-80% of forest

ecosystem respiration (Goulden et al. 1997, Law et al. 1999, Law et al. 2001a, Janssens et al. 2001, Yuste et al. 2005a, Davidson et al. 2006). Variations in weather and climatic factors may affect seasonal and annual soil respiration rates, and further contribute to interannual variations in ecosystem carbon balance (Barford et al. 2001).

In order to understand the role of soil as either sink or source of carbon, and to construct a precise global carbon budget, there have been many studies on influences of environmental factors on soil respiration. Soil respiration varies greatly among different ecosystems and depends on biotic as well as abiotic factors. Temperature and moisture are the most dominant environmental factors that dictate the temporal and spatial variations in soil respiration in an ecosystem (Wildung et al. 1975, Hanson et al. 1993, Raich and Potter 1995). While the relationship between soil temperature and soil respiration is well-documented (e.g., Lloyd and Taylor 1994, Davidson et al. 1998, Kätterer et al. 1998), extensive knowledge about the effects of soil moisture content on soil respiration is still yet to be established. Among the knowledge gaps that need to be bridged is the process of soil respiration during rain events. Since measuring soil CO_2 flux is technically difficult during rainfalls, most knowledge available today regarding soil respiration in response to rain is mainly based on post-rain data. Borken et al. (2003) observed a positive correlation between soil respiration and soil O horizon water content; however, their measurements were not taken during or immediately after rain events, and may underestimate the release of soil CO_2 induced by rainfall.

Soil respiration during rain events may be inferred from measurements of eddy covariance, a methodology that large-scale studies on global carbon budget have relied upon to understand the dynamics of annual carbon and water balances in various ecosystems

(Valentini et al. 2000, Baldocchi et al. 2001). Lately, increased CO_2 flux during and after rain events was observed from eddy covariance data (e.g., Flanagan et al. 2002, Lee et al. 2004, Xu and Baldocchi 2004), and it is suggested that the increase was due to soil CO_2 release. However, eddy covariance measurements often encounter instrumental failure in rain storms, and thus require post-field data analysis. When performing gap-filling in order to quantify net ecosystem production (NEP), it is usually assumed that the response function established under fair weather conditions can be extended to rainy periods (e.g., Falge et al. 2001), while the behavior and patterns of soil respiration during rain events and their roles in the ecosystem carbon balance are still not well understood. This casts doubts on the accuracy of current estimates of NEP, and leads to greater uncertainty in predicting the future global carbon balance.

The problem of soil respiration during rainfall is important particularly because ongoing global warming is expected to lead to more heavy and extreme precipitation in mid- and high latitude areas, primarily in the Northern Hemisphere, and to increase the risk of drought in most mid-latitude continental interiors (IPCC 2001, Ch. 9.3.6.2). The changes may have impacts on food production and ecosystem productivity (Fay et al. 2003). In the Northeast United States, it is observed that the frequency and intensity of heavy and extreme precipitation have increased over the twentieth century (Easterling et al. 2000, Karl and Knight 1998). While many studies have focused on the impacts of temperature increase, it is also critical to understand the effects of change in precipitation regime on the function and energy flow of an ecosystem. More complete knowledge of the effects of rain events to soil respiration will help to better predict not only impacts on primary productivity and vegetation distribution, but also potential changes in terrestrial carbon pools and carbon sink strength.

The overall goals of my study are to (1) detect response patterns and magnitudes of soil respiration during rain events under different site conditions and management approaches, (2) identify the mechanisms through which soil moisture influences the evolution of soil CO_2 during and following rain events, (3) determine the major contributor of rain-induced CO_2 pulses, and the driving forces for their temporal and spatial variability, (4) examine effects of rainfall on different ecosystems through comparison of field results from the three study sites, and (5) estimate the amount of rain-induced carbon release in an ecosystem and contribute to the construction of site-specific models that can effectively account for rain-induced soil respiration.

My research approaches include manipulative field experiments and laboratory incubation experiments. The main focus is on the field experiments, which investigated short-term, in-situ response of soil respiration to wetting through simulated wetting in the field, and on-site measurements during the process of wetting. Field experiments are carried out at two New England forests and Nebraska agricultural fields. The forests are characterized by warm and dry summers, with a future projection of more frequent and intensive precipitation. Peterjohn et al. (1994) suggested that moisture will have increasing importance when soils in temperate forests experience warming. The agricultural site is characterized by arid climate conditions with a future projection of more intensive drought. With the combined data from field experiments, laboratory incubation, and long-term eddy covariance measurements, this study will contribute to a more complete understanding of the effects of precipitation on soil respiration, more precise estimates of annual net ecosystem production, and better predictions of feedback on the climate system via terrestrial carbon cycles in a warmer future world.

1.2. SOIL RESPIRATION AND MOISTURE CONTENT

Soil respiration is the emission of CO_2 from soils to the atmosphere, which is assumed to be represented by soil surface CO_2 efflux, a time rate of soil respiration. It is common for ecological studies to measure soil CO_2 efflux as a key indicator of soil respiration.

Soil respiration is comprised of root respiration and heterotrophic decomposition of soil organic matter, including plant litter, fine root turnover, and dead microorganism biomass. A study at Harvard Forest showed that root respiration, belowground organic matter decomposition, and aboveground litter decomposition accounted for 33%, 30% and 37% of the total soil respiration respectively (Bowden et al. 1993). Epron et al. (2001) found that rhizosphere respiration represented 30-60% of soil respiration in a beech forest. Based on various published data, Hanson et al. (2000) reported that the mean values of decomposition contribution to total soil respiration in a whole year or during one growing season was 54.2% for forest ecosystems and 39.6% for non-forest ecosystems. Based on radiocarbon data, a study at Harvard Forest estimated that 59% of soil respiration was derived from photosynthate carbon residing in the plant and soil for less than one year (including root respiration), and 63% of soil respiration occurred in the upper 15 cm of the soil profile (O and A horizons) (Gaudinski et al. 2000).

1.2.1. Primary abiotic drivers of soil respiration

In addition to the amount of soil organic matter, physiological and ecological characteristics of plant communities and litter quality, there are also environmental factors

that affect the temporal and spatial variation in soil respiration of an ecosystem, such as temperature (Reich and Schlesinger 1992, Lloyd and Taylor 1994, Davidson et al. 1998, Kätterer et al. 1998), soil moisture content (Orchard and Cook 1983, Linn and Doran 1984, Martin and Bolstad 2005), substrate availability and input (Clein and Schimel 1993, Xu et al. 2004, Hibbard et al. 2005), soil pH-value (Reth el al. 2005), and gas diffusivity (Davidson et al. 1995). Soil respiration is site-specific and driven by a combination of elements. Xu and Qi (2001) identified that in a Californian ponderosa pine plantation, 84% of spatial variation in soil surface CO_2 flux was explained by fine root biomass, microbial biomass and soil physical and chemical properties; and 76-95% of temporal variation was explained by soil temperature and moisture. Soil temperature and moisture are the primary abiotic drivers of soil respiration, and they may affect both root respiration and soil organic matter decomposition (Edwards 1975, Palta and Nobel 1989, Borken 2002).

It has been well established that soil temperature is the dominant controller of soil respiration and normally has a positive correlation with soil respiration (Edwards 1975, Hanson et al. 1993, Lloyd and Taylor 1994, Raich and Potter 1995). Trumbore et al. (1996) reported that carbon turnover time in the Sierra Nevada Mountains decreased with elevation, indicating that an increasing temperature led to shorter turnover time and thus greater CO_2 released from soils, which is especially important to terrestrial ecosystem carbon cycles under global warming. The temperature dependence of soil respiration is commonly described by the following function forms:

(a) Power function:

$$F = \alpha T^b \qquad (1.1)$$

where F is soil CO_2 flux, T is soil temperature in degrees Celsius, α is a site-specific

coefficient and b is exponent;

(b) Exponential model:

$$F = a \times e^{bT} \quad (1.2)$$

where F is soil CO_2 flux, T is soil temperature, a is a site-specific constant and b is an exponent;

(c) Q_{10} values:

$$F = F_{10} \times Q_{10}^{(T-10)/10} \quad (1.3)$$

where Q_{10} is the factor that respiration increases by upon 10 degree C increase in temperature, and F_{10} is the reference respiration at 10°C;

(d) Lloyd and Taylor (1994, a modification of Arrhenius equation):

$$F = A \times e^{-308.56 / (Tk-227.13)} \quad (1.4)$$

where A is a constant that may change with environmental and physiological variables, and Tk is soil temperature in degrees Kelvin.

In general, soil moisture content only becomes a limiting factor when it is above or below a certain optimum range, such as during severe drought when microbial activities are curbed by physiological stress (Keith et al. 1997, Davidson et al. 1998) and under poor-drained or anaerobic conditions where oxygen becomes limiting (Linn and Doran 1984, Moncrieff and Fang 1999). It is common to detect the effects of soil moisture on soil respiration in the field by identifying the residuals of temperature-dependent soil respiration models (Savage and Davidson 2001, Borken et al. 2002). The residuals imply deviation from model-predicted soil respiration due to factors other than soil temperature, such as rain events and drought.

Within an optimum range, soil respiration usually increases with soil moisture content

(Orchard and Cook 1983, Linn and Doran 1984, Broken et al. 2003) until reaching a turning point of maximal soil CO_2 flux. Orchard and Cook (1983) reported that even with wet soil, a slight decrease in water potential led to 10% decrease in microbial activity. The turning point of maximum was at 20.6 % (vol) in soil moisture content in a coniferous forest in the Sierra Nevada Mountains (Qi and Xu 2001). However, soil respiration within an optimum range of soil moisture is often variable in the field, and others have reported cases where soil respiration appeared to be insensitive to change in soil moisture within an optimum range (Bunnell and Tait 1974, Reichstein et al. 2003). Soil respiration decreases dramatically if soil moisture drops below a certain threshold. The threshold was 12% (vol) (-150 kPa in soil matric potential) at Harvard Forest (Savage and Davidson 2001), -80 kPa in a European beech, spruce and pine forest (Borken et al. 2002), 15% (vol) in a European temperate maritime pine forest (Yuste et al. 2003), and 15% (vol) in grasslands at and near Sierra Nevada (Xu et al. 2004).

While soil moisture content is often secondary in determining soil respiration rate, many studies have shown that including soil moisture into soil respiration models could improve the predictive power and utility of these models (Bunnell and Tait 1974, Hanson et al. 1993, Potter et al. 1993, Leiros et al. 1999, Qi and Xu 2001, Rey et al. 2002, Reichstein et al. 2003, Yuste et al. 2003, Martin and Bolstad 2005, Reth et al. 2005). The combined effects of soil temperature and moisture on soil respiration is usually modeled using a temperature function multiplying a moisture function (e.g., Potter et al. 1993, Hanson et al. 1993), or a linear equation with temperature term and moisture term (e.g., Leiros et al. 1999). An example of the former is a model by Hanson et al. (1993):

$$F = (R_b Q_{10}^{(T/10)})(1 - Cf/100) \quad (1.5)$$

where

$$R_b = (k\ W_s\ R_{max}) / ((k\ W_s) + R_{max}) \quad (1.6)$$

In the above equations, F is soil CO_2 flux, R_b represents the effects of soil water content on soil respiration, T is soil temperature in °C, Cf is the percent coarse fraction of soil, W_s is the soil water content in volume percent, k is a constant determining the rate of change of R_b with respect to W_s, and R_{max} is the maximum value of R_b when W_s reaches 100%. The basic assumption of such of multiplicative formulation is that the effects of temperature and moisture on soil respiration are independent.

Leiros et al. (1999) used two multiple linear equations to fit their data:

$$F = a\ T + b\ W_s + d \quad (1.7)$$

$$F = a\ T + b\ W_s + c\ T\ W_s + d \quad (1.8)$$

where T and W_s are soil temperature and water content, and a, b, c and d are fitting constants. Leiros et al. (1999) found by multiple regressions that equation 1.8, which includes the term of the product of temperature and moisture, usually better explained the variation of soil CO_2 flux.

Soil moisture content and temperature may be confounded factors of the variation in soil respiration (Davidson et al. 1998). Soil temperature affects soil moisture content by influencing evapotranspiration, and thus soils with higher temperature usually have lower moisture content. Some researchers also pointed out that Q_{10} values are often affected by soil moisture conditions (Lloyd and Taylor 1994, Kirschbaum 1995, Xu and Qi 2001). Accompanying the confounding effect between soil temperature and soil moisture content, it is also common in the field to see low soil temperature with high soil moisture content early in the growing season due to snow melt, and high soil temperature with low soil moisture

content later in the growing season due to plant uptake of soil water. Martin and Bolstad (2005) found that there was a linear correlation between soil temperature and moisture during a drought year, whereas during a non-drought year there was no significant correlation. Qi and Xu (2001) separated the temperature and moisture effects on soil respiration in a temperate coniferous forest by plotting soil CO_2 flux data from two separate groups, one with higher soil moisture content and the other lower, against soil temperature. The results showed good correlations for both groups ($R^2 = 0.86$ and 0.73), and moisture appeared to affect the coefficient term but not the exponent term of the respiration-temperature power function.

The effect of soil temperature and moisture on soil respiration is also interdependent. Wetting (rain irrigation) following droughts in a European spruce forest showed that temperature during wetting was critical. Wetting taking place at a time with high temperature induced much greater release of soil CO_2 than that at a time with lower temperature (Borken et al. 1999). Conversely, field research in a Mediterranean coppice oak forest where water is often limiting in the summer showed that soil respiration was correlated with soil temperature only when soil moisture was above the threshold of 20% (vol) (Rey et al. 2002).

1.2.2. Variation in soil respiration as a function of soil moisture

Laboratory incubation experiments have shown a consistent relationship between soil respiration and soil moisture content (Orchard and Cook 1983, Linn and Doran 1984, Borken et al. 2003, Xu et al. 2004); however, this relationship is more complicated and variable in field conditions. Reth et al. (2005) measured soil CO_2 flux across three meadows, two agricultural fallows, and one forest in Germany, and found that only meadow soils responded

to changes of relative soil water content, and fallow soils and forest soils did not show such effect. Borken et al. (2002) found temporal variation in soil moisture had little effect on annual soil respiration rate in two European forest sites. One explanation for the lack of effect of soil moisture on soil respiration may be hydraulic lifting during periods of water stress (Caldwell and Richards 1989, Dawson 1993, Caldwell et al. 1998). Water uptake by deep roots in moist soils may be transferred up and released in upper drier soils, and thereby temporarily relieves moisture stress for decomposition. Since hydraulic lift occurs mainly at night when plant stomata are closed and water remains in upper soils until plant transpiration resumes, the fluctuations of soil moisture may or may not be detected depending on the depth and frequency of soil moisture sampling.

The sensitivity of soil respiration to change in soil moisture depends on soil temperature and some other environmental as well as biological factors (Reichstein et al. 2003). Wildung et al. (1975) found in an arid temperate mountain grassland, that soil respiration started to increase with soil moisture only when the temperature was above 6°C, but was still hugely dependent on temperature. However, when the temperature was above 15°C, soil respiration increased significantly and had a strong correlation with soil moisture ($R^2 = 0.83$, $P < 0.01$). Xu et al. (2004) also found in grassland and grassland/savanna ecosystems that soil respiration was regulated by temperature and not by moisture when soil water content was above 15% (vol) (-0.8 MPa), but it started to decrease with soil moisture when soil moisture was below the threshold of 15% (vol).

Hanson et al. (1993) found that variation in soil respiration in an upland oak forest in Tennessee was accounted for by variation in climatic factors, but not by different topographic positions. Although temperature was the dominant controller, they found that during a period

of time when soil temperature was nearly constant, soil respiration was regulated by soil moisture (it declined with soil moisture). Yim et al. (2003) also suggested that soil moisture is more important in explaining temporal variation than spatial variation in soil respiration. However, a study conducted in a broadleaf forest in Wisconsin by Martin and Bolstad (2005) found that the annual release of soil carbon decreased with increasing annual soil moisture means for the study sites (R^2 = 0.32 and 0.19 for 1998 and 1999), and that the topographic position played an important role in determining soil water content at a given time as well as the annual range of water conditions. Savage and Davidson (2001) found at both Harvard Forest and Howland Forest, ME, that soil respiration in spring and summer showed a decreasing trend across sites with decreasing soil drainage class. Upland well drained sites normally had higher soil CO_2 flux than poorly drained wetland sites.

Soil compaction and texture also make a difference. A study on agricultural lands found that soil respiration in a maize crop was significantly higher on wetter soil, but when moisture was not limiting, soil respiration was lower where soil was more compacted (Rochette et al. 1999). A study on a lemon farm showed that variation in soil moisture contents due to differences in soil textures did not affect soil respiration, but after irrigation, soil CO_2 flux was much higher on sandy (more porous) soil surface than on soils with more silt or clay content (Bouma and Bryla 2000). Kelliher et al. (1999) found that soil respiration in a Siberian pine forest was regulated by surface water content instead of soil temperature or spatial distribution of roots and soil carbon, which was a result of the poor water storage capacity of the sandy soil. Field research conducted in southeastern mixed pine hardwood stands in Georgia and Alabama showed that soil CO_2 flux in the clayey stands (higher soil moisture) was greater than that in the sandy stands (lower soil moisture) during the growing

season; in addition, soil CO_2 flux was correlated to soil temperature in sandy stands only under no-drought conditions, whereas in clayey stands soil CO_2 flux correlated to soil temperature under both drought and no-drought conditions (Dilustro et al. 2005).

1.2.3. Drought

Drought can reduce soil respiration at a monthly or annual scale via soil moisture depletion (Davidson et al. 1998, Borken et al. 1999, Savage and Davidson 2001, Borken et al. 2002, Reichstein et al. 2002, Martin and Bolstad 2005) and contribute to interannual variations in the ecosystem carbon balance. When comparing annual soil respiration in a broadleaf forest in Wisconsin in two consecutive years, Martin and Bolstad (2005) reported that the annual soil carbon emission was about 14.6% less in a (mild) drought year than in a no-drought year. While decreased release of soil carbon was observed during drought, carbon uptake by vegetation can also decrease (Reichstein et al. 2002). Reichstein et al. (2002) reported that temperature sensitivity of soil and ecosystem respiration, as well as plant water-use efficiency, all declined with increasing drought.

Drought also reduces root respiration (Palta and Nobel 1989, Rochette et al. 1991) and causes shifts in the dominance of microbial communities. Bacteria tend to be less drought-tolerant than fungi. Orchard and Cook (1983) found that bacterial activity was almost stopped at -1.5 MPa, whereas fungi could still survive due to hyphal extension. Jensen et al. (2003) also found an increase in C/N ratio during a drought at two European heathlands, indicating a change towards a more fungal-dominated microbial community.

1.2.3.1. Different drought effects

Not all sites respond to droughts the same way. A drought manipulation experiment was carried out at two heathlands, one drier with an average annual precipitation of 758 mm in Denmark, and the other wetter with an average annual precipitation of 1675 mm in the UK (Jensen et al. 2003). The drought treatment during the summer months resulted in constantly lower soil water content in the treatment plots than the control plots on the drier Denmark site, whereas on the wetter UK site, soil moisture in the treatment plots was only markedly reduced after 60 days of drought. This was probably due to the difference in soil texture. The soil at the drier site was a sandy podzol with thin organic layer, whereas that at the wetter site was a peaty podzol with a thick organic layer and a large soil carbon stock. As a result of the drought, the release of belowground CO_2 at the drier site decreased by 27%, while that at the wetter site increased by 22% (Jensen et al. 2003).

Palmroth et al. (2005) found a contrasting response of soil respiration to drought in a loblolly pine plantation and in an oak-hickory forest in Duke Forest, NC. In a year with mild drought, the annual CO_2 emission at the two stands was not statistically different. However, in a year with severe drought, soil respiration in the pine plantation decreased, whereas that in the hardwood forest increased. In the year with severe drought, drought effects on the physiological parameters (base respiration, i.e., respiration rate scaled to 0°C, and temperature sensitivity) led to a decreased difference in soil CO_2 response to temperature and moisture between the two stands, but to an increased difference in soil temperature and moisture between the two stands. Soil temperature was higher at the hardwood forest due to its deciduousness and thinner litter layer, and since soil respiration contributed by the effects of physiological parameters was similar to that in the pine plantation, the hardwood forest emitted more CO_2 during the year with severe drought.

Savage and Davidson (2001) found in Harvard Forest that soil respiration during summer drought was depressed at an upland well drained site, but increased at a low poorly drained wetland site due to soil drying. They concluded that decreased soil respiration in uplands during dry years may contribute to only a transient carbon sink, whereas increased respiration in wetlands could lead to substantial loss of soil carbon from terrestrial ecosystems to the atmosphere.

1.2.3.2. Uncertainties of drought impacts

The definition of drought is not articulated here, nor was it in most papers cited. Therefore, what was considered a drought by some might be deemed to be simply a relatively dry period by others. I do not address the problem of formulating a definition of drought, but instead follow the perceptions of respective research groups – it was a drought if they considered it to be one.

Drought may not affect soil moisture in an equal way, and soil respiration may not correlate to soil moisture during a drought. Borken et al. (2002) found that soil respiration decreased at spruce and beech stands in a European forest during a drought when soil moisture was -120 kPa; however, soil respiration at a nearby pine stand was unaffected, despite the soil moisture being lower (-263 kPa) there.

Drought may not always significantly lower soil respiration (Anderson 1973, Borken et al. 1999, Savsge and Davidson 2001). Borken et al. (1999) studied the effects of drought and wetting in a European spruce forest by creating drought conditions during two summers using roofs to prevent precipitation from reaching the treatment plots. They found that the effect of drought was not significant. Soil CO_2 emission was 12% less ($p>0.09$) on drought

plots than that on ambient plots in a year with severe drought, but had nearly no difference from ambient plots in the following year with a less-severe drought. The relatively small or no reduction in soil CO_2 emission might be because that while the surface layers were subject to more dramatic changes in moisture content, the water availability in the mineral soil was probably still high. Therefore, soil water storage capacity and deep-soil water availability to roots may also play an important role in determining drought effects (Reichstein et al. 2003, Reichstein et al. 2002).

1.3. RAIN EVENTS AND ENHANCED SOIL RESPIRATION

Studies have shown that increased rainfall variability (with the total amount of annual precipitation unchanged), decreased rainfall amount, or increased rainfall interval may all lead to a decrease in soil respiration (Knapp et al. 2002, Harper et al. 2005, Fay et al. 2000). While changes in precipitation patterns and annual precipitation greatly affect soil respiration and ecosystem carbon cycle, our current knowledge about soil respiration during rain events is far from conclusive. And this has casted major uncertainties on the estimates of annual soil respiration and ecosystem carbon balance.

Elevated soil respiration during and/or after rain events has been widely recognized, and most existing empirical models of soil respiration account for the effects of rainfall merely by looking at the changes in soil moisture content (e.g., Howard and Howard 1993, Davidson et al. 2000, Reth et al. 2005). However, CO_2 pulses following rain events may not necessarily be correlated to soil water content (Savage and Davidson 2001, Borken et al. 2002), and soil moisture is often measured for the mineral soil, which may not be able to reflect the rapid change in soil moisture at

upper layers during rain events. Moreover, it has been observed that even with just a little change in soil moisture, there can be a CO_2 flush immediately after wetting (Orchard and Cook 1983, Borken et al. 2003). However, due to technical difficulties associated with performing measurements during rain and the use of field sampling strategies, very few field observations were obtained during or immediately following rain events to capture the instantaneous response.

Few studies have tried to quantify the effects of wetting on annual soil respiration. A study in a temperate deciduous forest in Japan showed that the pulses of soil respiration after rain events contributed 16-21% of annual soil carbon flux at the site (Lee et al. 2002). A drought and rewetting experiment showed that post-drought wetting on the treatment plot increased the annual CO_2 emission by 51% compared with the no-drought plot (Borken et al. 1999). Xu et al. (2004) reported that peak values of rain-induced soil respiration were even higher than those of ecosystem respiration during times with vigorous growth and adequate soil moisture. Flanagan et al. (2002) reported in a study of temperate grassland in Canada that total ecosystem respiration was affected more by GPP and soil moisture than by temperature, and that all the days with maximum values of ecosystem respiration were associated with rain events, which, they suggested, was a result of increased soil CO_2 release driven by rain. Many other studies also suggested that rain-induced soil CO_2 pulses constitute a substantial fraction of the total annual soil respiration, and therefore may be key to understanding interannual variations in soil respiration and to determine a given ecosystem to be a source or sink of carbon (Savage and Davidson 2001, Flanagan et al. 2002, Xu et al. 2004, Yuste et al. 2005b).

1.3.1. Observations of rain-induced soil CO_2 pulses

Numerous soil drying and wetting experiments in synthetic laboratory environments have shown CO_2 pulses following wetting of dry soils that could last for hours or days (e.g., Birch 1958, Orchard and Cook 1983, Kieft et al. 1987, Clein and Schimel 1994, Franzluebbers et al. 2000, Borken et al. 2003, Xu et al. 2004). The maximum CO_2 pulse and the duration of the state of elevated CO_2 increased with wetting intensity. Orchard and Cook (1983) reported that CO_2 flux started to increase within one hour following wetting; and with a change in water potential of 5 MPa, microbial activity showed a 40-fold increase for a short period of time. The incubation experiment on O horizon by Borken et al. (2003) also reported an instant increase in CO_2 flux within 5 minutes after wetting, and the increase could be up to 9-fold depending on the amount of water added.

There were observations of decreased soil CO_2 flux in agricultural fields after heavy rainfall (Ball et al. 1999), which might be due to the anaerobic soil conditions caused by rainwater. However, many more field studies have observed increases in soil CO_2 flux following wetting (e.g., Anderson 1973, Rochette et al. 1991, Davidson et al. 1993, Hanson et al. 1993, Kelliher et al. 1999, Law et al. 2001b, Borken et al. 2002, Flanagan et al. 2002, Rey et al. 2002, Lee et al. 2002, Yuste et al. 2003, Huxman et al. 2004, Xu et al. 2004, Palmroth et al. 2005). Using manipulative field experiments to look into the mechanisms of rain-induced soil CO_2 pulses has been rare and still at its initial stage. Such relevant studies include Borken et al. (1999), Liu et al. (2002) and Sponseller (2007). Among all the aforementioned studies, an instant response to wetting was only addressed by Davidson et al. (1993), Borken et al. (2003), Xu et al. (2004) and Sponseller (2007).

The magnitude and duration of soil respiration pulse varied, and in most cases soil CO_2 flux data during and/or after rain events significantly deviated from the normal correlation between soil temperature and CO_2 flux. Rochette et al. (1991) observed a 9-fold increase in soil CO_2 flux in agricultural lands right after rain events, and CO_2 flux gradually decreased over time. Kelliher et al. (1999) reported a 52% increase in CO_2 flux after 12 mm of rainfall in a Siberian pine forest, and the respiration pulse disappeared the next day. Law et al. (2001b) observed a pulse of soil respiration after rain in a ponderosa pine forest, but it returned to the lower rate within a day. Lee et al. (2002) reported that soil CO_2 flux was up to 1.5 times pre-rain level soon after the onset of rainfall in a temperate deciduous forest in Japan, and the elevated CO_2 flux lasted for more than 6 hours despite the gradual decline in soil water content. Xu et al. (2004) observed 60 to 80-fold increases in ecosystem respiration in grasslands after rain events; the pulses were short-lived, and the daily CO_2 flux decreased exponentially with time, which also reflected the gradual drying-out processes of soil upper layers. Sponseller (2007) reported an increase in CO_2 flux of 30-fold immediately following wetting and flux returned to background level within 48 hours.

1.3.1.1. A case study: Change in CO_2 concentration in soil pores during rain events

A study by Xu et al. (2004) provided a close look at belowground CO_2 activities at the beginning of a rain event. The observations were recorded early August in 2003, and soil moisture content at the grasslands site in California was only 3% (vol) (-15 MPa) before 12.5 mm of rainfall. Soil CO_2 showed instantaneous response to the onset of rain event, and within one hour CO_2 concentration at 2 cm depth in the soil increased from 617 to 900 ppm (measured by a buried-in small solid state, non-dispersive infrared gas analyzer). The

increase carried on in the next 30 min at a rate of 181 ppm min^{-1} and soil CO_2 concentration leveled off at around 7100 ppm. Soil CO_2 concentration at the depths of 8 cm and 16 cm responded to rainfall with a time lag and with a less pronounced increase. The fact that soil moisture at these two depths did not change during the rain led Xu et al. to conclude that CO_2 increase at 8 cm and 16 cm depths was a result of diffusion of CO_2, produced near the soil surface, into deeper layers.

By directly measuring soil CO_2 concentration in situ, the case study confirmed the instantaneous response of soil respiration at upper soil layers during rain events, and demonstrates the belowground production and movement of CO_2.

1.3.2. Mechanisms of rain-induced soil CO_2 pulses

The pulses of soil respiration following wetting events may be a result of rapidly re-activated microbial activity due to increased water availability (Birch 1958, Orchard and Cook 1983, Saetre and Stark 2005), increase in microbial biomass (Griffiths and Birch 1961, Orchard and Cook 1983, Schnürer et al. 1986), and increased substrate availability. There are two sources of organic substrates: soil organic matter from plant litter, and organic substance of microorganism origin. Upon wetting, soil organic matter can be more accessible through desorption from the soil matrix (Seneviratne and Wild 1985) and thus increased exposure of organic surfaces to microorganisms due to the crumbling of organic aggregates (Birch 1959), and enhanced movement of dissolved organic carbon from litter to soil may stimulate carbon consumption of certain microbial population (Cleveland et al. 2007). Substrates of microorganism origin can be readily available from microbial biomass that died from desiccation in the preceding drying cycle or the shock of wetting (dramatic

change in turgor pressure can cause disruption of cell membrane and release of intracellular substrates) (Bottner 1985, Kieft et al. 1987, Van Gestel et al. 1991), and from mineralization of cytoplasmic solute from living microbial cells in response to the water potential shock from wetting (Fierer and Schimel 2003). These explanations do not necessarily exclude one another: it is likely that more than one of the processes mentioned above contribute to the CO_2 pulses concurrently, or on different timescales.

Little is known about root respiration in response to wetting. A study by Burton et al. (1998) on sugar maple reported reduced root respiration in response to a drought, while Bouma et al. (1997) reported that root respiration of citrus was not affected by a change in soil moisture as a result of drought or wetting. Borken et al. (1999) observed that post-drought increase in root growth showed a delay of weeks after wetting started. Other likely explanations for the soil CO_2 pulse include displacement of CO_2 in soil pores by rainwater, release of CO_2 dissolved in rainwater, and degassing due to a decrease in barometric pressure. However, the first two reasons account for too small an amount of CO_2 to explain the pulses (Oishi and Lee 2002; Lee et al. 2004); and degassing occurs only when pressure changes within a very short period of time, which is too short in timescale to really happen during rain events (Lee et al. 2004). Therefore, these explanations are of minor importance.

1.3.3. Factors affecting response patterns and enhancement sensitivity

While the response patterns of soil respiration to wetting vary, soil CO_2 flux enhancement triggered by rain events also have shown considerable variability. The magnitude of flux enhancement and the time needed to activate enhancement can be an indication of the sensitivity of soil respiration in response to rain events.

1.3.3.1. Initial, pre-rain soil moisture

Soil moisture conditions not only affect response patterns of soil respiration to rain events, but also determine enhancement sensitivity. Wetting does not necessarily lead to flux enhancement. The timing of rain may affect plant uptake and soil CO_2 emission. Rain-induced decrease in soil CO_2 flux can occur in wet soils as if anaerobic conditions result (e.g., Ball et al. 1999). When respiration pulses do occur, the magnitude of flux enhancement may depend on how dry the soil is prior to rain.

CO_2 flux enhancement following rain events was shown to depend on the length of the preceding rain-free period (Lee et al. 2002; Sponseller 2007). Borken et al. (2002) further suggested that rain-induced soil CO_2 flux was not correlated to the soil matric potential per se, but to the change in the soil matric potential, which means that enhancement due to wetting was stronger when the soil was drier and the change in the soil matric potential greater. This was also supported by field observations of a study on Californian grasslands by Xu et al. (2004). They found that the enhancement in ecosystem respiration following wetting was inversely related to the pre-rain ecosystem respiration rates, which reflected a strong dependency of flux enhancement on the difference between pre-rain and post-rain soil moisture conditions.

This finding is important given the projected decrease in soil moisture in most regions on earth during this century (Meehl et al. 2007), and should be particularly pertinent to rainfall following droughts. An example is from an oak forest in Mediterranean-climate Portugal, where sustained drought is typical in the summer and rainfall only comes at the end of summer. It was observed that during the spring and early summer, rainfall actually

enhanced CO_2 sequestration and the ecosystem was a temporary sink of carbon. However, at the end of summer, a relatively small amount of rainfall, following a long-developed drought, was able to trigger large CO_2 emission (Jarvis et al. 2007).

On the other hand, the effect of drought conditions may sometimes be outweighed by other factors in influencing rain-induced CO_2 flux enhancement. A drought and wetting experiment in a European spruce forest conducted by Borken et al. (1999) found that, while drought had only little impact on soil respiration, soil CO_2 flux increased immediately following wetting and continued to increase for 3 weeks until reaching the peaks, which were about 2 and 3 times the pre-rain level respectively for the two years. The lack of sharp peaks after the onset of wetting might be due to the slower wetting process in the field. Despite the higher intensity of wetting in the first year (more water was applied within a shorter period of time), soil CO_2 emission as a result of wetting was less in the first year. In the second year, although drought was of less severe duration, soil CO_2 emission after wetting was greater due to higher temperatures during wetting, and the cumulative carbon emission during the first 30 days after wetting represented one-fifth of the annual carbon release. Borken et al. (1999) therefore concluded that, for the release of CO_2 following wetting, the length of a drought period was not as critical as soil temperature and moisture conditions at the time of wetting.

1.3.3.2. Soil surface layers (O horizon)

Some studies have suggested that microbial biomass and activities in soil surface layers may provide the largest contribution to soil CO_2 flux enhancement following rain events (Borken et al. 1999, Savage and Davidson 2001, Lee et al. 2002, Rey et al. 2002, Yuste et al. 2003). The role of soil surface layers is important not only because they are

exposed to more changeable temperature and moisture conditions as well as frequent drying and rewetting cycles, but also because they represent a large organic carbon reservoir, and thus the supply of carbon for mineralization to microbial community is less limiting in these layers.

Studies have shown that recent litter input from current and previous growing seasons is a major source of CO_2 flux from the forest floor (Bowden et al. 1993, Gaudinski et al. 2000), and the turnover time for recent leaf litter was 2 to 5 years at Harvard Forest (Gaudinski et al. 2000). However, Buchmann (2000) found in a European spruce forest that soil respiration was not significantly reduced on plots where litter and other organic layers were removed, which suggested that mineral soil organic matter played the dominant role in soil CO_2 emission.

Litter on the forest floor is often porous and low in moisture content and water potential, which restrains microbial activities, and therefore it is likely to be more sensitive to wetting due to the relief from drought stress. O'Connell (1990) found that respiration rate of eucalypt litter was relatively constant when moisture content was greater than 100% oven dried weight (ODW), but decreased markedly when moisture was lower than 80% ODW. Schimel et al. (1999) found that moisture strongly controlled the decomposition of birch litter in the Alaskan taiga. Gärdenäs (2000) reported that litter moisture accounted for much of the spatial variation in soil respiration in a spruce forest. A study by Hanson et al. (2003) found that the estimate for annual soil respiration from an upland oak forest in Tennessee would increase by 23% if litter decomposition following wetting were included in the current ecosystem carbon model.

Savage and Davidson (2001) observed some positive residuals of soil CO_2 flux

measurements of their Harvard Forest upland temperature model that were not explained by soil moisture content. They suggested that these residuals could be a result of small precipitation events that wet only the upper litter and organic layers but were not detected by a time domain reflectometry (TDR) probe which was inserted into the mineral soil.

Measuring soil moisture in upper organic layers has been problematic due to their porous structure (Lee et al. 2002, Borken et al. 2003). Borken et al. (2003) were able to continuously measure soil moisture of the O horizon with DC half-bridge at Harvard Forest. They found that soil moisture fluctuated greatly in the O horizon and soil respiration was strongly affected by drying and wetting cycles in the O horizon. Residuals of soil respiration from a temperature-dependent model showed correlation with water content in the Oi horizon (R^2= 0.72) and the Oe/Oa horizon (R^2= 0.56). Their field observations were supported by laboratory incubation experiments. Wetting of soil samples of the O horizon led to instant, strong flux enhancement even with only 0.5 mm of water addition, and the magnitude of enhancement was comparable with those observed in the field when the temperature effect was accounted for.

1.3.3.3. Organic carbon pools

A difference in carbon pool sizes also affects flux enhancement sensitivity. Xu et al. (2004) found from two comparable study sites that, the one with less decomposable plant biomass and less soil carbon showed a much lower peak value after rainfall. Franzluebbers et al. (2000) also reported that short-term flux enhancement following wetting strongly correlated with the biologically active pools of soil organic matter - potentially mineralized carbon and microbial biomass. The amount of potentially mineralized carbon (in other words,

substrate availability) is associated with primary productivity as well as litter quality. Litter quality is influenced by the physical characteristics of the litter, lignin: N ratio, availability of carbon matrix to microbial community, the pH value, and concentrations of nutrients (Pastor and Post 1986, O'Connell 1990).

1.3.3.4. Nutrient input

In addition to effects of change in soil moisture due to rainfall, nutrients in rainwater may also play a role in soil CO_2 flux enhancement. Litter on the forest floor is usually poor in nutrients and has a high C:N ratio at the initial stage of decomposition. Nutrients, such as nitrogen in the form of nitrate (NO_3^-), may be brought in through precipitation and made available to facilitate litter decomposition. Birch also found increased release of nitrogen in the form of NO_3 as a result of wetting, which enhanced crop growth. Whether this is also responsible for soil respiration pulses during rain events still needs further investigation.

1.3.3.5. Rainfall amount and intensity

Some field observations found that carbon released through soil CO_2 flux enhancement following rain events was positively correlated to the amount of precipitation (Xu et al. 2004, Lee et al. 2002). Laboratory incubation also reported that peak values and duration of respiration pulses increased with intensity of water addition (Orchard and Cook 1983, Borken et al. 2003). However, the complexities of the relationship between flux enhancement and soil moisture was unfolded by a manipulative field study that tried to quantitatively analyze the response patterns and enhancement sensitivity of soil respiration.

A rain-simulation field experiment was conducted by Liu et al. (2002) to examine the

effects of different amounts of rainfall on soil respiration. 8 levels of rain simulation (0, 10, 25, 50, 100, 150, 200 and 300 mm of rainfall) were applied to plots in a tallgrass prairie ecosystem in Oklahoma. It was found that soil respiration was most sensitive to 10 mm and 50 mm treatments, which showed the highest CO_2 flux and sharp peaks. Soil CO_2 flux enhancement was lowest for 150 mm treatment. The decline of soil CO_2 flux after rainfall was faster for lower water treatment level, and slower for higher water treatment level. The fact that soil CO_2 flux enhancement did not necessarily increase with an increasing quantity of water addition, along with the rather scattered data points of soil CO_2 flux against soil water content, indicated a more complex process involving multiple variables, such as temperature, and the effects of precipitation amount versus intensity.

1.3.3.6. Tillage and no-till management practices

The production and transportation of CO_2 in agricultural soils is greatly influenced by soil structural quality and water content associated with tillage and compaction. Ball et al. (1999) found that gas diffusivity was lower and water content higher in no-till plots than in plowed plots. Lampurlanes et al. (2001) also found that soils under no-till practice had higher water content than those under minimum tillage or subsoil tillage. They suggested that in semiarid areas, soils with low water holding capacity would benefit from no-till practice since it supported greater and deeper water accumulation in the soil profile and greater root growth.

Studies have shown that the change from tillage to no-till management practices could increase soil carbon sequestration in agricultural lands by reducing CO_2 emission (Reicosky and Lindstorm 1993, Kern and Johnson 1993, Smith et al. 1998, West and Post

2002). Increase in carbon sequestration as a result of change from tillage to no-till was greatest in the top 7 cm of soil and moderate in 7 to 15 cm depth, but no significant increase was observed below 15 cm depth (Kern and Johnson 1993, West and Post 2002). Less intensive tillage (reduced tillage) did not appear to sequestrate significantly more soil carbon than conventional tillage (Kern and Johnson 1993, West and Post 2002). The effectiveness of no-till practice also depends on soil texture. Jarecki and Lal (2005) found that soil organic carbon pools were increased under no-till management practice in a silt loam soil, but there was no effect of no-till practice in clayey soil.

A tillage experiment on an imperfectly drained clay loam soil in Scotland found that soil CO_2 flux was normally lower in the no-till plots than in the plowed plots. Soil CO_2 flux in plowed plots increased with rainfall, but flux enhancement did not necessarily increase with tillage intensity or plow depth. In no-till plots, CO_2 flux decreased dramatically after heavy rainfall due to reduced gas diffusivity and air-filled porosity (Ball et al. 1999).

1.3.3.7. Impacts of stress history

The effects of frequent drought and wetting on soil respiration at the ecosystem level are still uncertain. Some studies suggested that environmental and physiological stress from frequent drought and wetting may exhaust substrate availability and lead to a decline in soil respiration. Anderson (1973) suggested that the fragmentation of leaf litter during drought might facilitate microbial decomposition in the course of wetting. Laboratory incubation by Taylor and Parkinson (1988) showed accelerated decomposition of aspen leaf litter after 14 wetting and drying cycles, possibly due to cuticle damage or hydrolysis of cellulose that allowed easier penetration of microorganisms; but eventually decomposition slowed down as

a result of the exhausted supply of labile substrate. However, a decline in the enhancement of soil respiration after repeated wetting was not observed by Borken et al. (2003), and they suggested that this might be because mineralizable carbon was less limiting in the litter layer.

In addition to the depletion of labile substrate, frequent drought and wetting may also cause changes in microbial composition and declines in microbial diversity. A study on birch leaf litter in the Alaskan taiga found that microbial activity was greatly reduced even with one short drying and wetting event, which they suggested may be due to loss of critical litter decomposing organisms and enzymes during drying (Clein and Schimel 1994). Another study on birch leaf litter showed that, although litter respiration and microbial biomass did not decrease over time with repeated drying and wetting, the bacterial community appeared to be more susceptible to stress from drought and wetting shock, which led to a shift in microbial composition further toward fungal domination and a decline in potential bacterial diversity (Schimel et al. 1999). The study suggested that in ecosystems experiencing regular episodic drying and wetting events, such as irrigated agricultural fields, microbial activity was not a function of only substrate availability and climatic factors, but also the site-specific stress history.

A study by Knapp et al. (2002) on the effects of altering rainfall patterns in a grassland ecosystem in Kansas was conducted by increasing intervals of rain events while the total amount of annual precipitation remained unchanged; they found a 16% reduction of soil respiration as a result of increased rainfall variability. This seems inconsistent with what other studies have observed, especially in that, with extended drought and lower water moisture, soil respiration tends to show stronger enhancement upon wetting (e.g., Borekn et al. 1999, Xu et al. 2004). It is likely that Knapp et al. (2002) missed the respiration

enhancement during and/or immediately following rain events due to their sampling design (weekly measurement) and thus underestimated soil respiration. However, it is also likely that in the long run, a decline in the microbial population due to environmental and physiological stresses from prolonged drought and wetting shock, along with decreased primary productivity, may indeed cause reduced soil respiration. Further investigation is still needed to determine the real causes of these different conclusions.

1.4. SUMMARY

The causes, magnitude and duration of soil respiration pulses during and after rain have not been fully understood, and no simple conclusions can be drawn to serve as a comprehensive basis for predicting and quantifying precipitation effects on soil respiration. As a result of sampling strategies that rely on periodic field measurements instead of continuous monitoring, the effects of rain on soil moisture and thus on soil respiration are very likely to be underestimated. Even with studies that incorporated incidents or an amount of rainfall as a variable into their empirical models for soil respiration (e.g., Lee et al. 2002, Liu et al. 2002, Raich et al. 2002, Yuste et al. 2003, Palmroth et al. 2005), predicted values may still fail to reflect the reality since the instantaneous flux enhancement was usually overlooked in field measurements.

Currently available data suggested that patterns and magnitude of soil CO_2 flux enhancement during and/or after rain events may be determined by the degree of pre-rain drought and other factors. Although the magnitude and duration of rain-induced soil respiration pulse varies, the losses of soil CO_2 during and/or after rain events may be particularly important in areas with warm and dry summers. The frequency and intensity of

rain events may greatly influence the fluctuation of annual soil respiration and thus ecosystem carbon balance (Savage and Davidson 2001, Lee et al. 2002, Rey et al. 2002). As suggested by Reichstein et al. (2003), the effect of precipitation on soil respiration reaches further beyond its direct effect via soil moisture. While the effects of drought may not necessarily alter the pattern of annual soil respiration, variation in precipitation alone, or when combined with drought effects, may play a critical role in the fluctuation of interannual soil respiration and ecosystem carbon flow. An in-depth study of the rapid change in soil moisture content during rainfall and the ensuing effects on soil respiration is therefore essential to further comprehend and quantify the rain-induced emissions of soil carbon.

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Chapter 2

Short-Term Effects of Rain Events on Soil Respiration in Two Mixed-Hardwood New England Forests

ABSTRACT

Rain simulation field experiments were conducted in two temperate mixed-hardwood forests in New England: Great Mountain Forest, CT, in 2002 (GMF02); Harvard Forest, MA, in 2004 and 2005 (HF04 and HF05). In-situ measurements showed that on plots with intact O horizon, soil CO_2 flux increased as soon as the onset of 30-min rain simulation, peaked at an enhancement ratio of 1.52, 1.41 and 1.45 at GMF02, HF04 and HF05 during rain simulation, and returned to the pre-rain rate within 90 min after the rain ended. Less or no enhancement was observed from plots without O horizon. Thus, the rain-induced CO_2 pulses were mainly contributed by O horizon, likely due to reactivated microbial activity and enhanced substrate availability. Estimated growing season soil carbon loss during rain is 0.77, 1.15, and 0.80 t C ha^{-1} at GMF02, HF04, and HF05, although the value for HF04 may be overestimated due to the coarser observation intervals for the HF04 precipitation data.

Flux enhancement at all site-seasons showed negative correlations with soil temperature and pre-rain CO_2 flux. Rain intensity made significant difference in flux enhancement. Pre-rain soil moisture could account for both spatial and temporal variations in flux enhancement at HF04 and HF05, but not at GMF02. The negative correlation between enhancement magnitude and soil moisture was likely due to the moisture dependence of the sizes of reactivated microbial population and substrate pool. Flux enhancement at GMF02 was positively correlated with moisture increment of O horizon.

Flux contribution of O horizon to total soil respiration was 0.44, 0.26 and 0.29 at GMF02, HF04 and HF05. Spatial variation in flux contribution of O horizon showed a strong negative correlation to seasonal mean soil moisture of the plots across the two forests ($R^2 = 0.55$). Temporal variation in flux contribution of O horizon showed a positive

correlation to pre-rain soil moisture at GMF02, but a negative correlation to that at HF04.

Q_{10} values were averaged 2.54, 4.37 and 4.25 at GMF02, HF04 and HF05. At Harvard Forest, Q_{10} decreased with increasing soil moisture. Repeated wetting at Harvard Forest did not show significant impacts on soil respiration.

2.1. INTRODUCTION

Soil CO_2 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 as well as abiotic factors. Rain-induced soil CO_2 pulses have been widely observed (Birch 1958, Anderson 1973, Davidson et al. 1993, Xu and Baldocchi 2004), and can lead to substantial annual soil carbon loss (Lee et al. 2002, Lee et al. 2004). However, 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 CO_2 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, 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.

Constrained by the technical difficulties to measure in rain and the unpredictable nature of weather conditions, 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 CO_2 emissions. Moreover, eddy covariance techniques tend to suffer from instrumental malfunction during rainfall and necessitate data gap-filling, which is commonly performed under the assumption that response function established under fair weather conditions is also applicable during rainy periods (e.g., Falge et al., 2001). Given that rain-induced soil CO_2 pulses have been widely observed in various ecosystems, such assumptions bring the reliability of resulting models into question. The accuracy of current estimates of soil respiration and net ecosystem production (NEP) is therefore uncertain.

Regrowth of temperate forests in North America from abandoned farmlands has played a critical role in uptaking atmospheric carbon (Wofsy et al. 1993, Fan et al. 1998). The amount of carbon sequestered depends on interannual shifts in photosynthesis and respiration, which is greatly affected by interannual climate variations such as anomalies in soil temperature, snow, drought in the summer, and other factors. Interannual variations in net ecosystem exchange (NEE) by these forests can have significant impact on regional carbon balance (Goulden et al. 1996). Under ongoing climate change, mid- and high latitude areas in the Northern Hemisphere are expected to experience increasing precipitation variability, which entails heavier and more extreme precipitation (IPCC 2001, Ch. 9.3.6.2).

Hence, there is need to further understand the behavior and response dynamics of soil respiration in temperate forests during rain events in order to contribute to improved characterization of ecosystem productivity and the global carbon cycle.

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, and at Harvard Forest, Massachusetts, for two growing seasons in 2004 and 2005. Soil CO_2 flux measurements were made with a portable photosynthesis system. Field manipulative experiments allowed more control over environmental variables while reflecting on-site field conditions, and could provide complementary information to eddy covariance measurements. Rain simulation avoided the difficulties and unpredictability of measuring in natural rain events, and the use of the portable photosynthesis system allowed swift data collection. The standardized experiment protocol (i.e., identical site preparation and irrigation methods, known amount of water addition, and consistent measurement intervals) made it possible to quantify and compare rain-induced CO_2 pulses within and across sites. This same field method was also applied in an agricultural ecosystem in Nebraska in 2006 (see Chapter 3). We aim to identify the response patterns and magnitudes of rain-induced soil respiration, to probe into the underlying mechanisms responsible for the enhanced soil respiration, and to compare the results from the two forests. Our study sites at Great Mountain Forest and Harvard Forest are similar in many aspects, but differed in certain ways described below. In this chapter, the three site-seasons of our rain simulation experiments at Great Mountain Forest in 2002, at Harvard Forest in 2004 and 2005 are abbreviated as GMF02, HF04, and HF05.

2.2. METHODS

2.2.1. Site description

2.2.1.1. Great Mountain Forest, 2002

The experiment site is located in Great Mountain Forest, Norfolk, Connecticut (41°58'N, 73°14'W). The mean temperature at Great Mountain Forest site is 20°C in July and -7.2°C in January. Annual precipitation at the area is 1311 mm, and the average precipitation in June is 117 mm. 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. A preliminary study on soil organic matter content at the site found that mean forest floor thickness was 6.7 cm, and the forest floor soil bulk density was 0.16 g/cc. The soil organic matter stored in O horizon was estimated to be 6.7 kg m^{-2} (Wu 2002). Seven plots, each with a radius of 1 m were set up on a gentle slope near a meteorological tower and within the 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 meters 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.

2.2.1.2. Harvard Forest, 2004 and 2005

The experimental site is located on an east-facing, lower slope on the Prospect Hill Tract of Harvard Forest, Peterdsham, MA (42°53' N, 72°17' W). The mean temperature at Harvard Forest is 20°C in July and -7°C in January; the annual precipitation is 1100 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 estimated to be 7 kg m^{-2} (see Savage and Davidson 2001, Borken et al. 2003), which was comparable to Great Mountain Forest. The land was used as pastures until late 19th century (Foster 1992), as evidenced by the stone wall near the site. A total of twelve plots were set up with a block design within the footprint of an eddy covariance tower. Three blocks were created in May 2004. In 2005, one extra block was established at a higher and drier area at the site in order to include drier plots and to increase sample size. Each block contained three plots of radius of 1 m, and different treatments were randomly assigned to plots. Control plots were not treated with rain simulation or removal of O horizon. Treatments plots were treated with rain simulation, including plots with intact O horizon, and plots with O horizon removed (bare plots).

The two 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.

2.2.2. Rain simulation

Rain simulation experiments were carried out by spraying 6 mm or 12 mm of water with a watering can on treatment plots every one to two weeks during the growing season. No experiment was done on rainy days or right after it rained in order to avoid confounding effects. Simulated rain lasted for 30 minutes, a duration short enough to avoid flux fluctuation due to diurnal variations, but long enough to produce detectable responses. Soil CO_2 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 hours. Measurements were made at 7 time steps at 0, 10, 20, 30, 45, 60, and 120 min into experiment, denoted as t0 through t6 respectively. Soil temperature was measured at 10 cm depth; temperature change from the beginning to the end of the 2-hour experiment was normally within 1°C. The maximum soil temperature difference, in rare cases, was 1.8°C, likely due to brief occurrence of understory sunflecks. Water used for irrigation was ground water near the sites. The major drawback of using ground water is that its chemical properties are different from those of rain water, and therefore may introduce additional variables that may affect soil respiration. However, constrained by resources and field conditions, ground water was the most feasible, reliable and economical source of irrigation water. The manipulative field approach allowed us to better control environmental variables and to capture the immediate response, and also minimized 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.

At Great Mountain Forest, rain simulation was performed on the pilot plot for four times from August to December in 2001, and then on all plots every one to two weeks from

May to October in 2002. Rain simulation was carried out at Harvard Forest from May to October in 2004 and 2005. Soil CO_2 flux was measured with a portable photosynthesis system (model 6200, LI-COR, Inc., Lincoln, Nebraska, USA) coupled to a soil CO_2 flux chamber (model 6400-09, LI-COR, Inc.) and a soil temperature probe at Great Mountain Forest in 2002, and at Harvard Forest in 2004 and part of 2005, but most of the measurements in 2005 were made with a newer model (model 6400, LI-COR, Inc.). Field tests proved that measurements taken by the two photosynthesis systems were very close (relationship between measurements by the two systems: $y = 1.0494x - 0.0006$, $R^2 = 0.9856$). Soil moisture content was measured by 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, so that soils around the tubes could be stabilized. 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 analyses and statistical tests are performed with computer programs including Microsoft Excel, Matlab, and Sigmaplot.

2.3. RESULTS

2.3.1. Immediate pulse-like responses

Soil CO_2 flux on plots with O horizon increased immediately after the onset of rain, and dropped back to the pre-rain rate within 90 min after rain stopped (Fig. 2.1). For each two-hour experiment, baseline CO_2 flux was measured at the given plot right before the

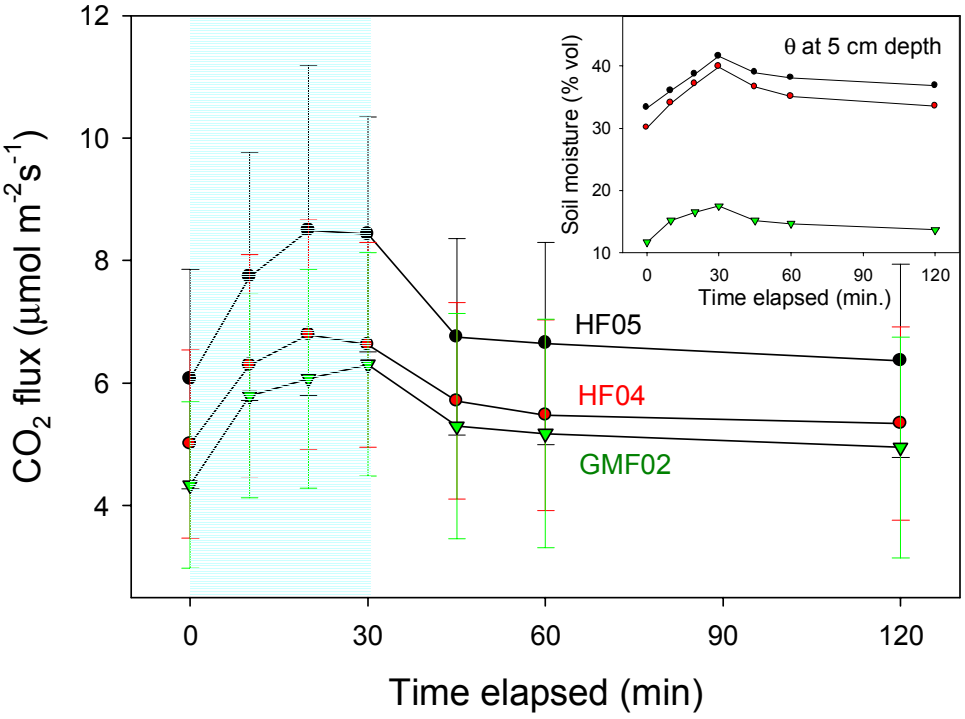

Figure 2.1. Average soil CO_2 flux and moisture during and following 30-min rain simulation on plots with O horizon at Great Mountain Forest in 2002, Harvard Forest in 2004 and in 2005. The blue area corresponds to the period of rain simulation. Each data point represents average CO_2 flux of replicate plots over the whole season. The error bars indicate the magnitude of seasonal variations during the growing season, and are calculated as the standard deviations of the distribution of site means (average flux across replicate plots) for each day of measurement.

commencement of irrigation (F_{t0}). To avoid the confounding effects of variation in soil temperature, moisture and inherent plot variability, CO_2 flux measured at different time steps since the commencement of irrigation (F_{ti}) is normalized by dividing by the pre-rain baseline flux (F_{t0}). The ratio obtained by the normalization is flux enhancement ratio (F_{ti}/F_{t0}). Enhancement ratio is greater than 1 when flux enhancement occurs. There were a total of 7 time steps (measurements) during the course of the 2-hour experiment. On plots with intact O horizon, the average maximum enhancement ratios over the season were 1.52 (± 0.31), 1.41 (± 0.25), and 1.45 (± 0.52) for GMF02, HF04, and HF05 respectively (Fig. 2.2). At GMF02 and HF05, average enhancement ratio peaked right after 30 min of rain simulation, whereas at HF04, it occurred at 20 min into rain simulation. While the average enhancement ratios at the three site-seasons appeared comparable, the magnitude of the CO_2 flux was in general lowest at GMF02 and highest at HF05, likely due to the difference in soil moisture (Fig. 2.1). The ensemble plots (Figures 2.1 and 2.2) did not distinguish between the two rain intensities. However, while the response pattern was quite the same, rain intensity did make a difference in enhancement magnitude. At GMF02 and HF05, flux enhancement induced by 12-mm rain simulation was significantly greater than that by 6-mm ones (Table 2.1). Average enhancement following 30-min irrigation (F_{t3}/F_{t0}) with 6-mm and 12-mm intensity was 1.34 and 1.66 at GMF02, and 1.23 and 1.93 at HF05. CO_2 flux before and after 30-min rain simulation at HF05 can be seen in Figure 2.3. Note that 12-mm irrigation at HF05 were all carried out in late growing season (between Aug. 27 to Sep. 18) and the sample size was small (n = 4). Over the season, the highest enhancement (F_{t3}/F_{t0}) observed was 2.20, 1.82, and 2.33 at GMF02, HF04, and HF05 respectively. Both the highest enhancement at GMF02 and HF05 were induced by 12-mm irrigation in late growing season.

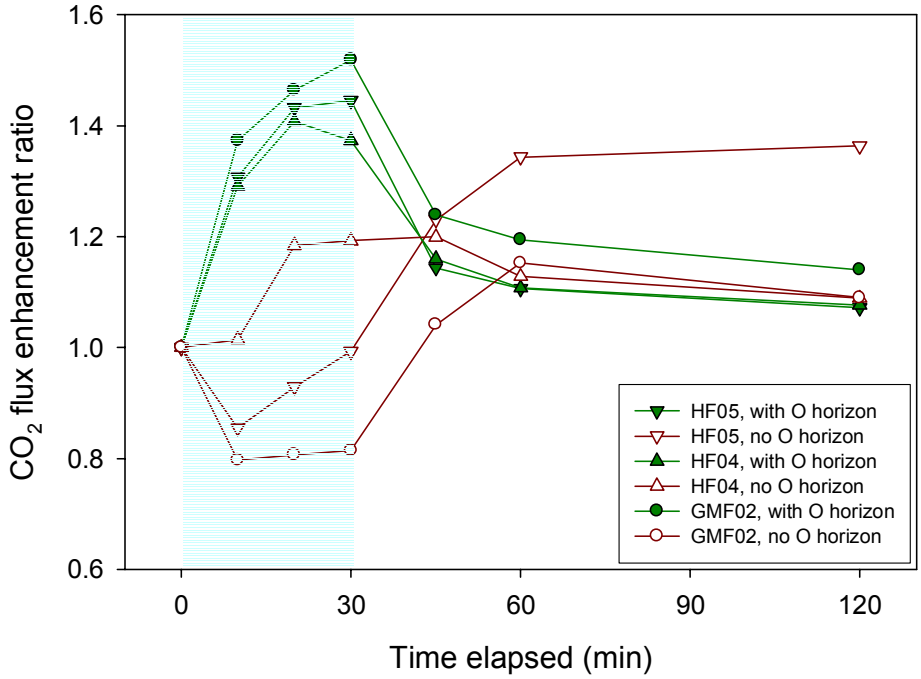

Figure 2.2. Ensemble plots of soil CO_2 flux enhancement ratio during and following rain simulation at Great Mountain Forest in 2002, and at Harvard Forest in 2004 and 2005. The blue area represents the 30-min rain simulation. Green symbols denote plots with intact O horizon, and brown symbols denote plots without O horizon. Each data point represents average enhancement of replicate plots over the whole season.

Table 2.1. Flux enhancement ratios following 30-min rain simulation (F_{t3}/F_{t0}) under different rain intensities (6 mm versus 12 mm). Enhancement ratio is the average of replicate plots. When enhancement ratio is < 1, instead of flux enhancement, there is suppression of soil respiration. The value of n is the number of experiments that a given rain intensity treatment was applied. When P value is lower than 0.05, the difference of rain intensity treatment is considered significant, and is marked red.

	Flux enhancement (F_{t3}/F_{t0})		
Plots with O horizon	**GMF02**	**HF04**	**HF05**
6 mm	1.34 ± 0.18 (n = 8)	1.39 ± 0.22 (n = 9)	1.23 ± 0.45 (n = 9)
12 mm	1.66 ± 0.32 (n = 10)	1.39 ± 0.09 (n = 3)	1.93 ± 0.31 (n = 4)
P value	**0.025**	0.9896	**0.0174**
Plots without O horizon			
6 mm	0.80 ± 0.65 (n = 8)	1.19 ± 0.35 (n = 9)	0.84 ± 0.33 (n = 9)
12 mm	0.82 ± 0.36 (n = 10)	1.20 ± 0.15 (n = 3)	1.33 ± 0.42 (n = 4)
P value	0.9392	0.9834	**0.0442**

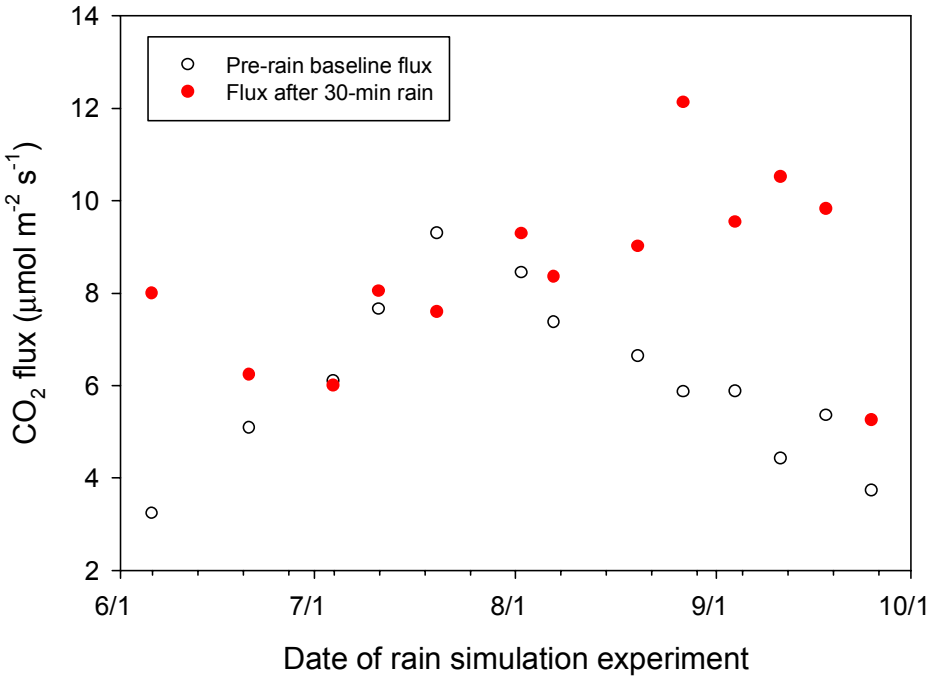

Figure 2.3. Pre-rain and post-rain CO_2 flux (F_{t0} and F_{t3}) over the season at Harvard Forest in 2005. The dates for 12-mm rain intensity were 8/27, 9/4, 9/11, and 9/18. The data points are the average flux of replicate plots on each field day.

The effects of rain intensity may also be reflected by the change in soil moisture. Flux enhancement ratios measured at the 7 time steps during the experiment overall showed a positive correlation with soil moisture increment (change in soil moisture content as a result of water addition) ($R^2 = 0.42$) (Lee et al. 2004). However, soil moisture increment did not have such strong effect on flux enhancement at Harvard Forest ($R^2 = 0.20$ in 2004, and 0.17 in 2005). Despite the same amount of water addition at all three site-seasons, soil moisture increment of the surface layer right after 30-min rain simulation was lowest at GMF02, and this was true for both plots with and without O horizon (Table 2.2).

Average baseline CO_2 flux on plots with versus without O horizon was 4.34 (± 1.36) vs. 2.64 (± 0.79), 5.01 (± 1.53) vs. 3.71 (± 1.11), and 6.07 (± 1.79) vs. 4.32 (± 1.28) μmol m^{-2} s^{-1} at GMF02, HF04 and HF05 respectively. CO_2 flux from plots without O horizon was consistently smaller than that from plots with O horizon, and showed much weakened or even no enhancement during rain simulation (Fig. 2.2). The distinct difference in response patterns and magnitude between plots with and without O horizon suggests that organic forest floor litter was the major contributor to increase in CO_2 flux during rain. While the response pattern and magnitude on plots with O horizon were very similar and consistent at all three site-seasons, plots without O horizon showed rather variable response patterns. At GMF02, CO_2 flux on 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 minutes of wetting, and then flux increased as rain simulation went on, and dropped back to the pre-rain value after rain stopped. At HF05, there was an initial decrease in CO_2 flux during the first 10 minutes of rain simulation, and then flux started to increase even after rain simulation stopped (Fig. 2.2).

Table 2.2. Soil moisture increment (change in moisture content) at O horizon (measured at 5 cm depth) immediately following 30-min rain simulation. The results for both 6-mm and 12-mm rain intensities are presented. The values are average of replicate plots. The value of n is the number of experiments that a given rain intensity treatment was applied.

	Soil moisture increment (% vol)		
Plots with O horizon	**GMF02**	**HF04**	**HF05**
6 mm	5.65 ± 2.59 (n = 8)	7.63 ± 3.20 (n = 9)	6.31 ± 2.53 (n = 9)
12 mm	6.07 ± 2.38 (n = 10)	16.31 ± 0.56 (n = 3)	12.65 ± 1.51 (n = 4)
Plots without O horizon			
6 mm	1.95 ± 1.27 (n = 8)	4.41 ± 1.70 (n = 9)	3.87 ± 1.81 (n = 9)
12 mm	4.21 ± 1.30 (n = 10)	9.01 ± 1.97 (n = 3)	7.47 ± 1.56 (n = 4)

2.3.2. Variations in flux enhancement

Unlike CO_2 flux over the growing season, which increased with temperature (Fig. 2.4), flux enhancement did not follow the same seasonal pattern (Fig. 2.5). Soil moisture regime was distinctly different at Great Mountain Forest and Harvard Forest (Fig. 2.6). During the growing season, especially from mid June to late August, flux enhancement at HF05 was clearly lower than GMF02 and HF04. Note that some of the high values at GMF02 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). If only look at HF04 and HF05, their differences of the enhancement trends from mid June to late August were resulted from the differences in baseline CO_2 flux and pre-rain soil moisture. Higher enhancement ratio corresponded to lower baseline flux and lower soil moisture.

To further explore the temporal variation in flux enhancement, we plotted the average flux enhancement ratio of replicate plots immediately following 30-min rain simulation (F_{t3}/F_{t0}) against the average pre-rain baseline soil CO_2 flux, soil temperature and moisture. When pre-rain baseline CO_2 flux and soil temperature were high, flux enhancement was low (Fig. 2.7 and Fig. 2.8). In both cases, the correlations were very strong at HF04 and HF05, moderate at GMF02 with 6-mm rain intensity, and rather weak at GMF02 with 12-mm rain intensity. The temporal variation in flux enhancement also showed a negative correlation with soil moisture of O horizon at HF05 ($R^2 = 0.44$ and 0.96 for 6-mm and 12-mm rain intensity), but no clear correlation was observed at HF04 or GMF02 (Fig. 2.9).

Another variable associated with pre-rain soil moisture and rain intensity was moisture increment. Immediately after 30-min rain, average flux enhancement (F_{t3}/F_{t0}) and

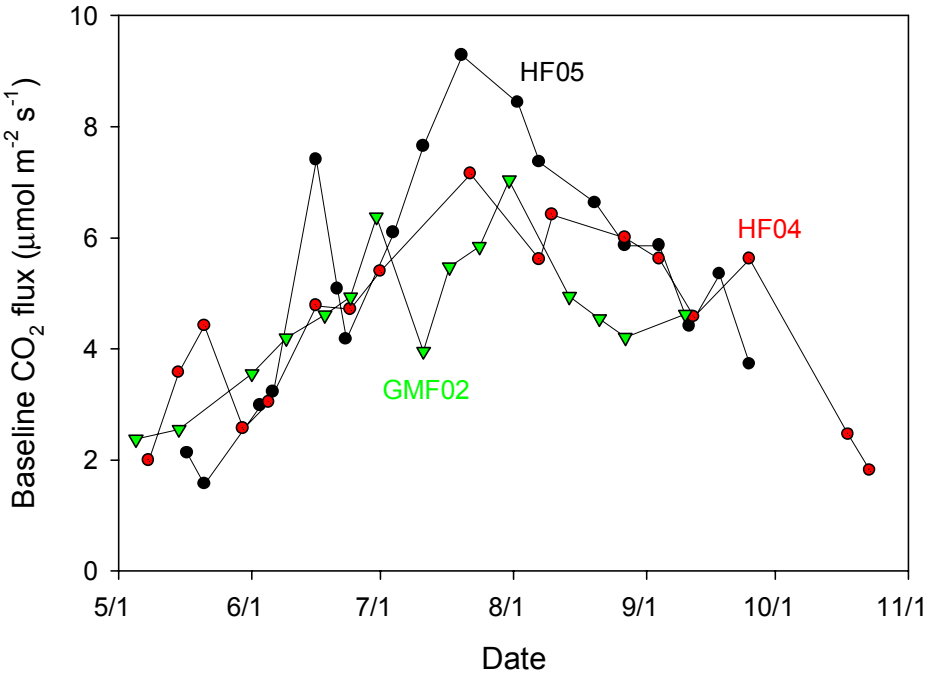

Figure 2.4. Baseline, pre-wetting soil CO_2 flux over the growing season at Great Mountain Forest in 2002, Harvard Forest in 2004 and in 2005. Each data point represents the average baseline soil CO_2 flux of replicate plots with O horizon on a field day.

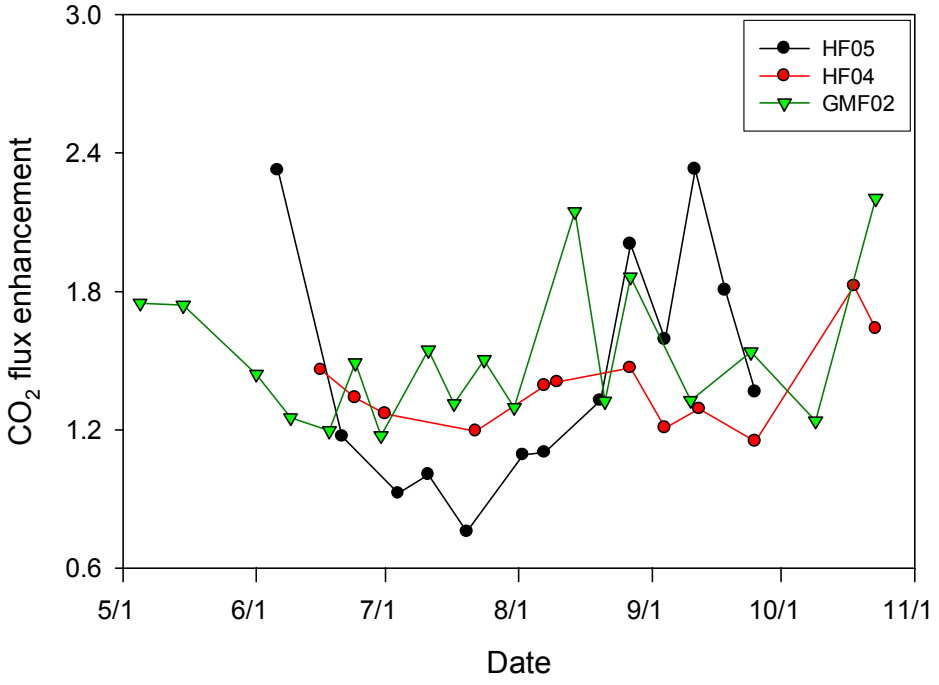

Figure 2.5. Flux enhancement over the growing season at Great Mountain Forest in 2002, Harvard Forest in 2004 and in 2005. The values used here are the enhancement ratio immediately following 30 min of rain (F_{t3}/F_{t0}), including both 6 and 12 mm irrigation intensity. Each data point represents the average enhancement ratio of replicate plots with O horizon on a field day.

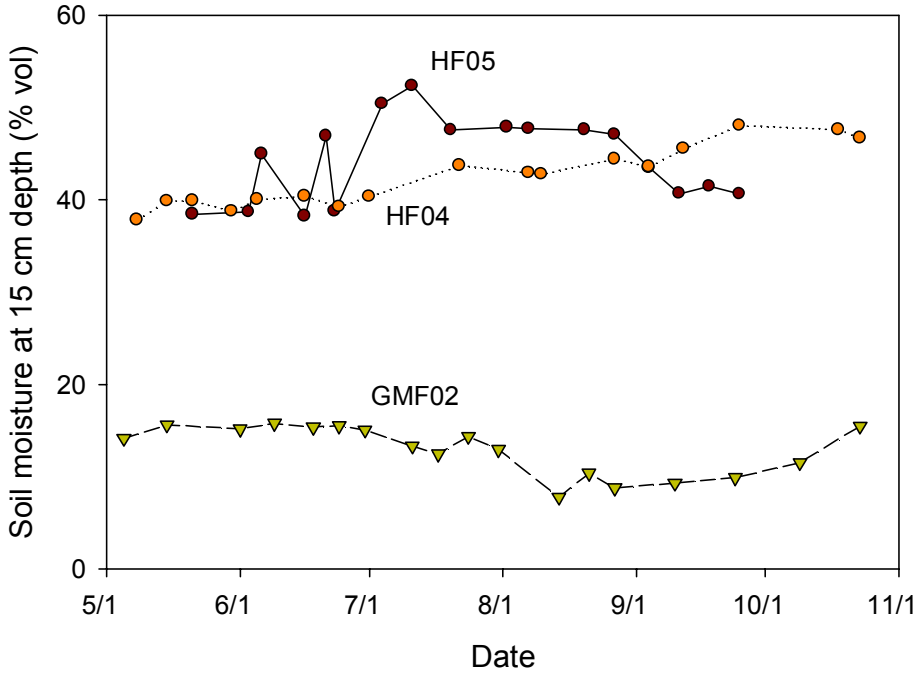

Figure 2.6. Pre-wetting soil moisture at 15 cm depth over the season at Great Mountain Forest in 2002, Harvard Forest in 2004 and in 2005. Each data point represents the average value of replicate plots with O horizon on a field day.

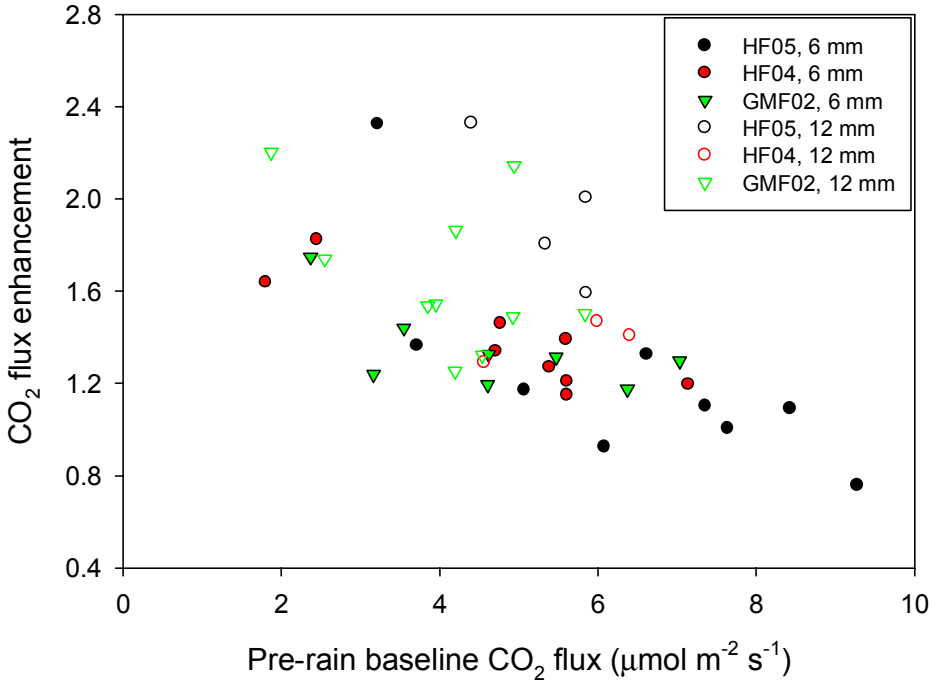

Figure 2.7. Flux enhancement vs. pre-wetting baseline CO_2 flux. Temporal variation in flux enhancement showed clear dependence on baseline CO_2 flux. Each data point represents the average enhancement following 30-min irrigation (F_{t3}/F_{t0}) of replicate plots on a field day. Correlations are shown as below:
GMF02, 6 mm: $y = -0.0721x + 1.6768$, $R^2 = 0.39$, $n = 8$;
GMF02, 12 mm: $y = -0.1206x + 2.153$, $R^2 = 0.19$, $n = 10$;
HF04, 6 mm: $y = -0.1178x + 1.9499$, $R^2 = 0.77$, $n = 9$;
HF04, 12 mm: $y = 0.0793x + 0.9387$, $R^2 = 0.72$, $n = 3$;
HF05, 6 mm: $y = -0.1669x + 2.2943$, $R^2 = 0.58$, $n = 9$;
HF05, 12 mm: $y = -0.3638x + 3.8838$, $R^2 = 0.63$, $n = 4$.

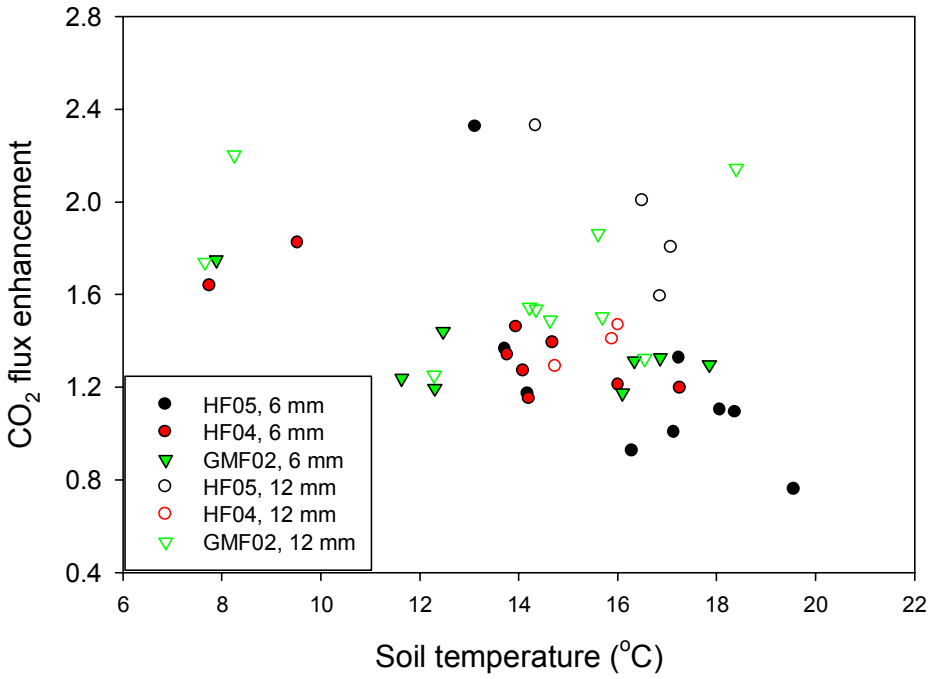

Figure 2.8. Flux enhancement vs. pre-wetting soil temperature. Temporal variation in flux enhancement showed temperature-dependence at Harvard Forest in 2004 and 2005, and GMF02 with 6-mm rain intensity, but showed no such correlation at GMF02 with 12-mm rain intensity. Each data point represents the average enhancement following 30-min irrigation (F_{t3}/F_{t0}) of replicate plots on a field day. Correlations are shown as below:
GMF02, 6 mm: $y = -0.0342x + 1.8186$, $R^2 = 0.40$, $n = 8$;
GMF02, 12 mm: $y = -0.0164x + 1.8857$, $R^2 = 0.03$, $n = 10$;
HF04, 6 mm: $y = -0.0635x + 2.242$, $R^2 = 0.73$, $n = 9$;
HF04, 12 mm: $y = 0.1239x - 0.5396$, $R^2 = 0.93$, $n = 3$;
HF05, 6 mm: $y = -0.1435x + 3.5843$, $R^2 = 0.51$, $n = 9$;
HF05, 12 mm: $y = -0.2221x + 5.5294$, $R^2 = 0.79$, $n = 4$.

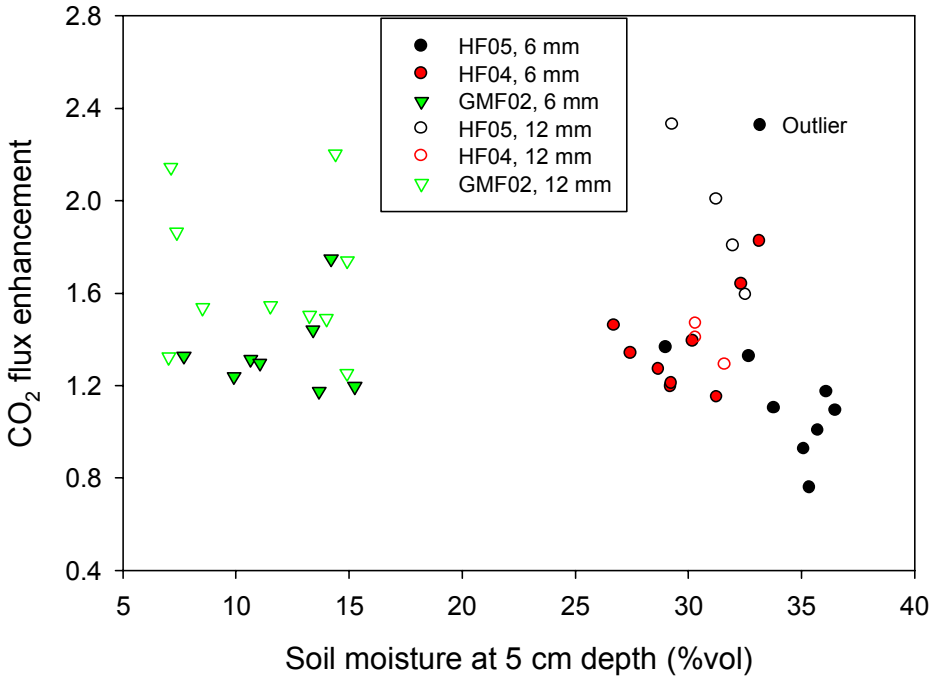

Figure 2.9. Flux enhancement vs. pre-rain soil moisture at 5 cm depth. The temporal variation in flux enhancement could be explained by surface soil moisture at Harvard Forest, particularly at HF05, but not at Great Mountain Forest. Each data point represents the average enhancement following 30-min rain (F_{t3}/F_{t0}) of replicate plots on a field day. Correlations are shown as below:
GMF02, 6 mm: $y = 0.014x + 1.1745$, $R^2 = 0.04$, $n = 8$;
GMF02, 12 mm: $y = -0.0126x + 1.8023$, $R^2 = 0.02$, $n = 10$;
HF04, 6 mm: $y = 0.0539x - 0.2224$, $R^2 = 0.27$, $n = 9$;
HF04, 12 mm: $y = -0.1132x + 4.8699$, $R^2 = 0.89$, $n = 3$;
HF05, 6 mm: $y = -0.0536x + 2.9304$, $R^2 = 0.44$, $n = 8$ (one outlier excluded);
HF05, 12 mm: $y = -0.2167x + 8.7106$, $R^2 = 0.96$, $n = 4$.

soil moisture increment showed negative correlation at HF05 (the correlations were moderate for 6-mm and strong for 12-mm rain intensity) (Fig. 2.10). Therefore, at HF05, flux enhancement decreased with increasing pre-rain soil moisture and moisture increment. At HF04, flux enhancement with 12-mm rain intensity appeared to decrease with increasing pre-rain soil moisture, but increase with increasing moisture increment (note that the sample size was very small: n = 3). At GMF02, with 6-mm rain intensity, flux enhancement (F_{t3}/F_{t0}) increased with moisture increment ($R^2 = 0.30$, Fig. 2.10), but showed no discernable relationship with pre-rain soil moisture.

The spatial variation in flux enhancement across the two New England forests showed a negative correlation to pre-rain soil moisture ($R^2 = 0.42$) (Fig. 2.11). Within each site-season, this pattern was very strong for plots at Harvard Forest ($R^2 = 1$ and 0.88 at HF04 and HF05), but not so at GMF02. The spatial variation in enhancement was analyzed by plotting the seasonal mean flux enhancement of each plot against the seasonal mean soil moisture at 15 cm depth. Although the ensemble enhancement ratios were similar across the three sites-seasons (Fig. 2.2), there was a wide range of enhancement ratios among individual plots. Plot A of HF05 had the highest average enhancement ratio (2.24), and plot C of HF05 the lowest (0.59, i.e., flux suppression). Our results indicate moisture dependence of flux enhancement ratio, which was higher on xeric plots and lower on mesic plots. Moisture dependence of flux enhancement was also manifested at a finer scale. Figure 2.12 shows the average flux enhancement over the 2-hour rain simulation on the four replicate plots with O horizon at Harvard Forest in 2005. Average soil moisture of each plot ranged from 26-71% (vol). Plots with lower pre-rain soil moisture showed greater flux enhancement, while plots with higher soil moisture showed less or even negative enhancement. Figure 2.13 shows soil

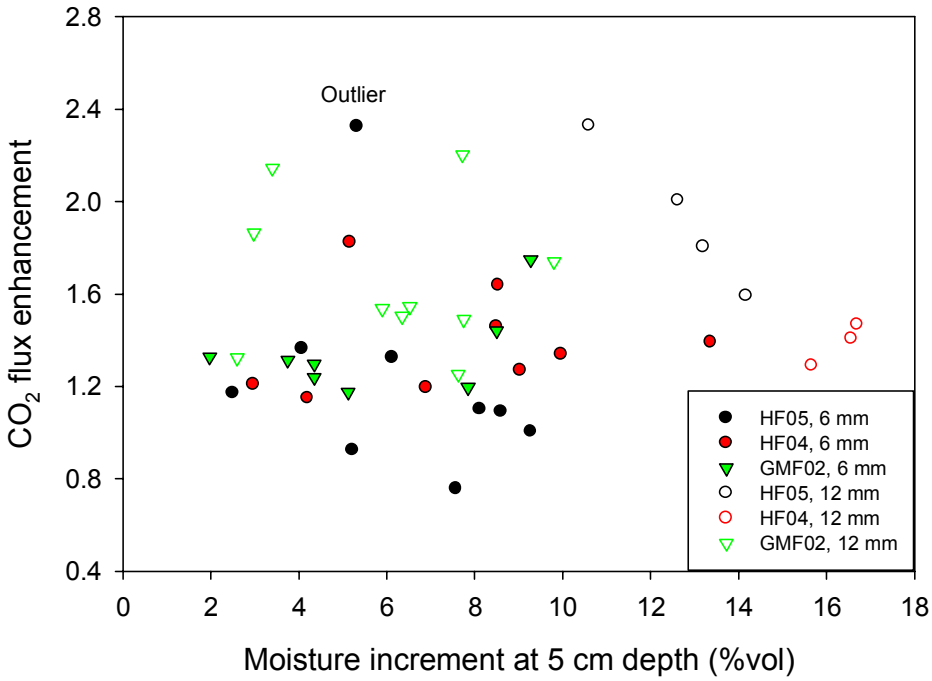

Figure 2.10. Flux enhancement vs. soil moisture increment at 5 cm depth. Each data point represents the average enhancement following 30-min rain (F_{t3}/F_{t0}) of replicate plots on a field day. Correlations are shown as below:
GMF02, 6 mm: $y = 0.0389x + 1.1221$, $R^2 = 0.30$, $n = 8$;
GMF02, 12 mm: $y = -0.0109x + 1.7261$, $R^2 = 0.01$, $n = 10$;
HF04, 6 mm: $y = 0.0092x + 1.3158$, $R^2 = 0.02$, $n = 9$;
HF04, 12 mm: $y = 0.1565x - 1.1656$, $R^2 = 0.95$, $n = 3$;
HF05, 6 mm: $y = -0.0364x + 1.3265$, $R^2 = 0.19$, $n = 8$ (one outlier excluded);
HF05, 12 mm: $y = -0.2056x + 4.5324$, $R^2 = 0.98$, $n = 4$.

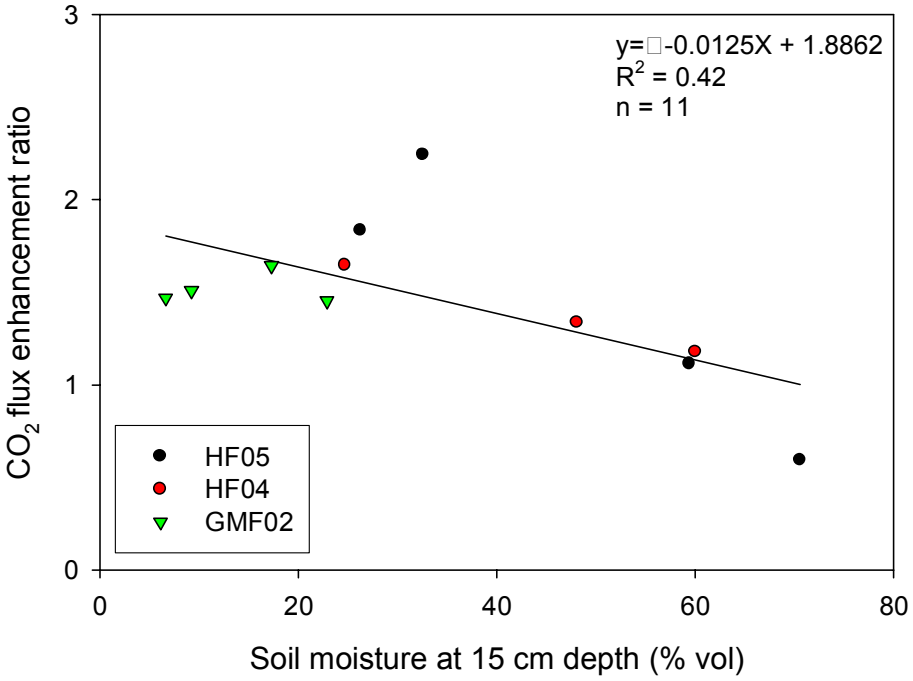

Figure 2.11. Flux enhancement of individual plots vs. pre-wetting soil moisture. Spatial variation in flux enhancement across the plots showed moisture-dependence. The data points are the seasonal mean enhancement of each plot following 30-min rain. Correlations within each site-season are:
GMF02: $y = 0.0014x + 1.4989$, $R^2 = 0.01$, $n = 4$;
HF04: $y = -0.0132x + 1.9721$, $R^2 = 1$, $n = 3$;
HF05: $y = -0.0325x + 2.9793$, $R^2 = 0.88$, $n = 4$.

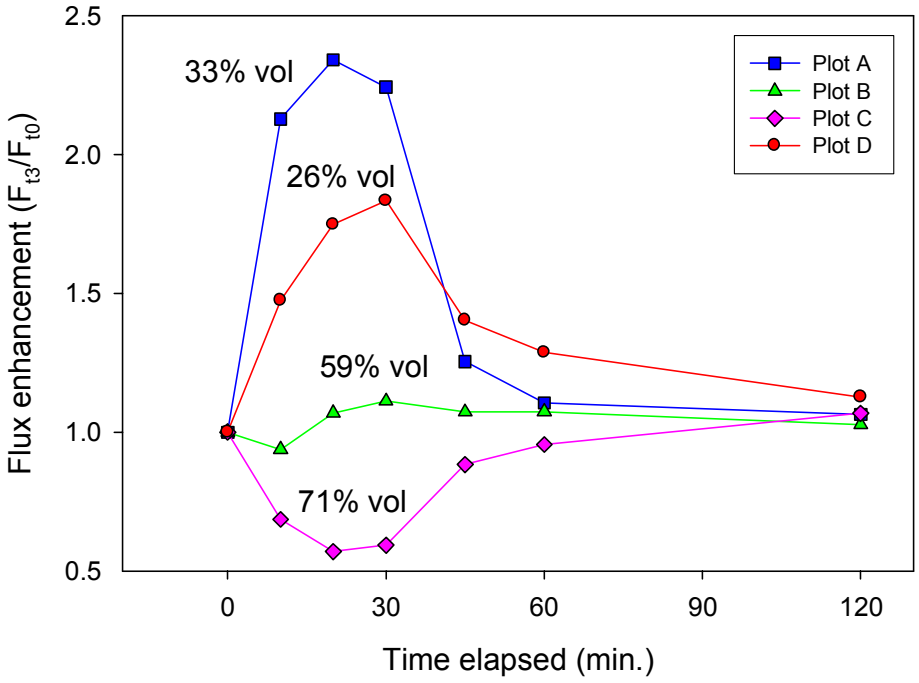

Figure 2.12. CO_2 flux enhancement at the four replicate plots over 2-hour rain simulation at HF05, with their corresponding average soil moisture. Each data point represents the seasonal average of flux at each time step.

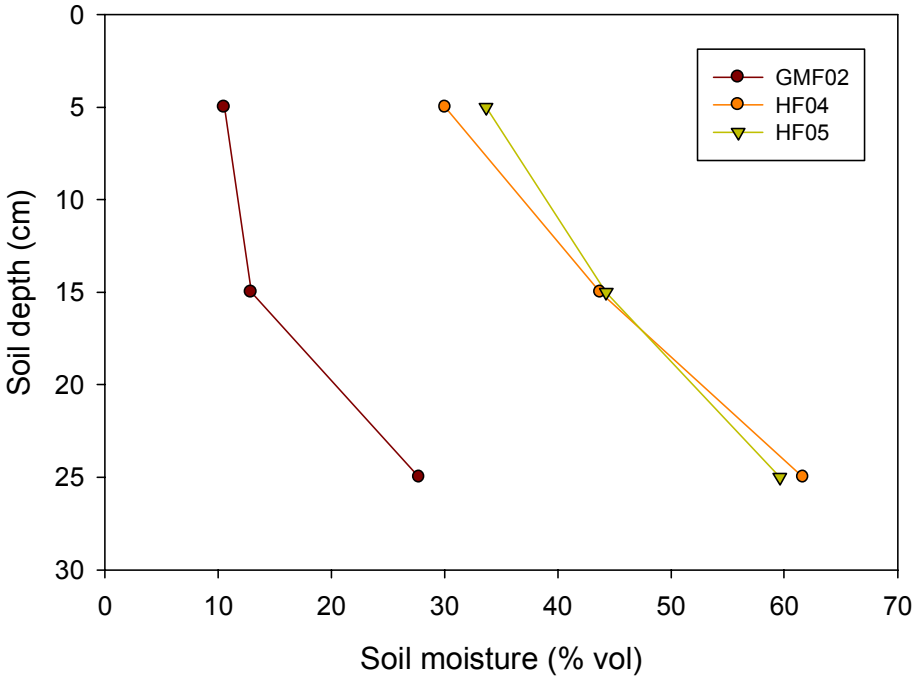

Figure 2.13. Average soil moisture profile at Great Mountain Forest in 2002, Harvard Forest in 2004 and 2005. The values of the data points are the average of replicates' seasonal mean soil moisture.

moisture profile at the three site-seasons. Soil moisture content at GMF02 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 decrease in the average soil moisture content at 25 cm depth in 2005 was due to the addition of a new set of plots located at a higher and drier spot. The increase in soil moisture at Harvard Forest was likely caused by an elevated water table, a consequence of beaver damming activities in a near-by pond, which inundated the lower part of an adjacent trail in 2005.

For bare plots, flux enhancement showed a clear trend to decrease with increasing pre-rain soil moisture over the season at HF04 and HF05 (Fig. 2.14). Especially at HF04, soil moisture of all depths appeared to be good predictors of the temporal variation in flux enhancement on bare plots.

2.3.3. Flux contribution of O horizon to total soil respiration

To quantify the relative contribution of O horizon to the total soil respiration, we first compared the pre-rain CO_2 flux at plot with O horizon (F_O) and 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.

$$\text{Flux contribution of O horizon} = \frac{F_O - F_B}{F_O} \qquad (2.1)$$

This method is based on the assumption that soil respiration on plots in a given block/pair was identical before one of them was treated with O horizon removal.

Flux contribution of O horizon was highest at GMF02 (0.45 ± 0.11), and was similar at HF04 and HF05 (0.26 ± 0.07 and 0.29 ± 0.07). Temporal variation in flux contribution

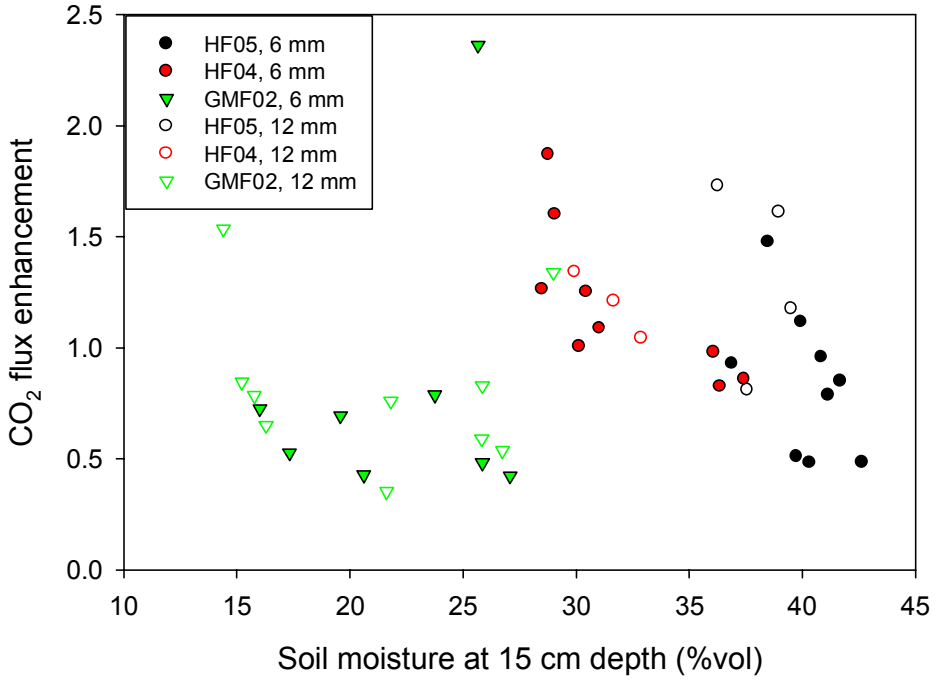

Figure 2.14. Flux enhancement vs. pre-rain soil moisture at 15 cm depth on **bare plots**. The temporal variation in flux enhancement could be explained by soil moisture at HF04, and at HF05 with 6-mm rain intensity. Each data point represents the average enhancement following 30-min rain (F_{t3}/F_{t0}) of replicate plots on a field day. Correlations are shown as below:
GMF02, 6 mm: $y = 0.0414x - 0.1074$, $R^2 = 0.07$, n = 8;
GMF02, 12 mm: $y = -0.0102x + 1.0393$, $R^2 = 0.02$, n = 10;
HF04, 6 mm: $y = -0.0732x + 3.5343$, $R^2 = 0.57$, n = 9;
HF04, 12 mm: $y = -0.099x + 4.318$, $R^2 = 0.97$, n = 3;
HF05, 6 mm: $y = -0.0918x + 4.5325$, $R^2 = 0.23$, n = 9;
HF05, 12 mm: $y = -0.0673x + 3.8941$, $R^2 = 0.05$, n =4.

of O horizon could be explained by pre-rain soil moisture, but showed no significant correlation with soil temperature. In Figure 2.15, each data point of flux contribution was the average of replicate plots measured on a given field day. Flux contribution of O horizon was 0.31-0.56 at GMF02; 0.1-0.35 at HF04; and 0-0.42 at HF05. Pre-rain soil moisture was 7.8-15.8% (vol) at GMF02; 37.8-48% (vol) at HF04; and 38.4-52.3% (vol) at HF05. The values of average soil moisture here were slightly different from those used with flux enhancement data. As flux contribution data required only pre-rain measurements, which could be obtained without performing rain simulation experiment, more data points were available for analysis. Over the season, flux contribution of O horizon at GMF02 increased with increasing pre-rain soil moisture ($R^2 = 0.75$); however, an opposite trend was observed at HF04 ($R^2 = 0.45$) with the highest values of flux contribution (>0.3) all occurred at the beginning of the growing season (May and June) (Fig. 2.15). No clear trend was found for HF05.

Spatial variation in flux contribution of O horizon showed a strong negative correlation with mean pre-rain soil moisture ($R^2 = 0.55$) (Fig. 2.16). The seasonal mean flux contribution of individual plots at the 3 site-seasons ranged from 0 to 0.55. Average pre-rain soil moisture among plots varied greatly from 6.6 to 70.6% (vol). The results suggest that, spatial variation in flux contribution of O horizon was strongly dependent on inherent site soil moisture condition; and at wetter sites, O horizon contributed less to total soil respiration.

2.3.4. Temperature sensitivity

CO_2 flux increases with soil temperature, and Q_{10} values serve as a measure of sensitivity of CO_2 flux in response to change in temperature. Table 2.3 shows Q_{10} values of

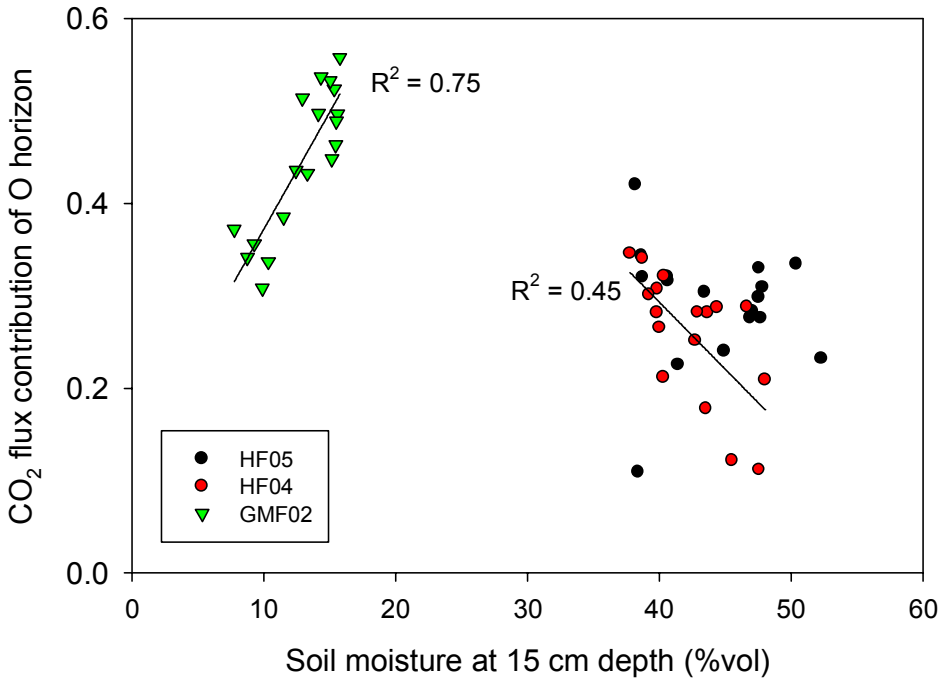

Figure 2.15. Flux contribution by O horizon vs. pre-rain soil moisture at 15 cm. Temporal variation in O horizon flux contribution showed opposite relationships with soil moisture at GMF02 and HF04 ($y = 0.03x + 0.12$, $R^2 = 0.75$, $n = 18$; $y = -0.02x + 0.87$, $R^2 = 0.45$, $n = 17$). Each data point represents the average flux contribution of replicates on a field day.

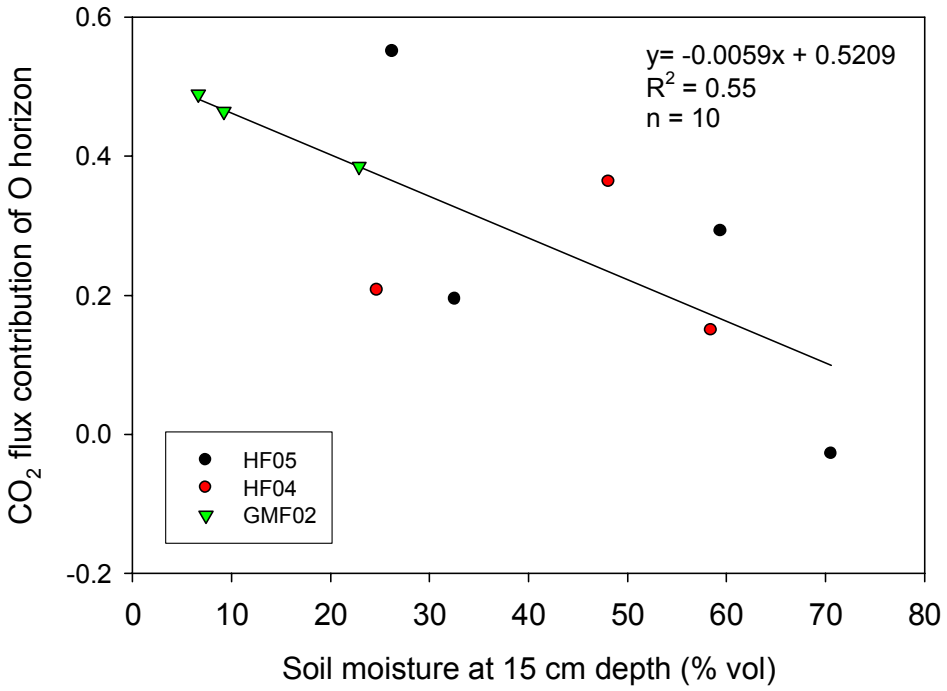

Figure 2.16. Flux contribution by O horizon of individual plots vs. pre-rain soil moisture. Spatial variation in flux contribution across plots of the three site-seasons could be explained by soil moisture. The data points are the seasonal means of each plot.

Table 2.3. Q_{10} values of individual plots at Great Mountain Forest in 2002, and Harvard Forest in 2004 and 2005.

Q_{10}		GMF02	HF04	HF05
Treatment plots	A	2.76	4.15	6.14
	B	2.88	4.00	4.22
	C	2.03	4.03	4.50
	D	2.50		4.12
Control plots	A0		6.55	5.77
	B0		3.38	3.87
	C0		4.12	4.20
	D0			4.85

the three site-seasons, calculated from baseline CO_2 flux from treatment and control plots, both of which were with intact O horizon. Q_{10} values at HF04 and F05 ranged from 3.38 to6.14, with an average of 4.37 at HF04, and 4.25 at HF05. These values are higher than those reported by Davidson et al. (1998), which ranged from 3.4 to 5.6 for the individual study sites at Harvard Forest, with an average Q_{10} of 3.9. Combined Q_{10} values of HF04 and HF05 decreased with increasing soil moisture ($R^2 = 0.42$) (Fig. 2.17). Q_{10} values at GMF02 ranged from 2.03 to 2.88, and did not show clear relationship with soil moisture. Our results support the general observation that Q_{10} values are often affected by soil moisture conditions (Lloyd and Taylor 1994, Kirschbaum 1995, Xu and Qi 2001).

2.3.5. Effect of repeated wetting

A t-test was performed to detect impacts of repeated wetting on treatment plots. Baseline CO_2 flux showed no significant difference between treatment and control plots at Harvard Forest in 2004 ($p<0.95\%$) and 2005 ($p<0.59\%$). Statistically, our two-year rain simulation experiments did not appear to alter site conditions. However, it is unclear whether this would remain true if rain simulation experiments were to be carried on for additional seasons.

2.4. DISCUSSION

2.4.1. Rain-induced CO_2 pulses in different ecosystems

In our study, soil CO_2 flux increased within the first 10 min of rain simulation, peaked immediately following the end of the 30-min rain simulation, started declining and returned to the pre-rain level within 90 min after rain stopped. The average flux enhancement ratio

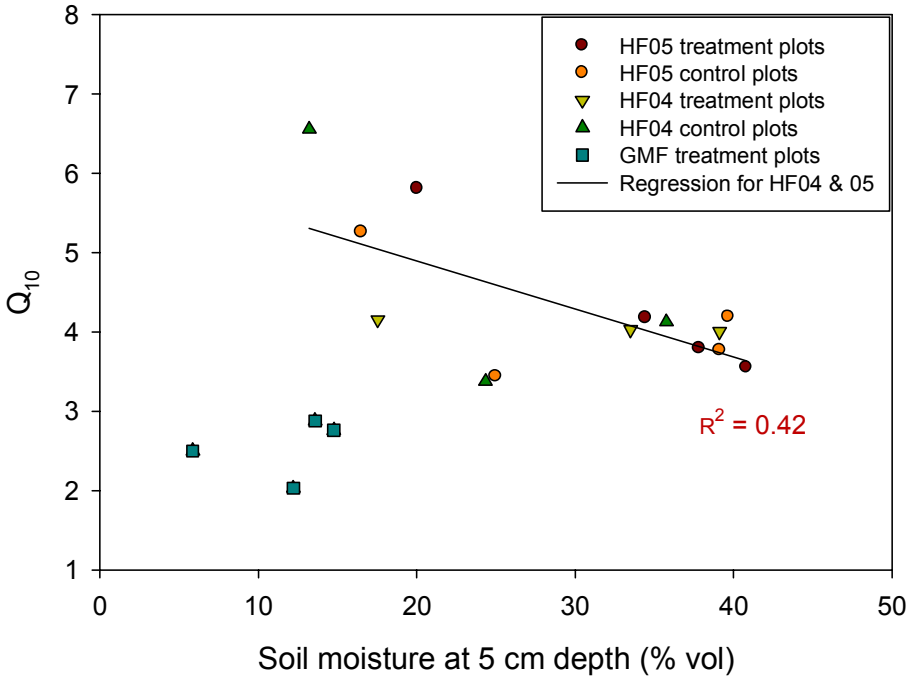

Figure 2.17. Q_{10} vs. soil moisture at 5 cm depth. Combined Q_{10} values of HF04 and HF05 showed a negative relationship with soil moisture ($y = -0.06x + 6.11$, $R^2 = 0.42$). The data points represent the respective Q_{10} values of individual plots, including treatment plots and control plots where O horizon was intact. Note that there were no control plots at Great Mountain Forest in 2002.

immediately following the 30-min rain simulation was 1.52 (GMF02), 1.41 (HF04), and 1.45 (HF05) on plots with intact O horizon. These values are comparable to the enhancement ratios of 1.52 in a Siberian pine forest (Kelliher et al.1999) and 1.5 in a temperate deciduous forest in Japan (Lee et al. 2002). Observations from these two studies were made following natural rain events, and therefore the amount and intensity of rain could not be standardized. However, the comparable numbers indicate that our results are roughly in line with those in other forest ecosystems as well as from natural rain events.

The enhancement ratio at GMF02 was smaller than the results from our laboratory incubation experiment on forest litter, which showed a 10-fold enhancement within 1 min (Lee et al. 2004). This suggests that, while laboratory data can usually hint the direction of wetting effects, they can not be directly extrapolated to field conditions. The higher enhancement ratio from laboratory experiments may be a result of increased access to organic matter due to disturbance of soil structure during sample preparation.

Immediate response was also reported by other rain simulation field experiments at an Arizona desert ecosystem (Sponseller 2007) and Nebraska soybean fields (unpublished results, see Chapter 3), as well as from laboratory incubation experiments (Borken et al. 2003, Sponseller 2007). Rapid increase in CO_2 flux was also observed from natural rain events in a tropical forest (Davidson et al. 1993), a temperate deciduous forest (Lee et al. 2002), a Mediterranean oak forest (Rey et al. 2002), and a grassland/savanna ecosystem (Xu et al. 2004). Some studies found a delayed pulse (e.g., Griffiths and Birch 1961), or a pulse within the first hour after wetting, followed by a second peak hours later (Orchard and Cook 1983). Our results showed very short-lived CO_2 pulses, which may be due to the relatively small amount of the simulated rainfall (Sponseller 2007), and fast drying-out process of soil upper

layers in the field, as also observed by Xu et al. (2004) and Kelliher et al. (1999). Indeed, regardless of rain intensity, CO_2 flux at all three site-seasons started declining along with declining soil moisture after rain stopped, which implies a possibility that if given more water or longer period of rain, flux enhancement may be greater and last longer. Our laboratory incubation results showed that under constant temperature, elevated CO_2 flux could be sustained for hours after the initial peak when litter substrate remained moist (Lee et al. 2004). Therefore, substrate availability appears not to be a limiting factor for the fluxes measured in our experiments. On the other hand, limited or no enhancement on plots without O horizon may be a consequence of limited available substrates as well as smaller microbial population. Some rain simulation experiments observed post-wetting soil CO_2 pulses that lasted for hours or even days; examples are experiments in a European forest (Borken et al. 2002), a tallgrass prairie ecosystem (Liu et al. 2002), and a semi-arid grassland (Huxman et al. 2004). Since our research aimed at short-term response during and immediately following rain events, we do not have information beyond the 2-hour experiment period. However, given that flux enhancement appeared to be restrained by fast declining soil moisture in our experiments, it seems unlikely that a second peak would be observed after the 2-hour observation time.

There was a distinct difference in response patterns between plots with intact O horizon and those with O horizon removed. Since data beyond the 2-hour experiment time frame are not available, it is not clear whether there was delayed enhancement on plots without O horizon. Based on our existing field data, we could not separate heterotrophic respiration from autotrophic respiration by fine roots and rhizosphere activities. However, it is more likely that rain-induced flux contribution was dominated by heterotrophic respiration.

One piece of evidence is that, our lab incubation experiment on leaf litter, which contained no living roots, showed immediate CO_2 pulses upon wetting with even greater enhancement magnitude than that observed in field (Lee et al. 2004). This is further supported by a published field study using isotope tracer (^{14}C) to trace the source of soil CO_2 flux in a temperate deciduous forest at Oak Ridge, Tennessee. Based on the change in the ^{14}C-signature of CO_2 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 CO_2 flux (Cisneros-Dozal et al. 2007). Soil microbes are most abundant in the top few centimeters of soil (Woods 1989), where leaf litter and plant detritus provide decomposition substrate rich in labile carbon. Water addition on plots with intact O horizon not only enhances microbial activities/populations that have been suppressed by water deficiency on well-aerated forest floor (Birch 1958, Orchard and Cook 1983), but also facilitates movement of dissolved organic carbon from litter into deeper soils for decomposition (Cleveland et al. 2007). While fine roots are most abundant in O horizon (for example, 50% of fine root biomass was present in 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 (H□gberg 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).

2.4.2. Likely mechanisms of rain-induced soil CO_2 pulses

Several explanations of rain-induced CO_2 pulses have been proposed. They can be

generalized into the following: (1) reactivated microbial activities by water addition (Orchard and Cook 1983, Bottner 1985, Saetre and Stark 2005); (2) rapid increase in microbial biomass (Griffiths and Birch 1961, Orchard and Cook 1983, Schnürer et al. 1986, Lundiquist et al. 1999); and (3) increased substrate availability for microbial mineralization. Increased substrate availability may result from i) 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); ii) lysing microbial cells due to water potential shock from wetting (Kieft et al. 1987); iii) cytoplasmic solutes released by viable microbes in response to water potential shock (Fierer and Schimel 2003, Lovieno and Bååth 2008). These processes may take place concurrently, or in different timescales during/following a rain event.

Our rain simulation triggered increase in CO_2 flux within just minutes after the onset of rain, often before change in moisture content in mineral soil could be detected. This almost instantaneous and short-lived response was most likely dominated by microbial activity and not root respiration. Low water potential of the porous, exposed surface litter layer often curbs microbial activity and enzyme movements. Wetting relieved the desiccating stress for dormant microbes in litter layer, and created a temporarily favorable environment for soil microbes 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 increased right after wetting, microbial population only showed linear instead of the normal exponential increase, and exponential growth only took place 7 hours 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. And the phenomenon of decoupling between soil respiration and microbial growth was referred to as "wasteful metabolism" (Lovieno and Bååth 2008).

Our results can not provide conclusive information as to the source of substrate used by the reactivated microbes creating the initial pulses. Substrates of both microbial origin and from plant litter are possible sources for microbial metabolism in our study. However, substrates of microbial origin appear to be more readily available and likely fuel for the observed rapid microbial activity upon wetting. Fierer and Schimel (2003) found that ^{14}C-labeled microbial carbon, instead of non-biomass soil organic carbon, was the primary substrate of the respiration pulse immediately following wetting. And although the wetting event did release some structurally protected soil organic matter, the additional soil organic carbon did not contribute as much to the resulting CO_2 pulse. Similarly, Kieft et al. (1987) found that increase in water potential caused significant release of biomass carbon and thus enhanced soil respiration. They also found that the release of intracellular materials in response to increased water potential accounted for a greater fraction of the enhanced respiration than did dead biomass from preceding desiccation. Halverson et al. (2000) found no cell lysis in response to an increase in water potential from -3.0 to -1.0 MPa. Fierer and Schimel (2003) further proposed that the observed microbial C pulse was not from cell lysis (because they did not find decrease in microbial population), but rather from mineralization of cytoplasmic solutes released by viable cells in response to water potential shock, through which soil microbes can raise their intracellular water potential and avoid lysis (Halverson et al. 2000). This hypothesis is supported by a study by Lovieno and Bååth (2008), which estimated soil bacteria growth using leucine or thymidine incorporation: cell proliferation is

accompanied by incorporation of radiolabeled leucine into protein molecules and radiolebeled thymidine into nucleotides. Normally, the two incorporation rates correlate very strongly. However, in this study, it was found that the incorporated leucine/thymidine ratio decreased after wetting. A likely explanation is that amino acids in microbial osmo-regulatory solutes were released by microorganisms into the environment in response to the water potential shock from wetting, and the increased amino acids diluted the radiolabeled leucine (also an amino acid), resulting in a lower leucine incorporation rate (Lovieno and Bååth 2008). Earlier research by Saetre and Stark (2005) also supports this conclusion, who found an initial nitrogen pulse following wetting, which was probably caused by an ephemeral N-rich substrate pool.

Evidence from the abovementioned studies suggest that the labile substrate pool initially used by soil microbes after wetting was mainly of microbial origin. Still, substrates of microbial origin and from plant litter both remain possible sources for microbial consumption upon wetting, and which one dominates in a given case may be a function of conditions such as relative availability, timescales for wetting events, and seasonal fluctuations in moisture. Moreover, if cytoplasmic solutes alone were responsible for the rain-induced CO_2 pulses, then shouldn't plots without O horizon also show some degree of enhancement upon wetting, when labile microbial carbon was released? Of course this may be explained by lower microbial abundance or different microbial composition on plots without O horizon. The labile carbon pool released by microbes is small (Fiere and Schimel 2003, Saetre and Stark 2005), and can be exhausted soon after wetting. Therefore, it is likely that if our rain simulations lasted longer, the main substrate used for soil respiration would eventually shift to plant organic matter.

2.4.3. Estimated amount of soil carbon release during rain

Models of soil respiration not taking rain-induced CO_2 pulses into account are very likely to underestimate soil CO_2 flux; so are 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 measurements not been made during rain simulation. And if measurements started 90 min after rain stopped, some plots would have misleadingly suggested no enhancement.

Soil CO_2 release during rain in the growing season can be roughly estimated as

$$F = F_{t0} \times (\overline{F_{t3} / F_{t0}}) \times t_{rain} \quad (2.2)$$

where F is the total soil CO_2 released during rainy periods, F_{t0} is the seasonal average baseline CO_2 flux of a site, mean F_{t3}/F_{t0} is the site-specific average enhancement ratio of 6-mm irrigation, which is used here as the average enhancement ratio during rain, and t_{rain} is the total time of rainy periods during growing season (May to October). Based on our results, at GMF02, average baseline CO_2 flux is 4.34 μmol m^{-2} s^{-1}, and the average enhancement ratio of 6-mm irrigation is 1.34 (Table 2.1). The total time of rain during the growing season of 2002 is 305 hours. Thus, the average soil CO_2 flux during rain is 5.82 μmol m^{-2} s^{-1}, and the total soil carbon loss to the atmosphere over 305 hours is estimated to be 0.77 t C ha^{-1}. Table 2.4 shows the values of parameters for estimating soil C release during rain at the three site-seasons. Using the same calculation method, during the growing season at HF04, average soil CO_2 flux during rain is 6.96 μmol m^{-2} s^{-1}, and the total rain-induced soil C release is 1.15 t C ha^{-1}. At HF05, average soil CO_2 flux during rain is 7.47 μmol m^{-2} s^{-1}, and estimated soil C release durian rain is 0.80 t C ha^{-1} in the growing season of 2005. Estimated

Table 2.4. Parameters for estimating rain-induced soil C release during growing season (May to October). Data of Great Mountain Forest are obtained from Prof. Xuhui Lee's website (http://pantheon.yale.edu/~xhlee/Site/Home.html); data of Harvard Forest are from Harvard Forest website (http://harvardforest.fas.harvard.edu:8080/exist/xquery/data.xq?id=hf001).

Parameters	GMF02	HF04	HF05
Avg. baseline CO_2 flux (F_{t0}) (μmol m^{-2} s^{-1})	4.34	5.01	6.07
Avg. enhancement ($\overline{F_{t3} / F_{t0}}$)	1.34	1.39	1.23
Total time of rain (hour)	305	383	248.5
Precipitation (mm)	482.1	678.7	822.4
CO_2 flux during rain (μmol m^{-2} s^{-1})	5.82	6.96	7.47
Estimated C loss (t C ha^{-1})	0.77	1.15	0.80
Observation intervals for precipitation (min)	30	60	15

carbon loss is greater at HF04 than HF05 due to more rainy hours at HF04 (Table 2.4). Given that HF05 had more precipitation (Table 2.4), it is quite unlikely that rainy hours at HF04 could be 135 hours or 54% more than those at HF05. The most likely explanation is the coarser observation intervals of the HF04 precipitation data (obtained from Harvard Forest online data archive). Observation intervals for the precipitation data of HF04 are 60 min, while those of HF05 are 15 min. Total time of rain is calculated as the sum of time whenever precipitation occurs. When any rain is observed, 15 min would be added to the total time of rain at HF05, whereas at HF04, 60 min would be added, which may result in overestimation of total rainy hours at HF04.

Our estimates of soil carbon loss during rain 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, and our estimation did not include the soil CO_2 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 carbon released as a result of rain could be of little consequence. 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

CO_2 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 hours, a single rain storm could 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 was emitted by soils subject to drying-rewetting cycles than by soils which remain constantly moist (Jarvis et al. 2007, Xiang et al. 2008). Laboratory experiments also found that overall bacterial population growth and respiration were 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, depending on site-specific conditions.

2.4.4. Moisture dependence of rain-induced pulses

Pre-rain soil moisture was a good indicator of rain-induced flux enhancement magnitude at Harvard Forest, but not at Great Mountain Forest. Spatial variation in flux enhancement across site-seasons showed a negative correlation to pre-rain site moisture (R^2 = 0.42). But within site-seasons, the correlations were particularly strong at HF04 and HF05 (Fig. 2.11). Similarly, a rewetting experiment on Mediterranean oak forest soil under controlled laboratory environment found that, the drier the soil was initially, the greater the flux response (Rey et al. 2005). Although wetter plots normally had greater soil respiration and maybe larger microbial biomass (Hunt et al. 1989), greater flux enhancement usually occurred on drier plots. One explanation is that, drier soil holds less water and more air in soil pores, and thus more CO_2 would be displaced by water upon wetting. However, a study

at Great Mountain Forest showed that, with our rain intensity (6-12 mm for 30 min), only 0.4-0.8 μmol m^{-2} s^{-1} of CO_2 was displaced (Oishi and Lee 2002), which is too small to account for the CO_2 pulses we observed. More likely explanations for the moisture dependence of enhancement magnitude are discussed below. (1) Dormant microbial population should be larger on drier plots than on wetter plot, and when water addition relieved the desiccation stress, CO_2 pulses from the wasteful metabolism of reactivated microbes would be greater on drier plots than on wetter plots. (2) Microbial activity and enzyme movements were suppressed by water deficiency on drier plots between two sequential rain events, and therefore relatively more soil organic substrate would be left unconsumed as compared with wetter plots at the time of wetting. (3) There could be more N-rich dead microbial biomass on drier plots due to desiccation, which provides more readily available substrate for consumption by living microorganisms. (4) Upon wetting, microbes on drier plots may suffer greater water potential shock than those on wetter plots, which led to either more microbial lysis, or more release of cytoplasmic solutes by surviving microbes in order to reach a new water potential equilibrium. Kieft et al. (1987) did observe greater release of biomass carbon along with greater increase in water potential. We also found a strong linear correlation between flux enhancement and change in soil moisture content at GMF02 ($R^2 = 0.42$). Similarly, Orchard and Cook (1983) found a log-linear relationship between enhancement magnitude and change in water potential due to wetting. These explanations are not exclusive from one another. The observed relationship between enhancement magnitude and soil moisture is therefore very likely to owe to the moisture dependence of the sizes of both the reactivated microbial population and the substrate pool.

Change in soil moisture (moisture increment) due to wetting did affect flux

enhancement. The correlations were strong at GMF02 ($R^2 = 0.42$), but less so at HF04 and HF05, probably due to the higher soil moisture at Harvard Forest site. Note that this correlation was obtained by plotting measurements made at the 7 time steps of all experiments/field days. However, when we selected only the enhancement ratio at the end of 30-min rain simulation (F_{t3}/F_{t0}), which should correspond to the maximum moisture change, the relationship between flux enhancement and moisture increment was weak (except for HF05 with 12-mm rain intensity) (Fig. 2.10). Although enhancement ratio (F_{t3}/F_{t0}) at GMF02 showed significant difference in response to the two rain intensities, it showed no discernable relationship with pre-rain soil moisture or moisture increment (Figures 2.9, 2.10, 2.11, and 2.14). This seems to suggest that, either F_{t3}/F_{t0} was not a good measure of enhancement for a given experiment at GMF02, or there were other factors that undermined the effects of soil moisture. Overall, flux enhancement (F_{t3}/F_{t0}) was highest at GMF02 in the ensemble plot (Fig. 2.2), while soils at GMF02 held the lowest pre-rain soil moisture and moisture increment among the three site-seasons (Table 2.2) due to fast water loss through well-drained soils at the site. This may suggest that (1) with the driest soils and highest flux enhancement among the three site-seasons, GMF02 still followed the pattern that lower soil moisture corresponded to higher flux enhancement; (2) the effect of moisture increment is site-specific, depending on site moisture condition, soil characteristics and substrate availability, and thus higher moisture increment does not necessarily mean greater enhancement.

Many studies have observed greater rain-induced soil CO_2 release after longer rain-free period (Lee et al. 2002, Xu et al. 2004, and Jarvis et al. 2007). In a rain simulation experiment in an Arizona desert, Sponseller (2007) reported greater CO_2 loss with increasing

time between rain events, and concluded that rain-induced pulses were fueled by a resource pool that was replenished by accumulation of organic substrate from plant litter and dead microbial biomass, nutrient mineralization, and increase in microbial biomass during rain-free period. However, our results from the two New England forests showed no significant correlation between flux enhancement and rain event interval. Our experiment plots at any given site-season were not so distant from one another as to have different rain-free period. Despite the same rain event interval for the plots at a given site-season, soil moisture varied greatly. Soil moisture reflects the combined effects of precipitation amount and interval, evaporation, topography, throughfall, and soil properties. In our study, rain event interval alone was not sufficient to explain the spatial variation in flux enhancement, and pre-rain soil moisture content and increment appeared to be better indicators. Moisture-dependence was manifested differently at Great Mountain Forest and Harvard Forest due to differences in moisture regimes and soil properties.

2.4.5. Flux contribution of O horizon

Flux contribution of O horizon was quantified based on pre-rain CO_2 flux from plots with and without O horizon. Our results showed that at Harvard Forest, less than 30% of soil respiration came from O horizon, a fraction which is lower than numbers reported in other studies conducted at Harvard Forest. At a well-drained site at Harvard Forest, 63% of annual soil respiration came from O and A horizons, and 59% was derived from photosynthate carbon residing in the plant and soil for less than one year (including root respiration) (Gaudinski et al. 2000). In a decade-long trenched-plot experiment with root exclusion, Melillo et al. (2002) reported that microbial respiration contributed to 80% of annual soil

respiration at Harvard Forest. More specifically, Bowden et al. (1993) found that aboveground litter accounted for 37% of annual soil respiration, and belowground litter and live roots contributed 30% and 33% respectively. Davidson et al. (2006c) reported that based on mean annual sums, O horizon contributed to 40-48% of the total CO_2 efflux at Harvard Forest. However, comparison with these studies may not be valid due to difference in experiment methods. The purpose of our study was not to sharply distinguish between autotrophic and heterotrophic respiration, but rather to identify possible sources of CO_2 emission upon wetting. Plant roots were not excluded from the experiment plots, and therefore measured soil CO_2 flux included both microbial and fine root respiration. Assuming that flux from O horizon was dominated by microbial respiration, then the reason for such differences between our results and other studies' may be that, instead of calculating the annual flux contribution, our data was only obtained from the growing season when root respiration was most vigorous. The difference may also derive from variation in biotic and abotic factors among experiment sites.

Temporal variation in flux contribution of O horizon showed opposite relationship with soil moisture in the two forests (Fig. 2.15). At the drier GMF02, flux contribution of O horizon increased with soil moisture over the season. However, at HF04, flux contribution decreased with soil moisture. The opposite trends seem to suggest a potential soil moisture between 20% and 40% (vol) for an optimal flux contribution. Such relationship does exist between 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. At poorly-drained sites at Harvard Forest, such a turning point of soil moisture was 12% (vol) (Davidson et al., 1998). We could not identify any relationship

between soil respiration and moisture at GMF02 or HF04 from our data, however, it is not surprising that one fraction of soil respiration, i.e., contribution from O horizon in this case, should follow the general relationship between soil respiration and moisture. More study is needed to locate sites within such an "optimal soil moisture range", if such a range does exist. In addition, since O horizon is exposed to most changeable environmental conditions, respiration from O horizon is likely to be the most sensitive and responsive to change in soil moisture. For example, in a temperate mixed oak forest, the times of lower soil respiration coincided with times of lower leaf litter flux contribution (Cineros-Dozal et al. 2006).

There was a wide range of soil moisture across the plots at all three site-seasons. Spatial variation in O horizon flux contribution showed strong negative correlation with site moisture ($R^2 = 0.55$). In a Californian ponderosa pine plantation, 84% of spatial variation in soil surface CO_2 flux was explained by fine root biomass, microbial biomass and soil properties. While soil temperature and moisture together explained less than 34% of spatial variation, they could explain 76-95% of temporal variation (Xu and Qi 2001). In our case, after removing the effects of temperature and intrinsic plot variation, soil moisture could explain spatial variation in flux contribution very well. At GMF02, the temporal and spatial variations in O horizon flux contribution curiously showed opposite trends as a function of soil moisture (Fig. 2.15 and Fig. 2.16). It is likely that the temporal fluctuations of flux contribution are dominated by newer and more labile carbon which is more responsive to the changeable environmental factors (e.g., soil temperature and moisture), whereas spatial variation in flux contribution reflects the activities of both new and older carbon, which is determined by the long-term, combined effects of inherent site properties (e.g., site productivity, soil characteristics, precipitation, evaporation, topography and hydrology).

2.4.6. Strength and limitations of manipulative experiment

Predetermined duration and amount of rain, along with standardized measurement time steps allowed us to quantify and compare the effects of rain in situ under repeatable protocols and controlled conditions, which would otherwise be impossible in natural rain events. Due to limitation of resources and manpower, we were unable to perform rain simulation at multiple plots simultaneously. Rain simulation and subsequent measurements had to be carried out on different plots sequentially, and intraplot and interplot difference in soil temperature would inevitably confound the effect of soil moisture. Intraplot confounding effect from soil temperature was avoided by having short experiment time. With few exceptions, the temperature difference from the beginning to the end of the 2-hour experiment rarely exceeded 1°C. The use of enhancement ratio (F_{ti}/F_{t0}) to normalize flux enhancement further eliminated the interplot confounding effects of temperature, inherent site productivity as well as other environmental factors, and made the replicate plots true replicates, through which comparison could be possible and meaningful. 6 mm or 12 mm of rain within 30 minutes was valid rain intensity as a light-to-medium rain storm for our study sites, and was strong enough to produce detectable response, but not so to significantly impact the site conditions. The total water added during the experiment season from June to September was 102 mm at Harvard Forest in 2005, equivalent to 25% of the summer time precipitation, and 6.5% of annual precipitation that year. Water used for rain simulation was ground water, which had different chemical properties from natural rain water. However, it provided a reliable and free water source in the field to sustain our experiments.

Even with the knowledge from field manipulative experiments, the uncertainties of

rain pulses remain, and the absolute flux during natural rain events may not be effectively predicted, mainly because of variable site conditions, changeable/inconsistent rain intensity and duration, as well as accompanying meteorological factors such as stronger wind speed and lower temperature during rain. Soil respiration during and/or following rain events significantly deviates from its normal relationship with soil temperature, but the magnitude and duration of CO_2 pulses varied greatly among studies as well as ecosystems, and appear to be experiment-specific (Borken and Matzner 2009). Response patterns and magnitudes are often site specific. Despite the uncertainties, we could still make rough estimations of rain-induced soil carbon release based on our results. Therefore, manipulative field experiments like ours not only contribute to a better understanding of the processes involved and improve the knowledge about mechanisms behind rain-induced pulses, but also provide some quantitative information that can serve as base for model building.

2.5. CONCLUSIONS

Rain simulation experiments provided complementary information for eddy covariance measurements and laboratory incubation experiments. A systematic field experiment approach with consistent field operation, standardized protocols, and in-situ measurements has allowed quantification and comparison of rain-induced soil CO_2 pulses across landscape as well as over time. Despite differences in soil properties, site hydrology, topography, land use history and species composition, soil respiration in response to rain at the two New England mixed-hardwood forests could be compared under our research method. Analysis of the observed response patterns and magnitudes also provides insights into the processes, dynamics and driving forces of rain-induced CO_2 pulses.

Soil respiration showed rapid increase within 10 minutes of the onset of rain, and the absence or presence of forest floor organic horizon led to marked differences in the response pattern. While plots with intact O horizon consistently showed rain-induced CO_2 flux enhancement with similar enhancement ratios at the three site-seasons, plots without O horizon responded with limited or even negative enhancement. These results, combined with a consideration of laboratory results and related findings reported in the literature, lead us to nominate microbial activity from organic horizon as the main contributor to the observed flux enhancement upon rain.

Flux enhancement showed robust negative correlation with pre-rain baseline CO_2 flux and soil temperature at all three site-seasons. Rain intensity had clear effects on flux enhancement at GMF02 and HF05, and it is likely that if given more water or longer irrigation, enhancement ratio will increase. Overall, average flux enhancement (F_{t3}/F_{t0}) was highest at GMF02, while pre-rain soil moisture and moisture increment at GMF02 were the lowest among the three site-seasons due to fast water loss through the well-drained soils. However, pre-rain soil moisture and moisture increment could not explain variations in flux enhancement at GMF02. On the contrary, at HF04 and HF05, pre-rain soil moisture could account for both temporal and spatial variations in flux enhancement, and lower soil moisture corresponded to higher enhancement ratio. Such relationship between enhancement magnitude and soil moisture is likely to result from the moisture dependence of the sizes of reactivated microbial population and substrate pool.

Pre-rain soil moisture also determined flux contribution by O horizon. Spatial variation in flux contribution across the three site-seasons showed a strong negative correlation with pre-rain soil moisture. Temporal variation in flux contribution from O

horizon showed clear dependence on pre-rain soil moisture, although the correlation was positive for GMF02, and negative for HF04. The opposite trends seemed to suggest a potential optimal soil moisture for maximum O horizon flux contribution, analogous to an optimal moisture level corresponding to the maximum soil respiration as commonly seen in the respiration-moisture relationship.

Q_{10} values at HF04 and HF05 are higher than those at GMF02, and decreased with increasing soil moisture. Our results support the general observation that Q_{10} values are often affected by soil moisture conditions.

Based on our experiment results of baseline CO_2 flux and enhancement ratio, we estimated that growing season soil carbon loss during rain is 0.77, 1.15, and 0.80 t C ha^{-1} at GMF02, HF04, and HF05 respectively, although the value for HF04 may be overestimated due to the coarser observation intervals for the HF04 precipitation data.

Results from our study enhance knowledge about the response pattern and magnitude of rain-induced CO_2 pulses at the two New England forests. When combined with eddy covariance measurements and laboratory incubation data, the study may further contribute to better understanding of rain-induced CO_2 release from forest ecosystems, improved prediction power of ecological models, and more precise estimates of ecosystem carbon flow.

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Chapter 3

Short-Term Effects of Soil Respiration in Response to Wetting on Nebraska Croplands

ABSTRACT

Simulated wetting experiments were performed on two Nebraska soybean fields (conventionally named as site 2 and site 3) in the Agricultural Research and Development Center (ARDC), Univ. of Nebraska at Lincoln. 6 mm of water was added within 30 min. Pre-wetting baseline CO_2 flux over the season averaged 3.76 (± 1.64) and 4.43 (± 1.57) μmol m^{-2} s^{-1} at sites 2 and 3. Soil CO_2 flux increased immediately upon the onset of wetting, peaked with an enhancement ratio of 4.25 (± 1.93) and 3.79 (±1.55) at sites 2 and 3 during wetting. CO_2 flux started to decline as soon as irrigation ended, and returned to the pre-wetting level within 90 min. Greater wetting intensity could lead to greater enhancement. The response patterns were similar to our results from New England forest ecosystems using the same research method, but enhancement raio and the potential of carbon loss was greater on the soybean fields. Estimated soil carbon loss due to wetting with the center pivot irrigation system during the growing season of 2006 was 0.02 t C ha^{-1}. Bare plots showed slightly lower enhancement, but the duration of elevated soil CO_2 flux lasted much longer than plots with residues.

Baseline soil CO_2 flux was correlated with soil moisture at site 2, but more affected by soil temperature at site 3. Average Q_{10} was 1.2 and 2.1 at sites 2 and 3. Q_{10} values at site 2 increased with surface soil moisture (R^2 = 0.46).

Baseline soil CO_2 flux was a good indicator of temporal and spatial variations in flux enhancement. Soil temperature had little effect on variation in flux enhancement. Soil moisture increment due to wetting increased with pre-wetting soil moisture, and was negatively correlated with flux enhancement at both sites, which suggests that oxygen may be the major limiting factor for flux enhancement on the soybean sites. Pre-rain soil moisture

showed a negative correlation with temporal variation in enhancement at site 2, but showed positive correlations with spatial variation in initial enhancement at both sites. Our results shed lights in the complexities of moisture dependence of wetting-induced carbon pulses in agricultural ecosystems.

3.1. INTRODUCTION

Agricultural soils represent a potential carbon sink to mitigate atmospheric CO_2 increases. Cropland covers 12% of earth surface (Wood et al. 2000) and 20% of the United States' land area (Economic Service Center, USDA, 2002). Sperow et al. (2003) estimated that U.S. cropland soils have the potential to sequestrate 5% of 1999 total U.S. CO_2 emissions, if improved management practices were widely adopted, such as decreased tillage (Reicosky and Lindstorm 1993, West and Post 2002) and crop rotation (Cambell and Zentner 1997, Jenzen et al. 1998). Agricultural soils appear to be a small contributor of greenhouse emissions. Agriculture sector accounts for 13.5 % of global greenhouse emissions, among which 6.5% is from agricultural soils, and 5.1% from livestock and manure (World Resource Institute 2005). In the United States, agriculture sector represents 6.2% of total greenhouse emissions, 3.6% of which is from agricultural soils and 2.5% from livestock and manure (World resource Institute 2005). In the statistics, no CO_2 emissions are considered as directly contributed by agriculture sector. Nitrous oxide (N_2O) from agricultural soils and methane (CH_4) from livestock and manure are the only greenhouse emissions by agricultural sector. This is mainly based on the assumption that net ecosystem production (NEP) of cropland is above or equal to zero, meaning cropland is carbon sink or carbon neutral.

However, in a three-year study with eddy covariance measurements in Nebraska no-till cropland, it was found that after accounting for carbon removed by grain harvest and CO_2 released from irrigation water, two out of the three experiment fields were slight or moderate sources of carbon. Both carbon source sites were irrigated, and the carbon neutral site was fed by natural rain. While irrigation increased yield, additional soil moisture also enhanced ecosystem respiration, which offset increased gross primary production (GPP) (Verma et al.

2005).

This brings the carbon neutral assumption into question, and suggests the need for a careful examination of how soil carbon dynamics are altered by agricultural practices. Bursts of soil respiration following rainfall or irrigation have often been observed in cropland ecosystem (e.g., natural rain events: Birch 1958, Rochette et al. 1991; irrigation: Calderón and Jackson 2002; rain simulation experiments: Murphy et al. 1998, Burger et al. 2005, Steenwerth et al. 2005). On the other hand, temporary suppression of soil respiration can also occur on croplands due to reduced CO_2 diffusion upon wetting (Rochette et al. 1991, Bouma et al. 1997, Ball et al. 1999). Depending on the amount of carbon present and water available, elevated soil respiration could last for hours or days. Although the pulse-like CO_2 fluxes are often short-lived, they could be up to 10 times higher than the pre-wetting level (Calderón and Jackson 2002, Rochette et al. 1991, Millard et al 2008). From studies in other ecosystems, it appears that the more severe the drying, the greater soil CO_2 release on subsequent wetting (Xu et al. 2004, Rey et al. 2005, Sponseller 2007). If it turns out to be applicable to agricultural ecosystems, this pattern can be particularly pertinent for irrigated cropland soils, which are subject to frequent drying and wetting cycles. While irrigation is critical to increase yield and organic residues in croplands with water deficit, the ensuing loss of soil carbon to the atmosphere due to increased soil moisture may undermine the advantages from irrigation.

Therefore, a precise estimate of the loss accompanying the gain of carbon attributed to irrigation is crucial in determining the efficacy of mitigating atmospheric carbon increase and the accumulation rate of soil carbon stock. Carbon sequestration in cropland soils can be enhanced only by increased additions of crop residues and root organic matter, or reduced

decomposition. Despite all available technology and knowledge, carbon sequestration potential of croplands is not infinite and permanent (e.g., Bremer et al. 2008). It is suggested that, soil carbon stock in irrigated croplands will increase over time, and eventually may return to the level prior to its conversion for agriculture (Lal et al. 1998). Time required for such recovery may be 15 to 50 years (Lueking and Schepers 1985, Wu et al. 2008). In order to have a better understanding of ecosystem carbon budget and a more realistic prediction of time needed for croplands to reach a "carbon neutral" state, wetting-induced soil carbon losses have to be taken into account when constructing empirical models.

While the effects of practices such as crop rotation and reduced tillage intensity on soil carbon sequestration have been well studied (e.g., Havlin et al. 1990, Collins et al. 1992, Carter 1992, Franzluebbers et al. 1995), investigations on the impacts of irrigation/rain on soil carbon dynamics appears to be fewer. Most of the studies trying to quantify soil respiration have not targeted on respiration rates during and immediately following wetting; in-situ measurements of soil CO_2 often do not cover the periods during or immediately following wetting as a result of episodic sampling strategies, and difficulties of measuring in rain or during irrigation (e.g., Burger et al. 2005). Results from these studies may underestimate CO_2 released during and immediately following rain/irrigation, since rapid and drastic increase in CO_2 flux upon the onset of wetting has been reported (Lee et al. 2004). While soil respiration during wetting may be inferred from measurements of eddy covariance (Xu et al. 2004, Lee et al. 2004), it is rare that optimal meteorological and environmental conditions exist to allow and facilitate an accurate estimate of soil CO_2 emission. Besides, eddy covariance technique tends to malfunction during rainfall and requires data gap-filling, which has been performed under the assumption that response function established under fair

weather conditions is also applicable during rainy periods (e.g., Falge et al. 2001). Given that numerous studies in forest, grassland, as well as agricultural ecosystems have observed wetting-induced soil CO_2 pulses, the apparent inconsistency between model assumption and field observations has cast doubts on the accuracy of current estimates of soil respiration and NEP, and indicates a great need to understand the behavior and response dynamics of soil respiration during rain and irrigation.

This study aimed to explore the short-term response dynamics of soil respiration during and immediately following rain or irrigation. Manipulative rain/irrigation simulation experiments were carried out in soybean fields in eastern Nebraska, where soils are typically subject to the perturbation of large-scale irrigation and intensive thunderstorms in growing season. The fields were under no-till, corn-soybean rotating management system. In-situ CO_2 flux measurements were made with a portable CO_2 flux chamber during and immediately following simulated wetting. Response patterns and magnitudes were analyzed and compared with studies using similar methodology in forest ecosystems.

3.2. METHODS

The study site is located at the Agricultural Research and Development Center (ARDC), Univ. of Nebraska at Lincoln, Ithaca, Nebraska (41°09' N, 96°28' W), 32 miles from state capital Lincoln. Average high and low temperatures are 32°C and 19°C in July, and 0°C and -12°C in January. Annual precipitation is 619 mm. Soils here are deep silty clay loams. Soil series are Yutan, Tomek, Filbert, and Filmore. Our experiment plots were set up on three fields with different cropping systems and management:

Site 1: irrigated continuous maize (*Zea may*s L.), 48.7 ha, no till, no crop rotation. No

simulated wetting was performed on this site, but continuous soil CO_2 flux measurements were made with an automated system (see Appendix I, Fig. A1).

Site 2: irrigated maize-soybean (*Glycine max* [L.] Merr.) rotation, 52.4 ha, no till, crop of year 2006 was soybean.

Site 3: rain-fed maize-soybean rotation, 65.4 ha, no irrigation, no till, crop of year 2006 was soybean.

The three sites are within 1.6 km of each other. Since initiation in 2001 for a carbon sequestration project, they have been under no-till and best management practices for production scale maize systems. Before 2001, sites 1 and 2 had been under maize-soybean rotation system with no-till since 1998, whereas site 3 had a more various cropping history with tillage. Prior to initiation of the carbon project, all three sites were uniformly tilled by disking down to 10 cm to create a homogenous top layer and to incorporate the previous crop residue and P and N fertilizers (see Verma et al. 2005).

Simulated wetting was only performed on site 2 and site 3. Plots were set up with block design at dryland corner of site 2 (outside the range of the center-pivot irrigation system, i.e., received no irrigation water) and site 3. Therefore, both sites were not affected by irrigation and could be considered rain-fed systems. Each site had three blocks, and each block consisted of three plots: control plot (A_0), plot treated with irrigation and intact corn residues from the previous year (A), and plot treated with irrigation with corn residues removed (a). At each site, a total of nine 1m x 0.5m rectangular plots were set up on the interrows where no living plants were present aboveground. A map of the Agricultural Research and Development Center including our study sites and the experimental plot set-up are shown in Figure 3.1.

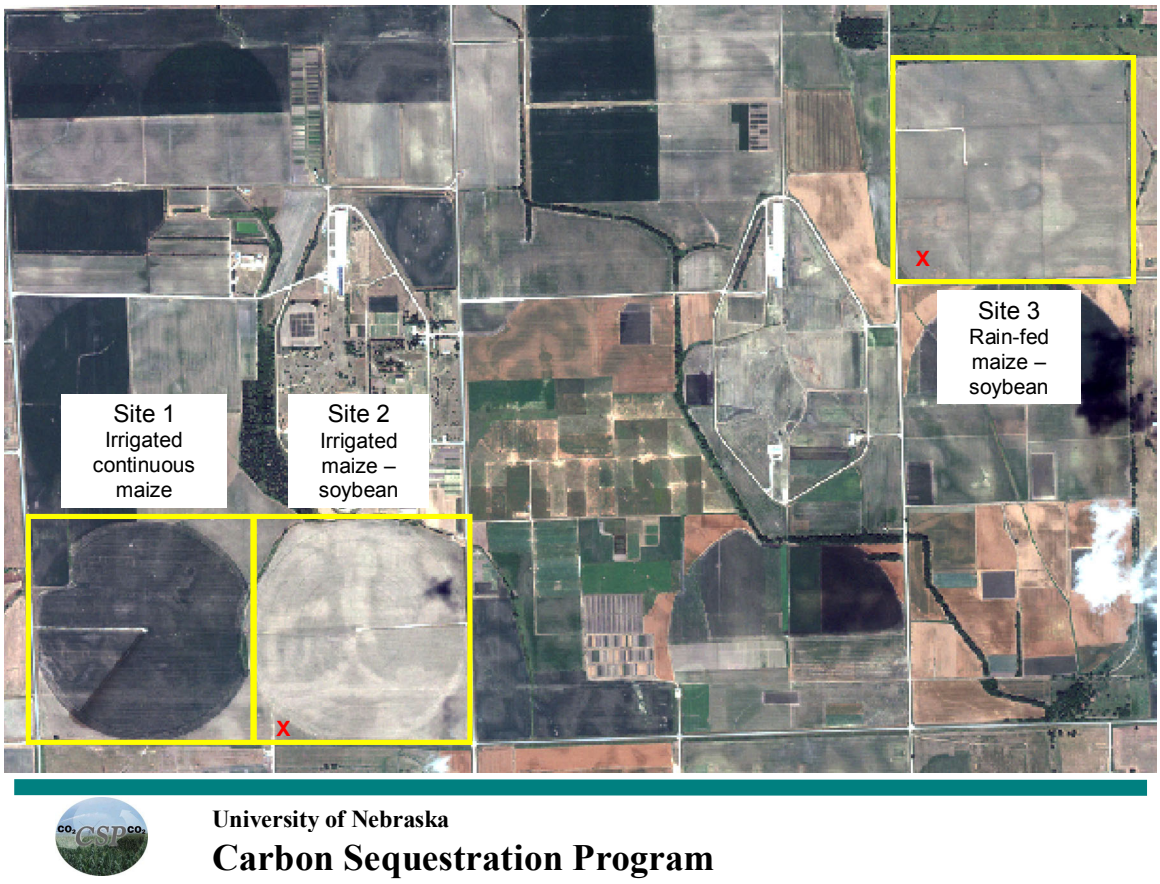

Figure 3.1. Map of the Agricultural Research and Development Center (ARDC), Univ. of Nebraska at Lincoln, Ithaca, Nebraska (41°09' N, 96°28' W), and experimental plot set-up. The red crosses at sites 2 and 3 indicate our experiment locations.

Rain simulation was carried out on the two soybean sites every one to three weeks during the growing season from June to September in 2006. 6 mm of water was evenly distributed on the treatment plots with a hand-held sprayer for 30 minutes. Water used wasground water obtained near the field of site 2. Soil CO_2 flux, temperature, and moisture content were measured right before, and at set time steps during and after rain simulation. Total observation time was 6 hours, and 9 measurements were made at 0, 10, 20, 30, 45 min, and 1, 2, 4, 6 hour into wetting. Instruments used were a portable photosynthesis system (LI-6400, Li-Cor, Inc.) coupled to a soil CO_2 flux chamber (Model 6400-09, Li-Cor, Inc.) and a soil temperature probe, and a portable soil moisture probe (PR1/4, Dynamax, Inc.) A week prior to the commencement of our experiment, PVC collars for measuring soil CO_2 flux were inserted around 2 cm into the soil. Plastic access tubes for soil moisture probe were also inserted into the soil, positioned to measure soil moisture at 5, 15, 25, and 35 cm depths. The inserted parts were left to be stabilized in the field for one week. No access tube for soil moisture probe was inserted into bare plots, so soil moisture of bare plots were not available.

3.3. RESULTS

3.3.1. Immediate response of CO_2 pulses

Pre-wetting baseline CO_2 flux over the season averaged 3.76 (± 1.64) μmol m^{-2} s^{-1} at site 2 (n = 8), and 4.43 (± 1.57) μmol m^{-2} s^{-1} at site 3 (n = 6). Soil CO_2 flux increased right away upon the onset of wetting, started to decline after the 30-min irrigation ended, and returned to the pre-wetting level within 90 min after irrigation stopped. Figure 3.2 shows CO_2 flux over the 6-hour experiment time at site 2 on a typical field day. Soil respiration on

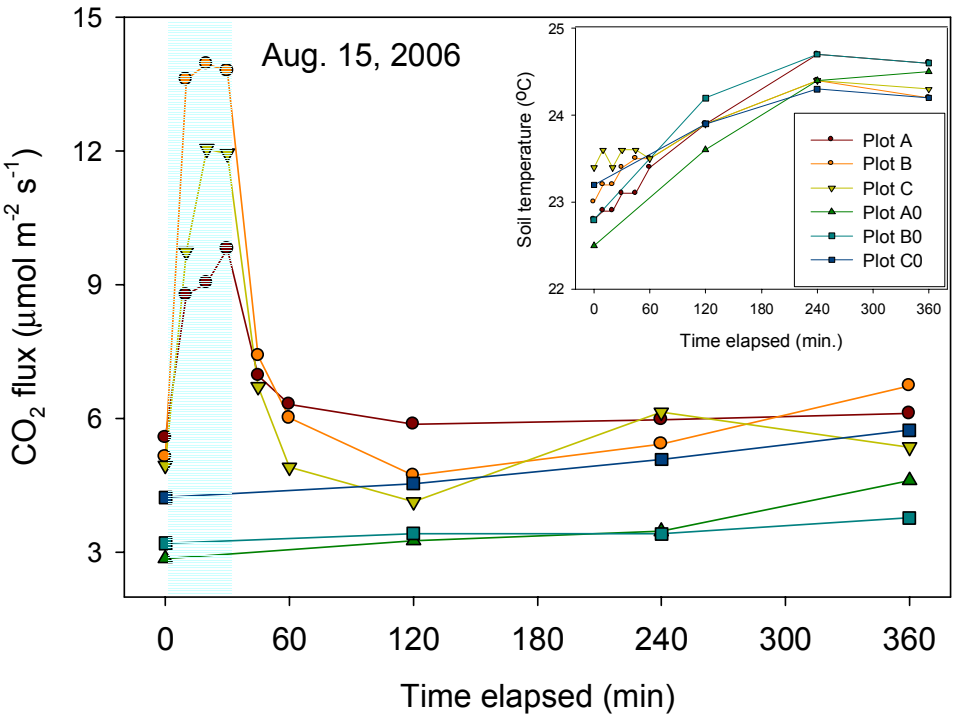

Figure 3.2. Soil CO_2 flux and temperature over the 6-hour experiment time at soybean field site 2 on Aug. 15th, 2006. The blue area represents the 30-min period of simulated wetting. A total of 6 mm of water was added in 30 min. Replicate plots A, B, and C were treated with wetting; control plots A0, B0, and C0 were not.

the treatment plots was enhanced by irrigation immediately, as opposed to that on the control plots, which followed the regular function of soil temperature. To avoid the confounding effects of variation in soil temperature, moisture and inherent plot variability, CO_2 flux measured at different time steps since the commencement of irrigation (F_{ti}) is normalized by dividing by the pre-rain baseline flux (F_{t0}). The ratio obtained by the normalization is flux enhancement ratio (F_{ti}/F_{t0}). Enhancement ratio is greater than 1 when flux enhancement occurs. Site 2 and site 3 showed similar response patterns to wetting, with the average maximum enhancement ratios of 4.25 (± 1.93) and 3.79 (± 1.55) respectively. At site 2, the enhancement ratio peaked at 20 min into wetting, whereas at site 3, it occurred right after the 30 min irrigation (Fig. 3.3). Over the season, the highest enhancement ratio immediately following the 30-min wetting was 6.49 at site 2 and 6.09 at site 3, both occurred in early growing season (June).

Simulated wetting was also performed on bare plots – plots where aboveground residues were removed, but only twice at site 2 and once at site 3 due to limited time and manpower. Soil moisture was not measured on bare plots. Simulated wetting on bare plots in early growing season (late June) resulted in enhancement ratios of 3.23 at site 2 and 3.37 at site 3. The flux enhancement on bare plots was only slightly lower than that on plots with intact residues, but the enhancement duration lasted much longer (Fig. 3.4). At site 2, 3.5 hours after rain stopped, average enhancement ratio was 2.11; at site 3, 5.5 hours after rain stopped, average enhancement ratio was 1.56. Even 24 hours after irrigation stopped, CO_2 flux remained elevated, as compared to the rather unchanged flux on the control plots during the same time period (data not shown). However, the other simulated wetting on bare plots at site 2 at the end of the growing season (mid September) presented very different results.

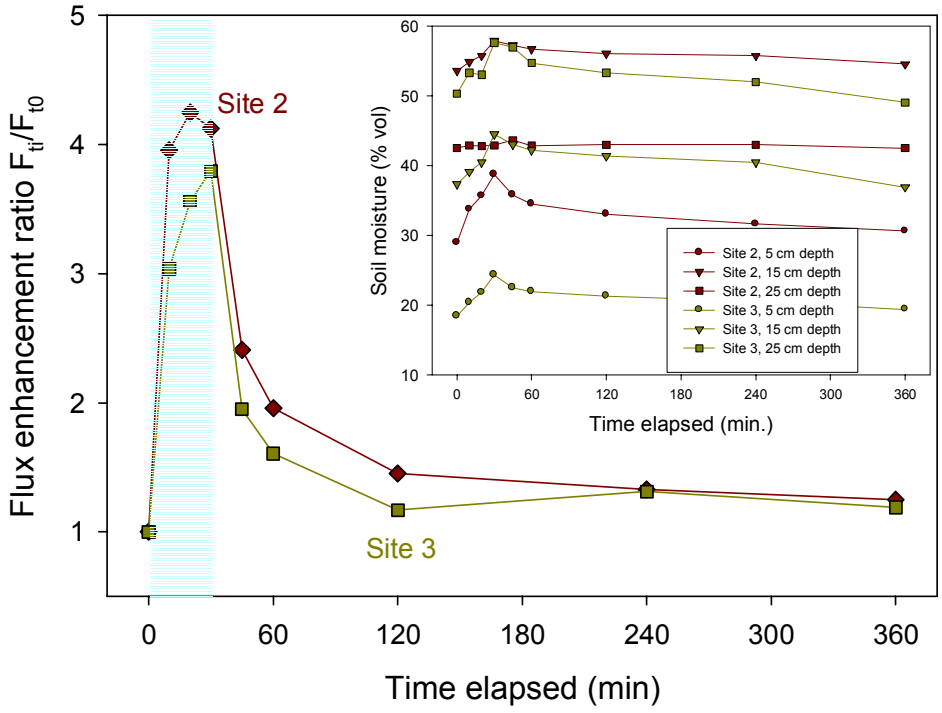

Figure 3.3. Average flux enhancement during and following 30-min wetting at soybean fields site 2 and site 3. Enhancement ratio was calculated as CO_2 flux measured at different time steps divided by the pre-wetting baseline flux. The blue area represents the 30-min simulated wetting, and the total water addition was 6 mm. The data points are the average enhancement ratios of three replicate plots at each site.

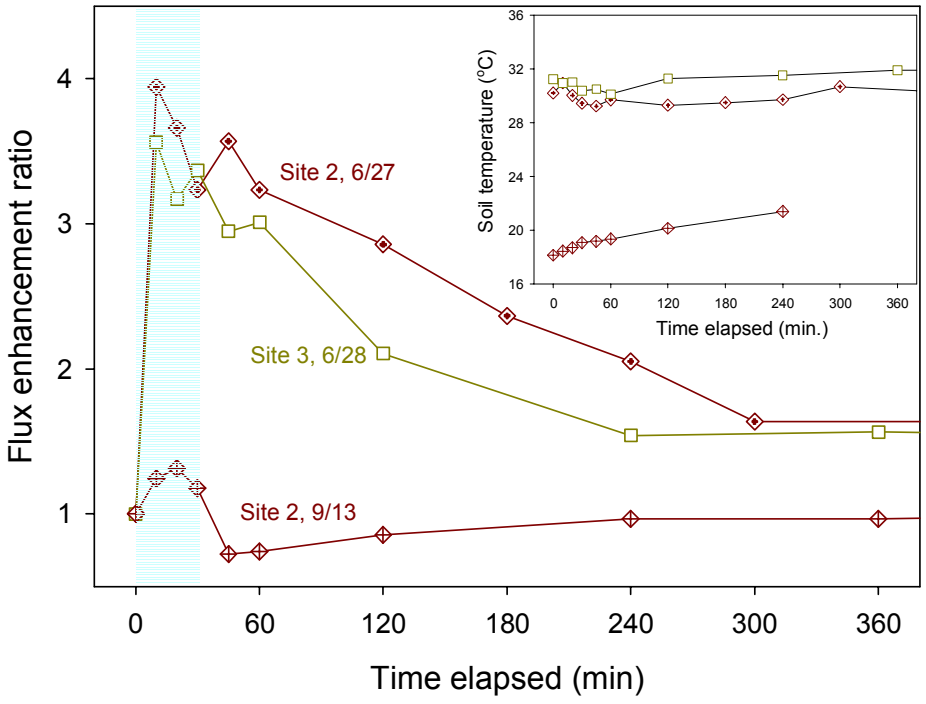

Figure 3.4. **Bare plot** flux enhancement during and following 30-min wetting at soybean site 2 on June 27 and September 13, and at site 3 on June 28. A total of 6 mm of water was added in 30 min. Enhancement ratio was calculated as CO_2 flux measured at different time steps divided by the pre-wetting baseline flux. The blue area represents the 30-min simulated wetting. The data points are the average enhancement ratios of three replicate plots at each site.

Soil temperature was lower than 20°C and soil was still moist from over 7.6 mm of rain three days before. Average flux enhancement at the end of the 30-min wetting was only 1.18, and continued to decrease even after irrigation ended. Flux enhancement started to increase 15 min after rain ended, and recovered to its pre-wetting level at the end of the 6-hour experiment (Fig. 3.4).

In addition to the regular 6-mm irrigations, pilot experiments with 18 mm of water addition within 30 min were carried out on site 2 in mid June. One-time wetting experiment was carried out on two plots with residues and two bare plots. These plots are not our regular experiment plots, and were treated with irrigation for only once. Figure 3.5 shows the measured flux values during wetting on the two plots with residues. Compared with the values from 6-mm wetting (Fig. 3.2), greater rain intensity did trigger greater CO_2 flux: enhancement ratios on the two plots are 18.29 and 9.64. On one of the bare plots, larger amount of water addition did not necessarily increase enhancement magnitude, but did produce delayed enhancement (Fig. 3.6). Compared with the 6-mm wetting experiment on bare plot at site 2 in late June, soil temperature during this pilot experiment was ~3°C higher. Enhancement peaked with a ratio of 3.52 within 10 min, but then started to decline. 30 min after irrigation ended, CO_2 flux was below its pre-wetting level and remained so for an hour. Enhancement only resumed 90 min after irrigation ended with a ratio of 2.50, and reached 3.0 in the following hour. The temporary suppression of soil respiration after wetting on agricultural fields due to decreased gas diffusivity has been widely reported (e.g., Rochette et al. 1991, Bouma et al. 1997, Ball et al. 1999), though the brief initial pulses are most often missed. On the other bare plot, greater wetting intensity did increase enhancement magnitude: CO_2 flux peaked with an enhancement ratio of 10.6 at 10 min into wetting, but

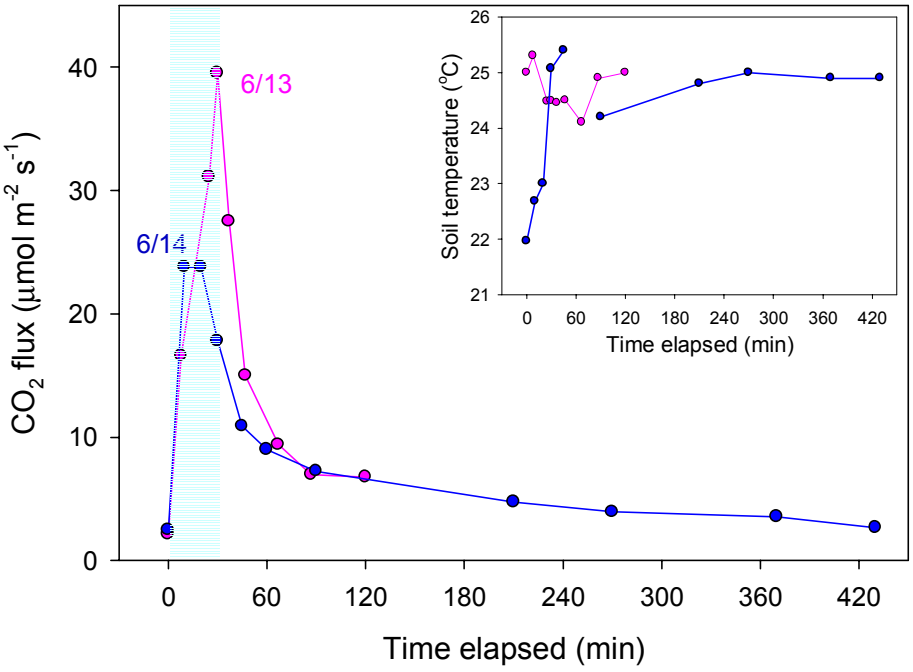

Figure 3.5. Soil CO_2 flux from 18-mm wetting on two randomly chosen plots with intact residues on site 2 (not our regular experiment plots). The first experiment was carried out on June 13, and the second one was carried out on June 14 on a different plot. The blue area represents the 30-min simulated wetting, and 18 mm of water was added within 30 min. The data points are the measured flux values of the one-time experiment on each plot.

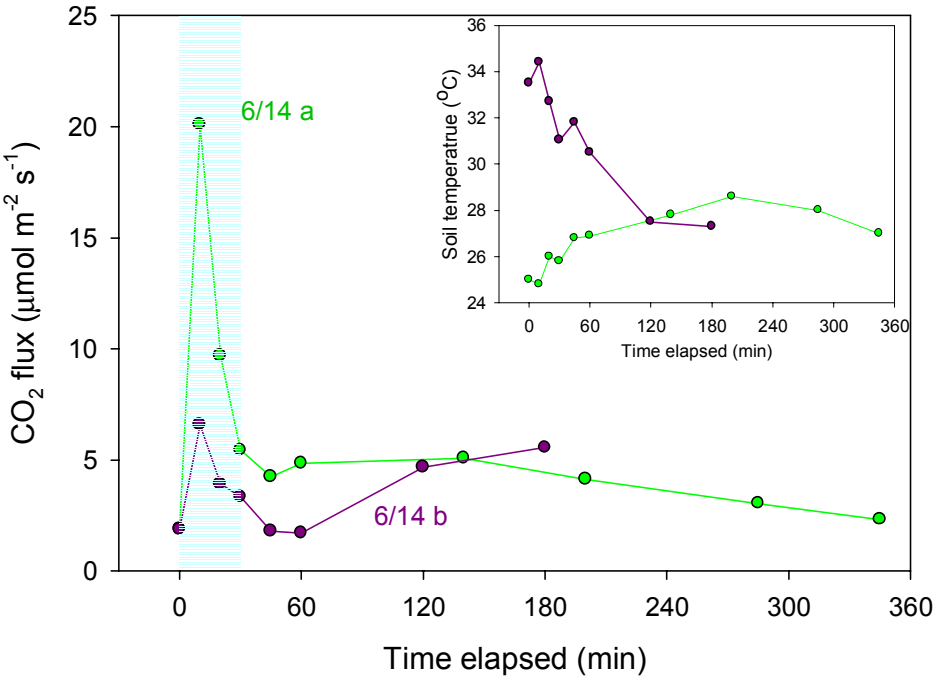

Figure 3.6. Soil CO_2 flux from 18-mm wetting on two randomly chosen **bare** plots on site 2 (not our regular experiment plots). Two experiments were carried out on two different plots on June 14. The blue area represents the 30-min simulated wetting, and 18 mm of water was added within 30 min. The data points are the measured flux values of the one-time experiment on each plot.

then started to decline to an enhancement ratio of 2.87 at the end of the wetting (Fig. 3.6). The results from these pilot experiments do not represent a general response pattern to 18-mm wetting, because there were no real replicates and experiment was not repeated. However, they provided some idea about the potential effect of greater wetting intensity.

3.3.2. Variations in baseline CO_2 flux at the two sites

Baseline CO_2 flux was higher at site 3 than site 2, which may be due to higher soil temperature (23.4°C at site 3, n = 6, versus 22.9°C at site 2, n = 8), or/and higher organic matter content at site 3. Total soil organic carbon to a 30 cm depth was 6.3 and 6.4 kg C m^{-2} at sites 2 and 3 respectively (Verma et al. 2005), though the value for site 2 was obtained from the irrigated area and our plots at site 2 were placed on an area beyond the radius of the center-pivot irrigation system.

Variation in soil CO_2 flux depended on site-specific factors. At site 2, soil moisture was the dominant factor, whereas at site 3, soil temperature seemed to play a more important role. Soil moisture of upper layers was higher at site 2 than site 3, as shown in the soil moisture profile (Fig. 3.7). Soil temperature, pre-wetting soil CO_2 flux, flux enhancement, and pre-wetting soil moisture over the season at the two sites are shown in Fig. 3.8 a and Fig. 3.8 b. Fluctuations in CO_2 flux loosely followed the seasonal pattern of soil temperature at site 3 ($R^2 = 0.58$), but barely showed such a trend at site 2 (Fig. 3.9). Temperature sensitivity of soil respiration was also higher at site 3, with average Q_{10} values of 2.1 at site 3, and 1.2 at site 2. While soil respiration at site 2 did not show much temperature dependence and sensitivity, it was more affected by change in soil moisture. At site 2, both CO_2 flux and Q_{10} values increased with soil moisture (Figures 3.10 and 3.11). A larger sample size would be

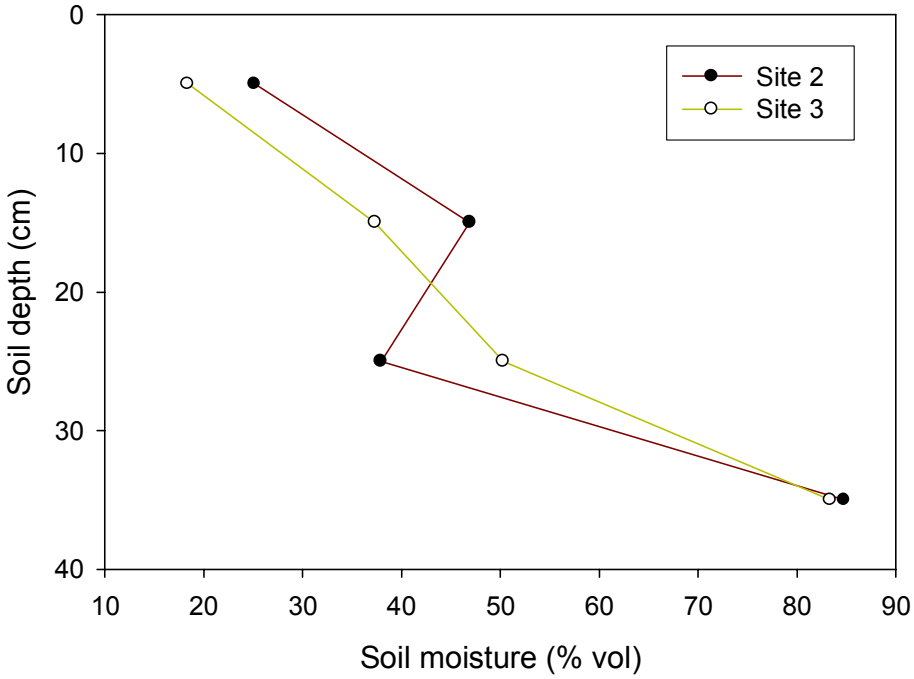

Figure 3.7. Soil moisture profile at soybean fields site 2 and site 3. The data points are the seasonal mean of replicate plots.

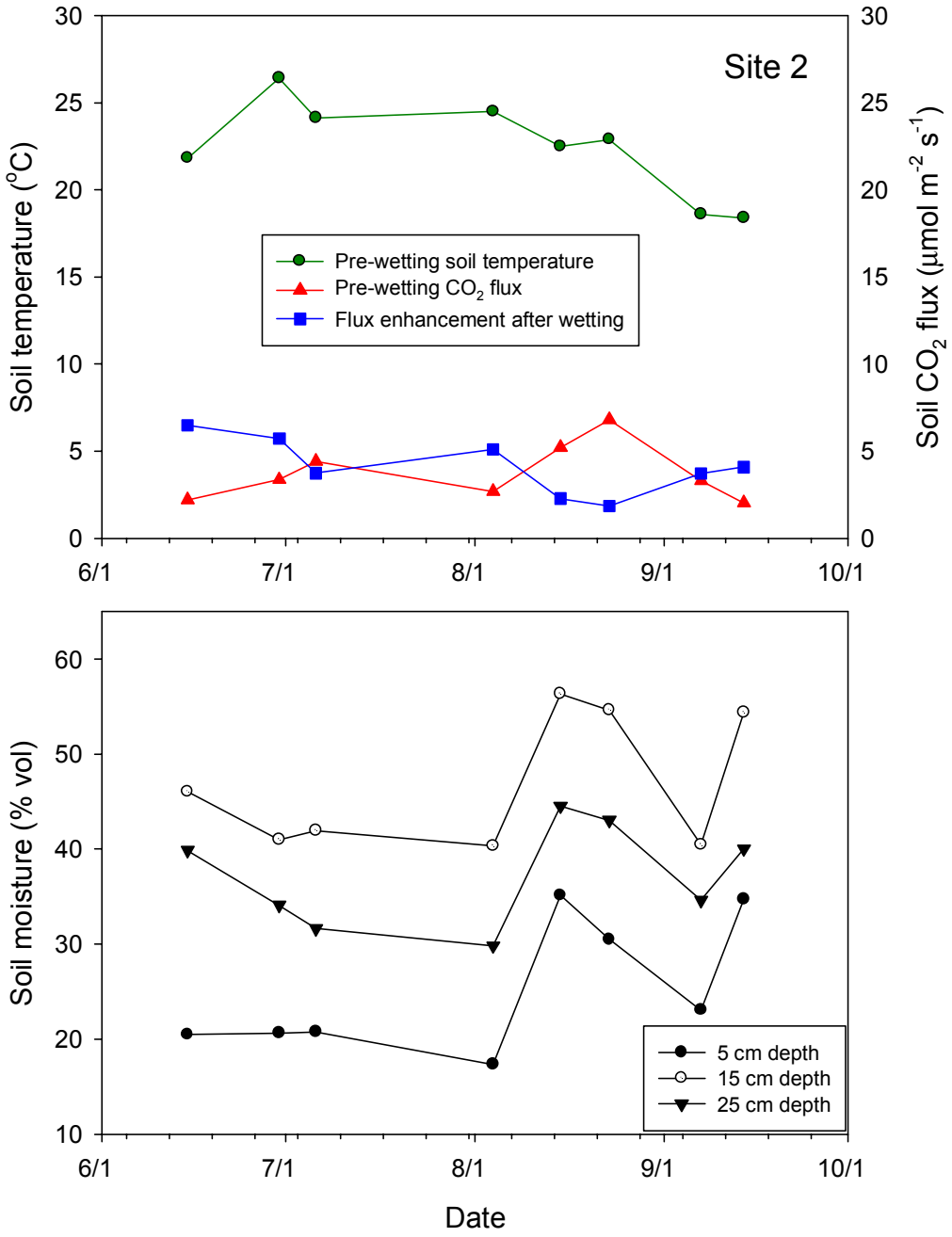

Figure 3.8 a. Pre-wetting soil temperature, soil CO_2 flux, flux enhancement immediately after 30-min wetting, and pre-wetting soil moisture over the season at site 2. The data points are the average values of replicate plots on each field day.

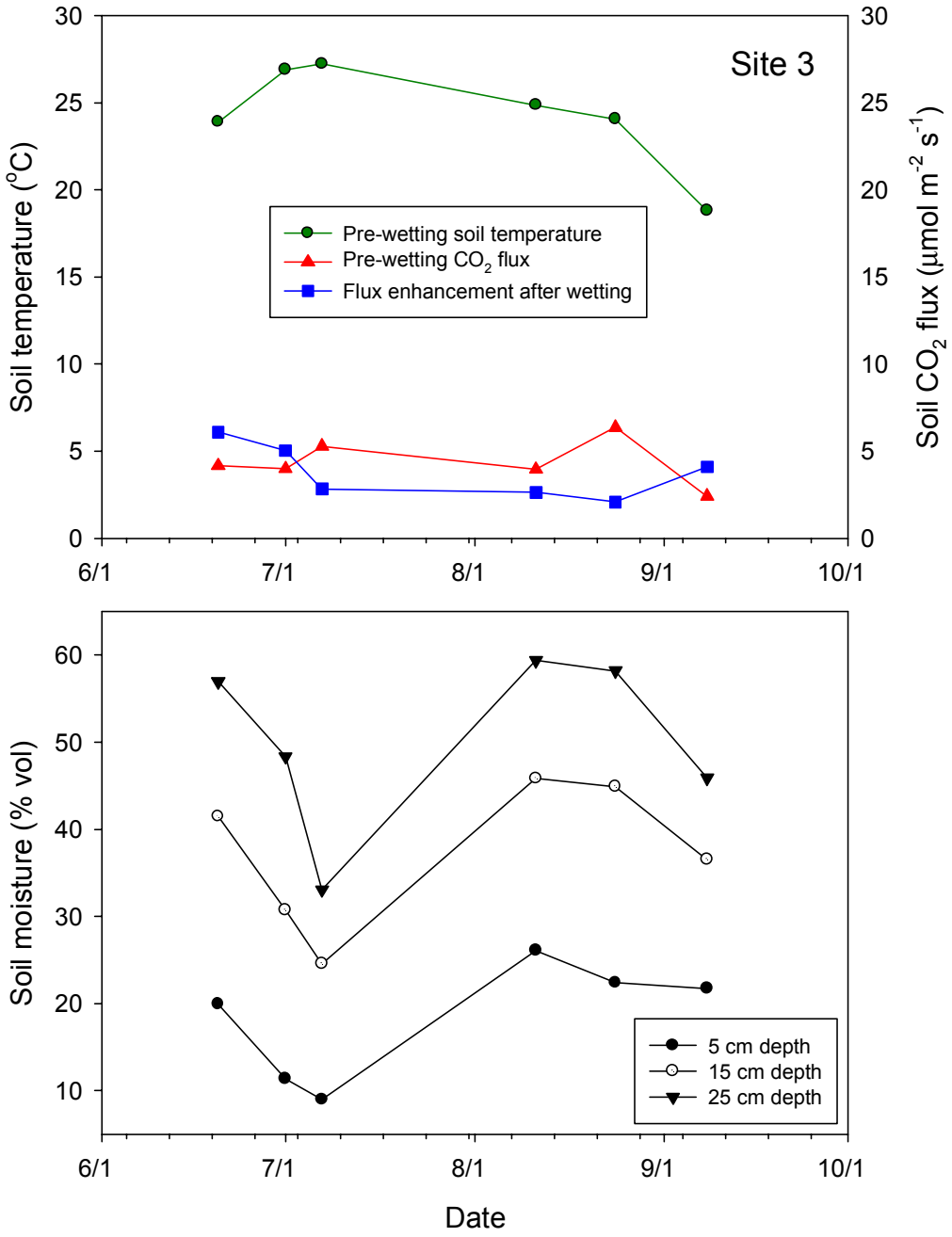

Figure 3.8 b. Pre-wetting soil temperature, soil CO_2 flux, flux enhancement immediately after 30-min wetting, and pre-wetting soil moisture over the season at site 3. The data points are the average values of replicate plots on each field day.

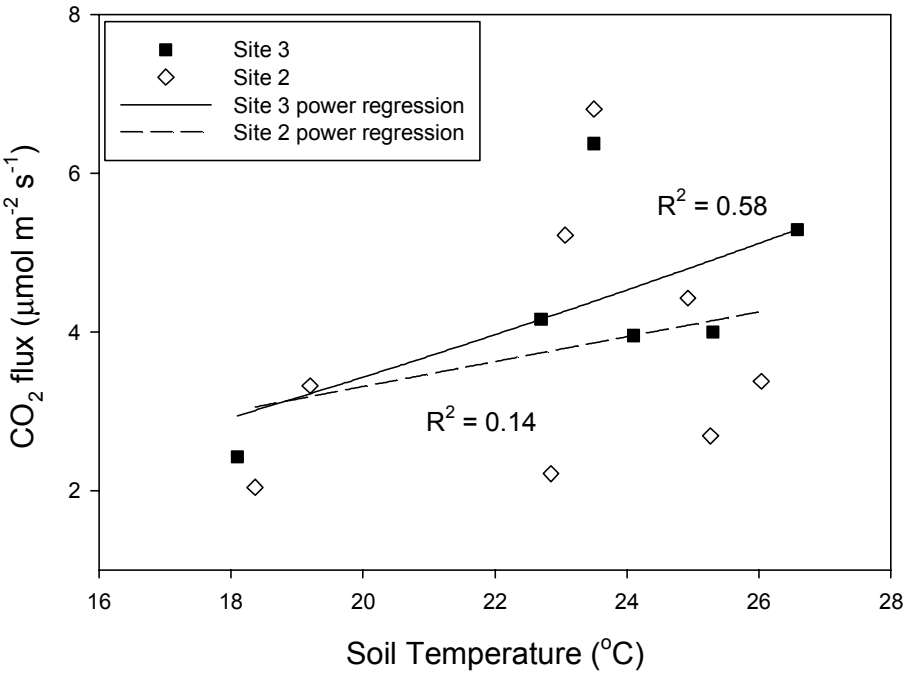

Figure 3.9. Pre-wetting baseline CO_2 flux and soil temperature over the season. Power regressions at site 2 ($y = 0.0766x^{1.2212}$, $R^2 = 0.14$, n = 8) and site 3 ($y = 0.0121x^{1.8591}$, $R^2 = 0.58$, n = 6). The data points are the average of replicate plots on each field day.

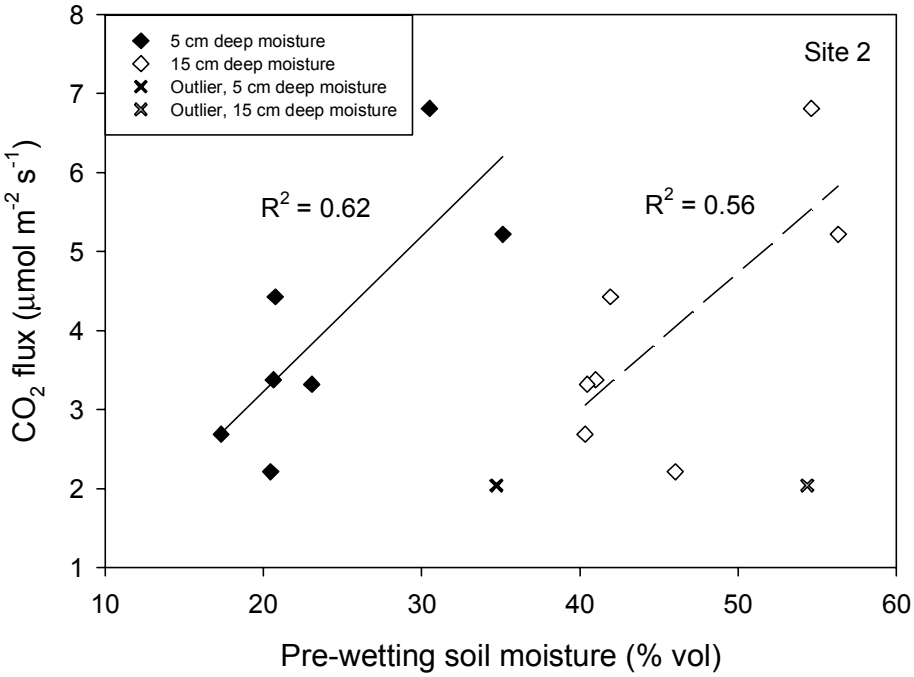

Figure 3.10. CO_2 flux vs. pre-wetting soil moisture at site 2. The trend lines are linear regressions of pre-wetting CO_2 flux and soil moisture at 5 and 15 cm depths ($y = 0.19x - 0.53$, $R^2 = 0.62$, $n = 7$; $y = 0.17x - 3.98$, $R^2 = 0.56$, $n = 7$). The data points are the average pre-wetting flux of replicate plots on each field day. The data of one outlier were removed to achieve better fit for the regression. The outlier was from a day in September with low temperature and high soil moisture following a heavy rain event 3 days before.

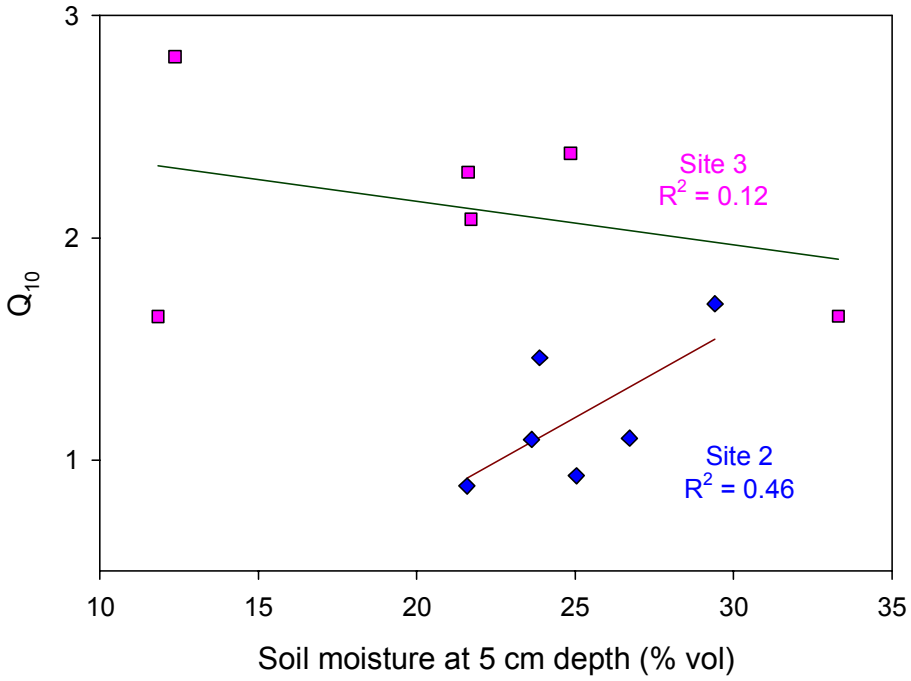

Figure 3.11. Q_{10} values vs. pre-rain soil moisture at 5 cm depth. The data points of each site consist of three control plots and three treatment plots with intact residues. Each data points Blue diamond denotes plots of site 2, and pink square denotes plots of site 3.

necessary to clarify whether the differences between site 2 and site 3 was genuine, and to identify the likely causes of such differences.

3.3.3. Comparison between soybean fields and New England forests

The field methods and experiment protocol of this study were also used by our simulated wetting experiments at two New England forest sites. With the same methods of site preparation and irrigation, and identical wetting intensity, observation intervals and instruments, the results from the forest sites and the soybean fields could be compared quantitatively, and provide some insights on the difference of wetting effects in different ecosystems. As far as we know, no other studies have employed experiment methods similar enough to ours for effective quantitative comparison.

Table 3.1 lists the baseline soil CO_2 flux, soil temperature, and pre-wetting soil moisture of plots with residues/O horizon at the two soybean fields and the three forest site-seasons (Great Mountain Forest in 2002, Harvard Forest in 2004 and 2005). Compared with the results from the New England forest sites, wetting-induced flux enhancement on soybean fields appeared to be more drastic. While baseline CO_2 flux at the soybean sites was generally lower than that at the forest sites, it increased up to much higher levels upon wetting (Fig. 3.12). Accordingly, at the end of 30-min wetting, average enhancement ratio at the soybean fields was 4.0, almost 3 times greater than that of the New England forest sites (averaged 1.47) (Fig. 3.13). The higher enhancement ratio suggests a greater potential of soil carbon loss from these fields during wetting.

The response pattern on bare plots at the soybean sites was also very different from that at the New England forest sites. Wetting-induced flux on bare plots was much greater at

Table 3.1. Average soil temperature and moisture at 5, 15, and 25 cm depths at soybean sites 2 and 3, and at Great Mountain Forest in 2002, Harvard Forest in 2004 and 2005. The New England forest sites are indicated as GMF02, HF04, and HF05 respectively.

	Soybean Site 2	**Soybean Site 3**	**GMF02**	**HF04**	**HF05**
Pre-wetting CO_2 flux ($\mu mol\ m^{-2}\ s^{-1}$)	3.8	4.4	4.3	5.0	6.3
Soil temperature (^oC)	22.9	23.4	13.8	13.0	15.0
Soil moisture (% vol)					
θ_{5cm}	25.1	18.4	11.6	30.1	33.3
θ_{15cm}	46.9	37.3	14.0	44.3	47.2
θ_{25cm}	38.0	50.3	26.4	61.7	59.5

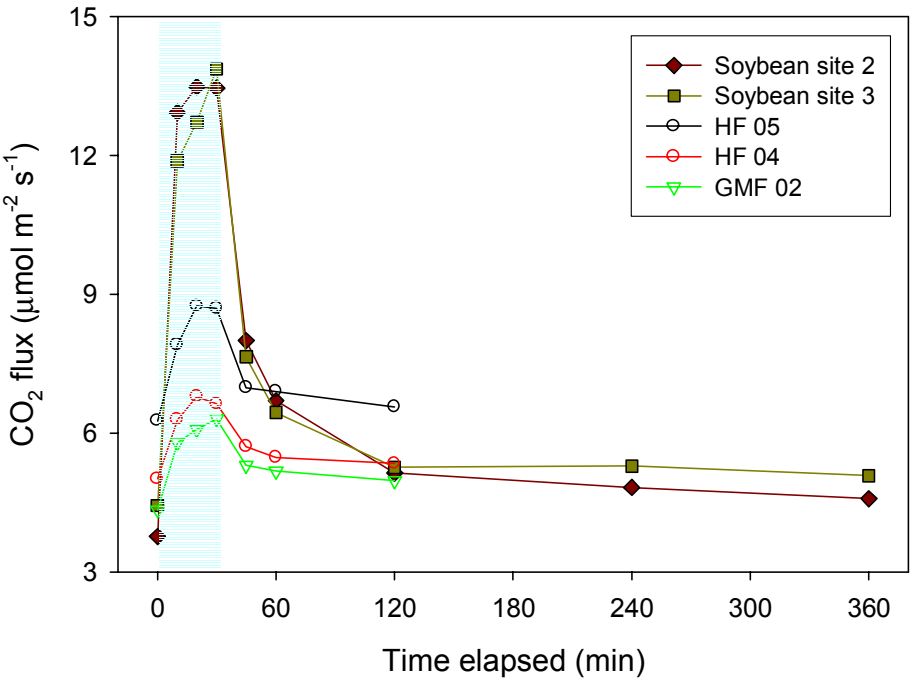

Figure 3.12. Average CO_2 flux over the observation time of simulated wetting at the two soybean fields (NE) in 2006, and at Harvard Forest (MA) in 2005 (HF05), Harvard Forest (MA) in 2004, and Great Mountain Forest (CT) in 2002. The New England forest sites are indicated as HF05, HF04, and GMF02 respectively. Blue area represents the 30-min simulated wetting. The data points are the average flux of replicate plots over the growing season.

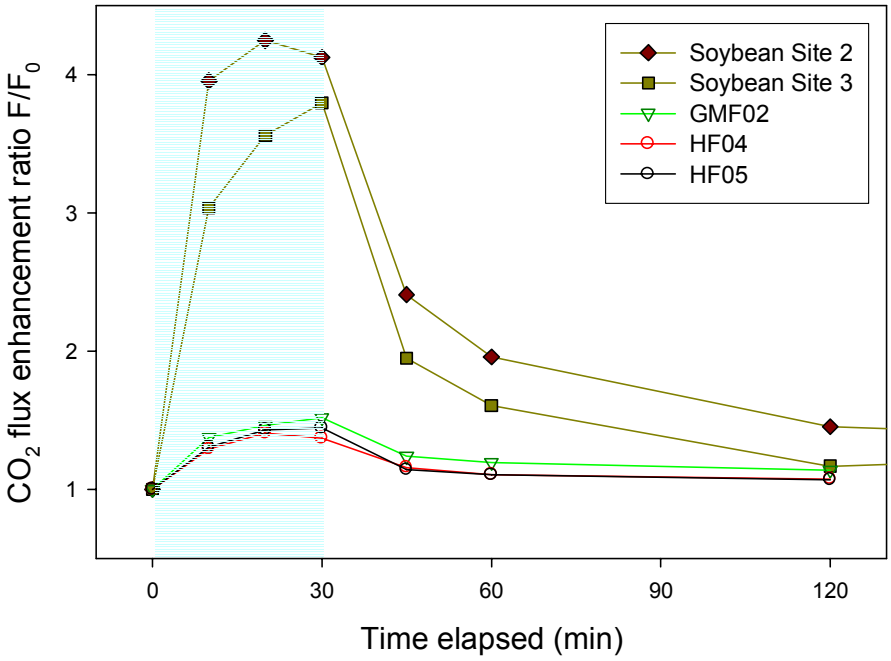

Figure 3.13. Average CO_2 flux enhancement ratio on plots with intact residues or O horizon in response to simulated wetting at soybean site 2 and site 3 (NE) in 2006, Great Mountain Forest (CT) in 2002, and Harvard Forest (MA) in 2004 and 2005. The New England forest sites are indicated as GMF02, HF04 and HF05 respectively. Blue area represents the 30-min simulated wetting. The data points are the average enhancement ratio of replicate plots over the season.

the soybean fields than that at the forest sites, where there was usually limited or no enhancement. Additionally, the extended enhancement duration after flux peaked at the soybean sites was not observed at the forest sites (Fig. 3.14).

3.3.4. Variations in flux enhancement

3.3.4.1. Temporal variations

Flux enhancement at the soybean sites was clearly dependent on pre-wetting flux and soil moisture, but only weakly on soil temperature. Temporal variation in flux enhancement could be explained by pre-wetting baseline CO_2 flux: the lower pre-wetting CO_2 flux there was, the higher enhancement. This relationship was stronger at site 2 than site 3 (Fig. 3.15). Pre-wetting CO_2 flux can be seen as an approximate of soil organic matter content, temperature, and moisture. Since pre-wetting CO_2 flux was dependent on soil moisture at site 2, temporal variation in flux enhancement was also negatively correlated to soil moisture at 5 and 15 cm depths, and the relationship was strongest immediately following 30 min of irrigation (Fig. 3.16 a). But a different trend was observed at site 3. When plotting enhancement upon 10 and 30 min into wetting (F_{t1}/F_{t0} and F_{t3}/F_{t0}) against surface soil moisture (5 cm depth), it appeared that flux enhancement was increasing with surface soil moisture until moisture content was greater than 20% (vol) (Fig. 3.16 b).

Soil moisture increment was averaged 8.54% (vol) at site 2, which was higher than the values at the New England forest sites, and 5.9% (vol) at site 3. On both soybean sites, flux enhancement (F_{t3}/F_{t0}) was negatively correlated with moisture increment of surface layer after 30 min of wetting (Fig. 3.17). This was different from the result from Great Mountain Forest, where flux enhancement increased with moisture increment. Our results suggest that

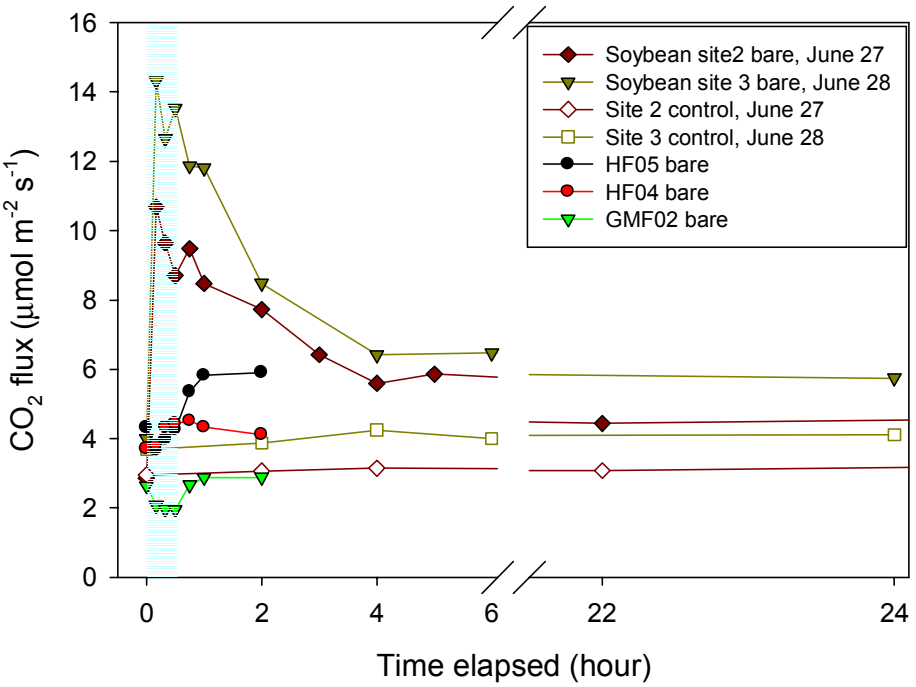

Figure 3.14. CO_2 flux in response to simulated wetting on **bare plots**. Presented here are data from soybean site 2 (on June 27, 2006), soybean site 3 (on June 28, 2006), Great Mountain Forest (CT) in 2002 (GMF02), and Harvard Forest (MA) in 2004 and 2005 (HF04 and HF05). Blue area represents the 30-min simulated wetting. The data points are the average flux of replicate plots. Because of the extended duration of elevated CO_2 flux, observation time for the bare plots on soybean sites was longer as compared to the regular treatment plots with intact residues. Accordingly, observation time was 28 hours at site 2 and 24 hours at site 3.

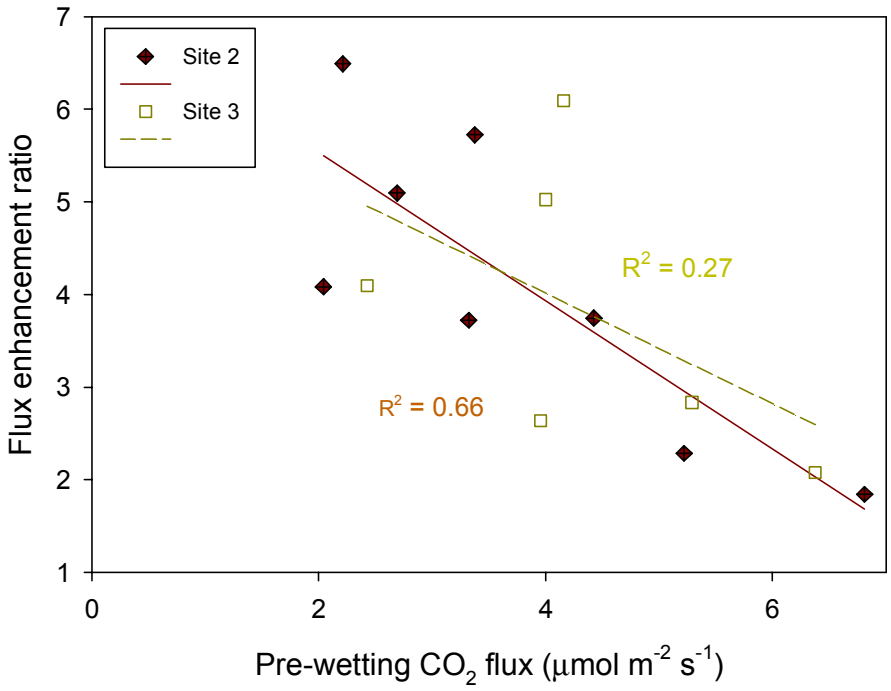

Figure 3.15. Flux enhancement vs. pre-wetting baseline CO_2 flux. Regression at site 2 was stronger than site 3 ($y = -0.80x + 7.13$, $R^2 = 0.66$, $n = 8$; $y = -0.60x + 6.40$, $R^2 = 0.27$, $n = 6$). The data points are the average enhancement of replicate plots following the 30-min irrigation (F_{t3}/F_{t0}) of each field day.

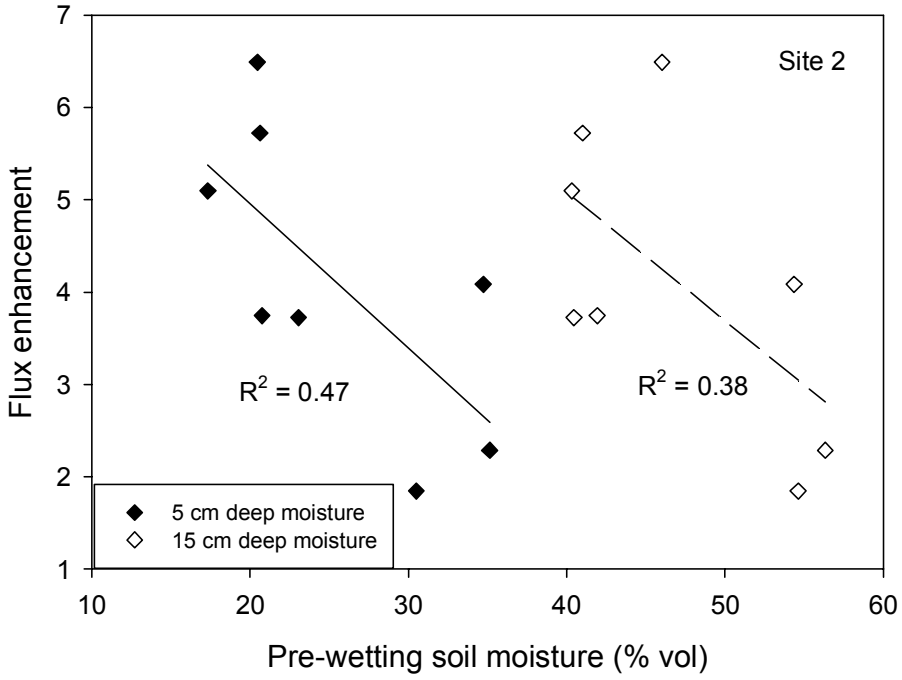

Figure 3.16 a. Flux enhancement vs. pre-wetting soil moisture at site 2. Temporal variation in flux enhancement showed dependence on soil moisture at 5 cm depth ($y = -0.16x + 8.06$, $R^2 = 0.49$, $n = 8$) and 15 cm depth ($y = -0.14x + 10.66$, $R^2 = 0.37$, $n = 8$). The data points are the average enhancement of replicate plots following the 30-min irrigation (F_{t3}/F_{t0}) of each field day.

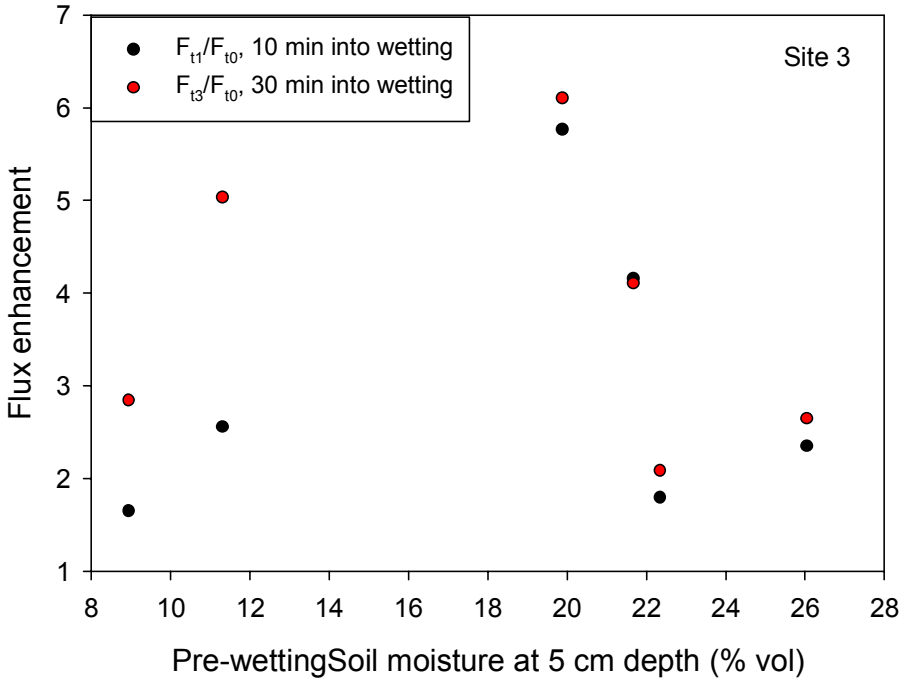

Figure 3.16 b. Flux enhancement vs. pre-wetting soil moisture at site 3. The data points are the average enhancement of replicate plots immediately following 10 and 30 min of wetting (F_{t1}/F_{t0} and F_{t3}/F_{t0}) of each field day.

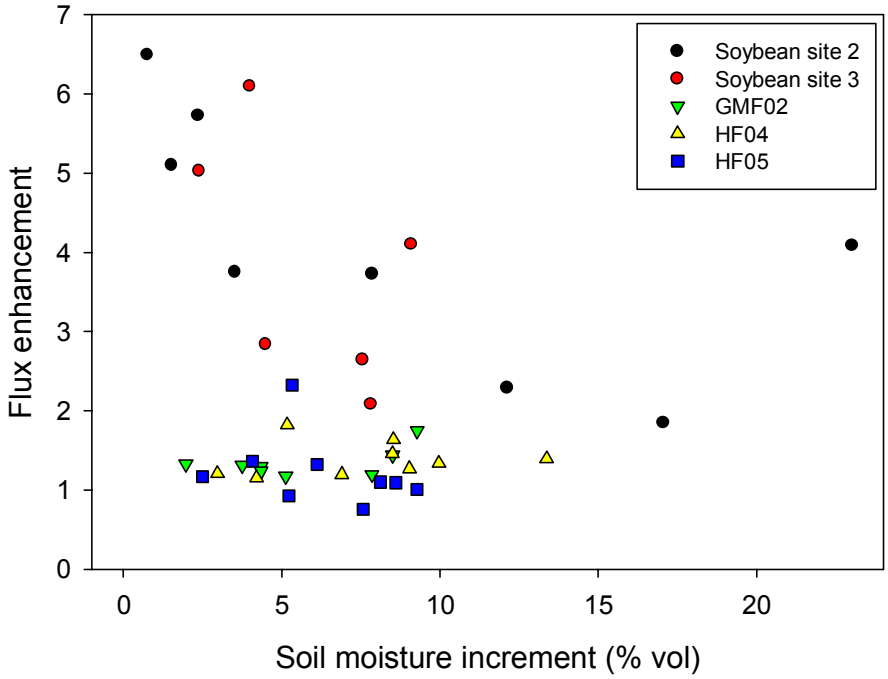

Figure 3.17. Flux enhancement vs. soil moisture increment at soybean sites and New England forest sites. Data presented are from the two soybean sites and from Great Mountain Forest (CT) in 2002 (GMF02), and Harvard Forest (MA) in 2004 and 2005 (HF04 and HF05). Soil moisture increment was average change in moisture content at 5 cm depth after the 30-min wetting of replicate plots. Flux enhancement was the average enhancement ratio following the 30-min irrigation (F_{t3}/F_{t0}) of replicate plots on each field day. The correlations are as below:
Site 2: $y = -0.127x + 5.2084$, $R^2 = 0.42$, $n = 8$;
Site 3: $y = -0.3357x + 5.7753$, $R^2 = 0.32$, $n = 6$;
GMF02: $y = 0.0389x + 1.1221$, $R^2 = 0.30$, $n = 8$;
HF04: $y = 0.0092x + 1.3158$, $R^2 = 0.02$, $n = 9$;
HF05: $y = -0.0364x + 1.3265$, $R^2 = 0.19$, $n = 8$ (one outlier excluded).

oxygen may be the limiting factor for soil respiration at the soybean sites, and that soil properties can indeed be a constraint to wetting-induced soil respiration. While greater moisture increment in soils may create a favorable environment for microbial activities, it could also decrease gas diffusivity and oxygen content necessary for microbial metabolism. Agricultural soils are more compact and with higher bulk density, and thus more prone to become anaerobic. Moisture increment was quite low at the beginning of the growing season, but increased over the season at both sites (Fig. 3.18). At site 2, the fluctuation of moisture increment over the season was in concert with baseline CO_2 flux (Fig. 3.18). Moisture increment showed strong positive correlations to pre-wetting surface soil moisture at both soybean sites and at Great Mountain Forest site, but not at Harvard Forest (Fig. 3.19). This seems to suggest that at drier sites, moist soils may have greater affinity to water and thus more able to retain water.

3.3.4.2. Spatial variations

Since there are site-specific factors dictating the behavior of soil respiration and its response to wetting on the two sites, cross-site correlations may not always be helpful. Spatial variation in flux enhancement among individual plots showed only weak dependence on soil temperature (Fig. 3.20), but had a more complicated relationship with pre-wetting CO_2 flux and soil moisture. Average enhancement ratios (F_{t3}/F_{t0}) of the six treatment plots ranged from 2.86 (plot C of site 3) to 4.26 (plot B of site 2). When combining data of all six plots from both sites, the pattern of low baseline flux corresponding to high enhancement still held (Fig. 3.21). But intrinsic differences of the two sites was clear, and the data points formed two distinct groups – plots of site 2 consistently had lower baseline flux and higher

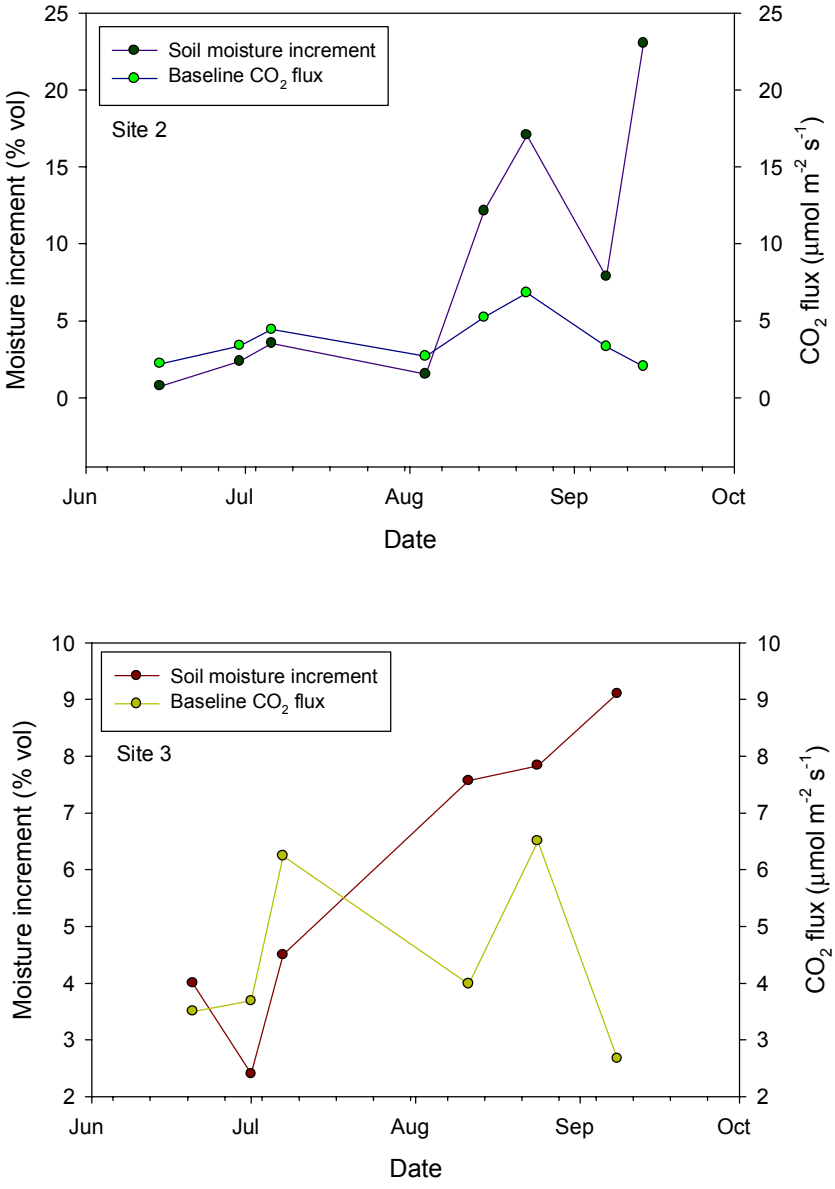

Figure 3.18. Soil moisture increment and baseline CO_2 over the season at sites 2 and 3. Soil moisture increment was the average of change in moisture content at 5 cm depth after the 30-min wetting of replicate plots. Baseline CO_2 flux was the average pre-rain flux of replicate plots.

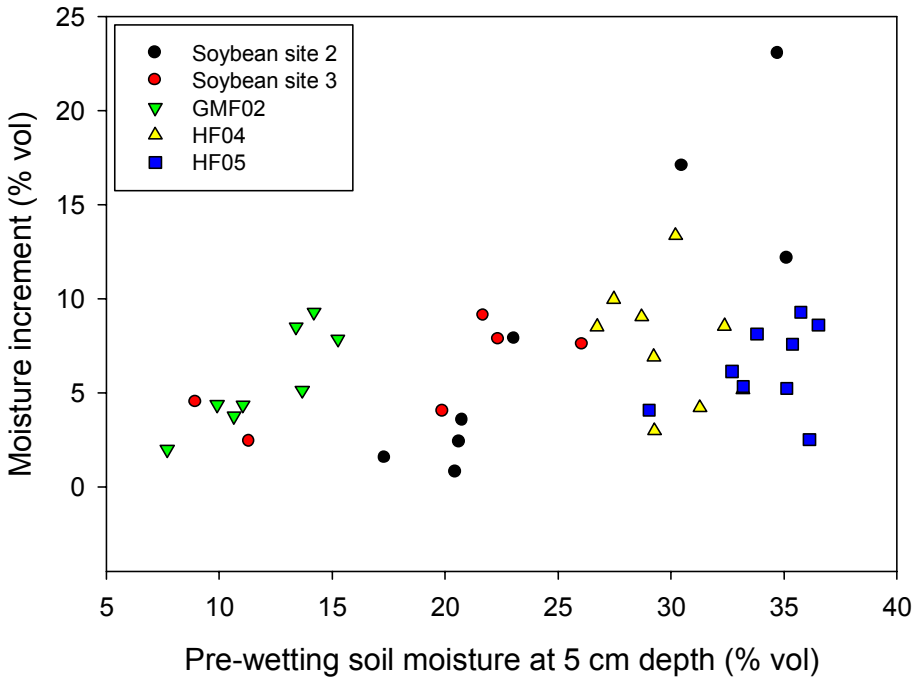

Figure 3.19. Soil moisture increment vs. pre-wetting soil moisture at the Nebraska soybean sites and New England forest sites. Data presented are from the two soybean sites and from Great Mountain Forest (CT) in 2002 (GMF02), and Harvard Forest (MA) in 2004 and 2005 (HF04 and HF05). Soil moisture increment was the average change in moisture content at 5 cm depth after the 30-min wetting. Soil moisture was the average of soil moisture at 5 cm depth of replicate plots. The correlations are as below:
Site 2: $y = 1.0459x - 17.955$, $R^2 = 0.81$, $n = 8$;
Site 3: $y = 0.2917x + 0.5356$, $R^2 = 0.56$, $n = 6$;
GMF02: $y = 0.8864x - 4.9718$, $R^2 = 0.77$, $n = 8$;
HF04: $y = -0.4194x + 20.133$, $R^2 = 0.08$, $n = 9$;
HF05: $y = 0.3453x - 5.4889$, $R^2 = 0.13$, $n = 9$.

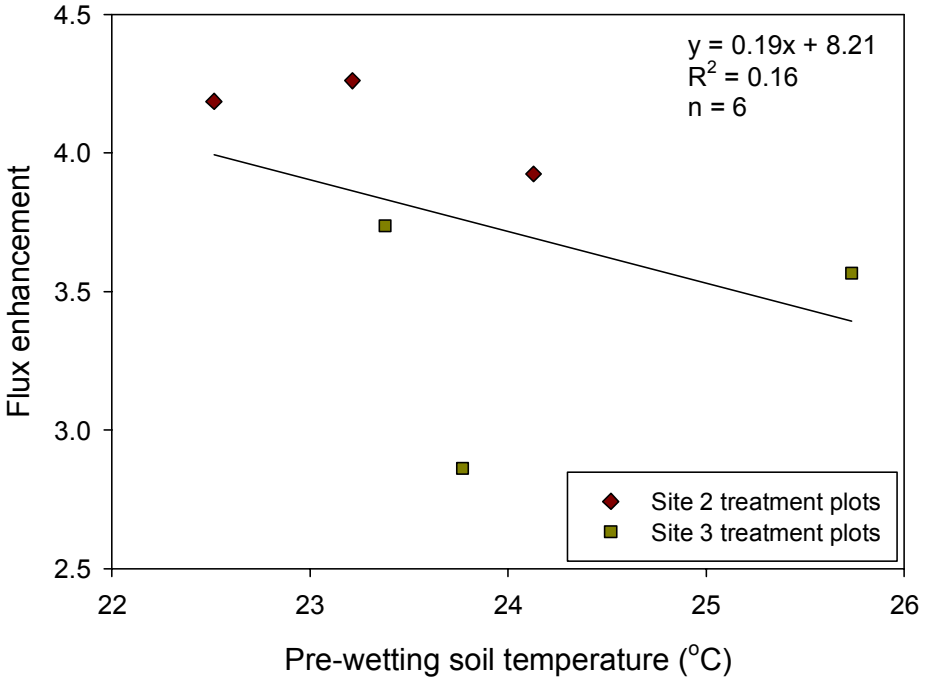

Figure 3.20. Average flux enhancement of individual plots vs. pre-wetting soil temperature. Spatial variation in flux enhancement had weak correlation with soil temperature. The data points are the seasonal average enhancement of each plot following 30-min irrigation (F_{t3}/F_{t0}).

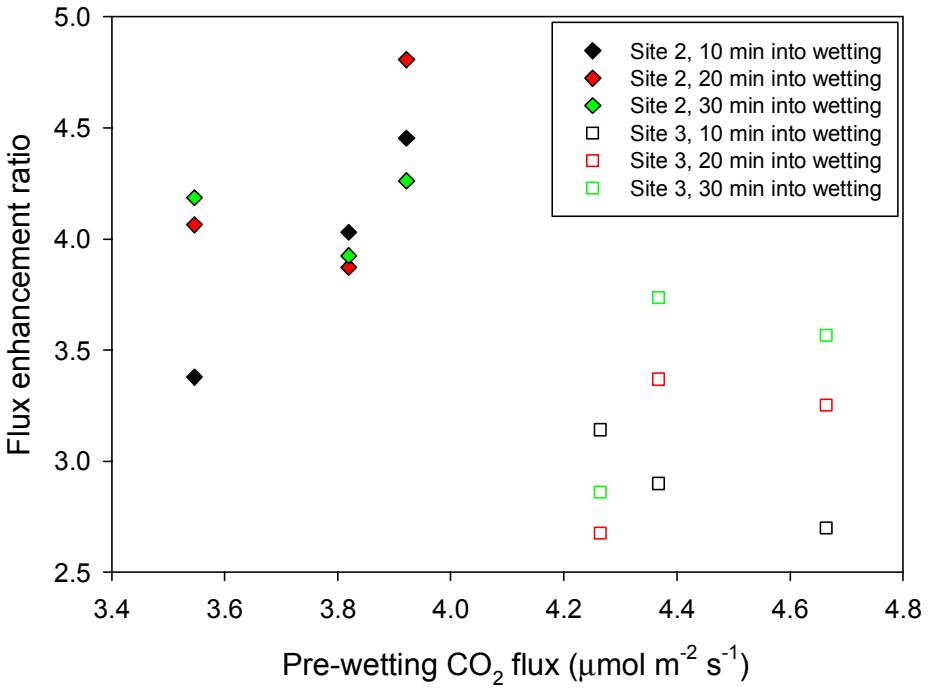

Figure 3.21. Flux enhancement of individual plots vs. pre-wetting soil CO_2 flux at time steps of 10, 20, and 30 min. during irrigation. Each data point represents the seasonal average of flux enhancement on one plot upon 10, 20, or 30 min into wetting (F_{t1}/F_{t0}, F_{t2}/F_{t0} , F_{t3}/F_{t0}). Solid diamonds denote plots of site 2, and open squares those of site 3. Black, red and green colors denote soil moisture at 10, 20, and 30 min into wetting.

enhancement than those of site 3 (Fig. 3.21). Therefore, it is more meaningful to look at the data of the two sites separately. CO_2 flux could only explain the spatial variation of initial enhancement (upon 10 min into wetting, our first measurement during irrigation). The two sites showed opposite trends: at site 2, enhancement increased with pre-wetting CO_2 flux (R^2 = 0.98, n = 3), whereas as site 3, enhancement decreased with increasing pre-wetting CO_2 flux (R^2 = 0.90, n = 3) (Fig. 3.21).

Figure 3.22 shows flux enhancement of individual plots versus pre-wetting soil moisture at different depths during irrigation. The data points represent the seasonal average of flux enhancement on individual plots upon 10, 20, and 30 min into wetting (F_{t1}/F_{t0}, F_{t2}/F_{t0}, F_{t3}/F_{t0}). Solid diamonds denote plots of site 2, and open squares those of site 3. Black, red and green colors denote soil moisture at 5, 15, and 25 cm depth respectively. Combined data of the two sties showed an increasing trend of enhancement with surface soil moisture at the beginning of wetting (R^2 = 0.63), but a decreasing trend with moisture at 25 cm depth (R^2 = 0.68) (Fig. 3.22). As irrigation progressed, the strength for soil moisture of these two soil layers to explain the variation in enhancement waned, and the strong correlation eventually shifted to the middle layer (15 cm depth) at the end of wetting (R^2 = 0.61) (Fig. 3.22).

When analyzing the data of the two site separately, we found that initial enhancement (F_{t1}/F_{t0}) increased with surface soil moisture (5 cm depth) at both sites (R^2 = 0.77 and 0.71 for sites 2 and 3). Enhancement after wetting (F_{t3}/F_{t0}) showed a negative trend with moisture of middle layer (15 cm) at site 2 (R^2 = 0.87), but a positive trend at site 3 (R^2 = 0.88) (Fig. 3.22). The positive correlations between flux enhancement and soil moisture are different from results of the New England forest sites as well as other studies (Xu et al. 2004; Rey et al. 2005). The reasons for such trends are unclear. But at site 2, the initial flux enhancement

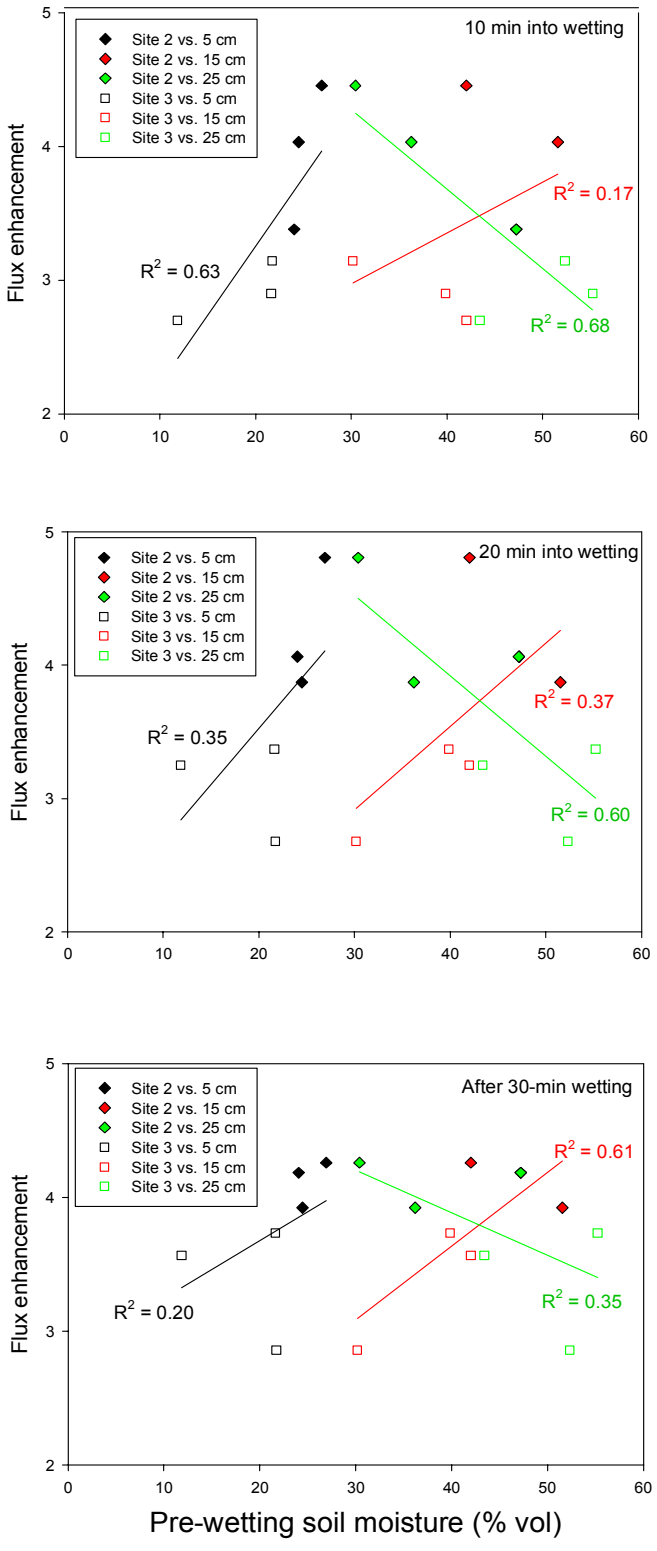

Figure 3.22. Flux enhancement of individual plots vs. pre-wetting soil moisture during irrigation at **10, 20, and 30** min. Data points are average enhancement over the season.

(F_{t1}/F_{t0}) also had a strong positive correlation with baseline CO_2 flux (Fig. 3.21), which increased with soil moisture. It is also likely that the initial enhancement (F_{t1}/F_{t0}) was increasing with moisture increment, since soils with higher soil moisture were more prone to retain water upon wetting (Fig. 3.19). A larger sample size would be necessary to verify and explain such trends.

3.4. DISCUSSION

The average flux enhancement ratios of 4.25 and 3.79 at the two soybean sites seem low compared to other studies on agricultural soils. For example, Calderón and Jackson (2002) observed 10 folds increase in CO_2 flux after irrigation, and Rochette et al. (1991) reported a 9 times increase after a 2-hour rain event. Flux enhancement depends on wetting intensity and duration (Orchard and Cook 1983, Borken et al. 2003, Borken and Matzner 2009). In our pilot experiments of 18-mm wetting, flux enhancement ratio could reach 18.29 (Fig. 3.5). However, excessive water could also curb soil respiration, especially on plots without residues (Fig. 3.6). The negative correlation between enhancement and soil moisture increment also suggests that oxygen availability may be the limiting factor for soil respiration at the soybean sites.

With our experiment results, it is possible to arrive at a rough estimate of soil carbon release due to irrigation at site 2 during the growing season. The estimate is based on two quantities that we measured, the enhancement ratio and the baseline CO_2 flux. However, we must take into account the fact that the duration that any spot remains under irrigation is not the total irrigation time, but in fact a much smaller number: at a given time, the center pivot irrigation system only covers a narrow rectangular strip. Additionally, the time any one spot

spends under irrigation is dependent on how far it is from the center of the site. However, the midpoint of the pivot can be chosen to estimate a typical number. (Other methods of obtaining an "average" number also yield similar or identical results). With the width of the irrigated zone at any instant denoted *w*, and the span of the pivot denoted *R*, the angle subtended, in radians, by the irrigated strip at the midpoint of the pivot is *2 (w/R)*. R is known to be 362 meters; we estimated *w,* within a factor of two, to be ~8 meters based on photographs of the irrigation system under operation. Thus, the angle subtended by the irrigated strip is ~2.5° and a typical spot will be under irrigation for about 0.7% (calculated as 2.5°/360°) of the time that the irrigation system is running. During the growing season, the total irrigation time was 432 hours; thus, in that time, a typical spot in the site received irrigation for approximately 3 hours. Multiplying 3 hours by the flux enhancement ratio (4.25) and the baseline CO_2 flux (3.76 μmol m^{-2} s^{-1}), we estimate that soil carbon loss to the atmosphere during irrigation over the whole growing season is 0.02 t C ha^{-1}. The estimate is only for carbon loss from irrigation at site 2, and not from natural rain events. The value did not take into account the enhanced soil respiration after irrigation ended.

Wetting-induced CO_2 pulses were most likely a result of increased microbial activity that had been suppressed by water deficit (Orchard and Cook 1983), or increased substrate availability from soil organic matter, dead microbial cells, and intracellular material released by living microbes in response to sudden water potential change (Birch 1958, Bottner 1985, Kieft et al. 1987, Fierer and Schimel 2003). More detailed discussion on mechanisms causing such CO_2 pulses can be seen in the discussion session of Chapter 2.

Enhancement ratio on bare plots was only slightly lower than that on plots with residues, but the enhancement duration on bare plots was much longer than that on plots with

residues. Such difference may owe to the depth to which water infiltrated into soil. Unlike wetting on plots with intact residues, where more water was retained on the surface by residues, irrigated water on bare plots moved further down into deeper soil, and provided moisture for decomposition of root residues and soil organic matter in lower layer. Infiltration process can be slow in soils with texture of silty clay loams, which led to the observed extended flux enhancement on bare plots. In cultivated soils, organic carbon distribution is more homogenous along soil profile (Woods, 1989). Since the soybean sites were under conventional tillage or moderate tillage by disking prior to the no-till practice, there should be considerable amount of substrate carbon in lower soil layers. Nonetheless, lack of surface residues should still have some bearing on the lower enhancement ratio on bare plots as opposed to plots with intact residues. As reported by Lundquist et al. (1999), soon after wetting, greater increase in microbial biomass carbon occurred in surface than deeper layer of agricultural soils, which may be due to higher substrate availability in surface layer as a result of wetting. Stripped of the insulating layer of crop residues, bare plots tend to have higher soil temperature than plots with residues. For example, based on available data from site 3, soil temperature in the afternoon during the growing season was averaged 30.4°C on bare plots, much higher than that of plots with residues (25.1°C) and control plots (26.6°C); soil CO_2 flux during the same measurement period was averaged 5.05 μmol m^{-2} s^{-1} on the bare plots versus 4.37 μmol m^{-2} s^{-1} on control plots and 5.10 μmol m^{-2} s^{-1} on plots with residues. Note that plots with resides were wetted several hours earlier and thus the flux was still slightly enhanced. The lower enhancement ratio upon wetting on bare plots may suggest that, belowground respiration usually dominated soil respiration on these soybean fields, but during wetting, a considerable portion of initial CO_2 pulses was contributed by surface crop

residues. Since wetting experiments on bare plots were carried out for limited times, more study is needed to further verify and understand our preliminary results.

Flux enhancement on plots with intact organic layer was 3 times greater at the soybean sites than the forest sites (Fig. 3.13). This could be due to differences in microbial composition and functions, or fertilizer addition on the soybean fields, which enables increased microbial N immobilization, and thus enhanced microbial population growth. However, the main reason for the greater enhancement at the soybean sites was most likely the much higher soil temperature at the soybean sites. Shielded by dense overstory canopy, the New England forest sites were exposed only to sunflecks, whereas the Nebraska soybean sites were often exposed to direct sunlight until later in the growing season when soybean canopy closed. Soil temperature at the soybean sites was therefore much higher than the forest sites, with a minimum difference of 7.9°C and a maximum difference of 10.4°C (Table 3.1). With optimal moisture conditions, wetting-induced soil CO_2 pulses are highest when soil temperature is high (Borken et al. 1999). Soil moisture at the soybean sites was higher than that at Great Mountain Forest, and slightly lower than that at Harvard Forest. Despite the difference in relative soil moisture condition, enhancement at the soybean sites was invariably higher than the forest sites, which should most plausibly be accounted for by the higher soil temperature at the soybean sites. Another possible explanation for the greater enhancement at the soybean sites could be higher organic matter content there. However, soil organic carbon to a 27 cm depth (including a forest floor thickness of 7 cm) was estimated to be 9.5 kg C m^{-2} at Great Mountain Forest (Wu 2002), which is higher than that at both soybean sites (6.3 and 6.4 kg C m^{-2} at sites 2 and 3 to a 30 cm depth, Verma et al. 2005).

Pre-wetting CO_2 flux was very similar for soybean site 3 and Great Mountain Forest, though soil organic carbon was lower and soil moisture was higher at all depths at soybean site 3 (Table 1). And the fact that wetting triggered greater CO_2 release from soybean site 3 than from Great Mountain Forest may suggest either that CO_2 concentration in soil profile was higher at soybean site 3 than Great Mountain Forest, or that displacement of CO_2 in soil pores is probably not a valid explanation for the observed CO_2 pulses. Soils of the Nebraska soybean sites are silty clay loams, whereas those of the New England forest sites are characterized as sandy loams. Soil bulk density at the no-till, more compacted soybean fields is 0.84, 1.09, 1.33, 1.30, and 1.31 g cm^{-3} for 0-2.5, 2.5-5, 5-10, 10-20, and 20-30 cm depths (Quincke 2006). In comparison, bulk density at Great Mountain Forest is lower: 0.16, 0.83, and 1.11 g cm^{-3} for 0-7 (forest floor), 7-17, and 17-27 cm depths (Wu 2002). Had gas displacement indeed played an important role in creating the CO_2 pulses, lower soil moisture and bulk density at Great Mountain Forest, and with identical rain intensity of 6 mm within 30 min, more CO_2 gas should have been displaced from forest soils than soybean fields. Hence our results may serve as a piece of evidence that biochemical processes, instead of physical displacement, account for the almost instantaneous soil CO_2 pulses upon wetting.

While there was limited or no enhancement on bare plots at the forest sites, there was considerable enhancement on bare plots at the soybean sites (Fig. 3.14). Such difference in response patterns of bare plots may be due to that: (1) the sandy loam soils of the New England forest sites have lower capacity to retain water, and thus irrigated water was quickly lost and soils dried up; (2) while the main source of labile carbon in forest floor was removed on bare plots in the forest sites, there may be greater amount of root-derived carbon and soil organic matter in lower layers of the soybean fields from previous plowing; (3) there may be

delayed enhancement on bare plots beyond our 2-hour observation time at the forest sites.

Baseline CO_2 flux at soybean site 2 showed rather weak temperature dependence. Similarly, Sey et al. (2008) also found that, on corn and soybean fields, CO_2 and N_2O contents in soil profile were not related to seasonal variation in soil temperature, but controlled more by soil moisture. As Skopp et al. (1990) pointed out, the effects of soil moisture content is a delicate balance between substrate mobilization and microbial requirements and adequately aerobic soil environment. Rochette and Gregorich (1998) found that during growing season, unless substrates are abundant and soil water content is optimal for microbial activities, the effect of temperature on soil gas content is often of little consequence. The moderate temperature dependence of site 3 may imply abundant organic substrate and optimal soil moisture condition (although lower than that of site 2) at the site. However, larger sample size is needed to clarify the strength of temperature dependence of soil respiration at site 3.

Compared with the experiments at the New England forest sites, observation time on the soybean fields was longer, and extended measurements beyond the 6-hour time frame were necessary in some cases. Constrained by time, manpower and accessibility to the sites during early or late hours, sometimes measurements were not as frequent and punctual as we would wish. It would be very helpful to be able to measurement *in-situ* CO_2 flux continuously. We tested an automated soil CO_2 flux system (model LI-8100, LI-COR, Inc.) on the irrigated corn field (site 1), and an example of continuous flux measurements for over a month with this automated, long-term system is shown in Appendix I (Fig. A1).

3.5. CONCLUSIONS

Wetting induced immediate but short-lived soil CO_2 pulses on soybean sites. At the end of the 30-min simulated wetting, the flux enhancement ratio averaged 4.0. The response pattern was very similar to that at the New England forest sites, but magnitude was almost 3 times greater due to the higher soil temperature at the soybean sites. On plots without crop residues, wetting-induced enhancement ratio was slightly lower than that on plots with intact residues. However, duration of elevated CO_2 flux on the bare plots lasted longer and extended beyond a day, a phenomenon observed neither on plots with intact crop residues, nor on bare plots at the New England forest sites. This indicates that, regardless of the presence or absence of crop residues, upon mild wetting events (such as 6 mm of water addition), the soybean fields have potential to lose more soil carbon than the New England forest sites, through either higher flux enhancement ratio, or longer duration of elevated CO_2 flux. Nonetheless, compared with forest ecosystems, wetting-induced carbon loss from agricultural soils could be constrained due to anaerobic conditions commonly seen in compact agricultural soils. While increased water addition indeed led to greater soil CO_2 loss from our soybean site, excessive water from heavy wetting was also observed to suppress soil respiration, producing delayed enhancement or no enhancement at all.

Based on our results, a rough estimation of wetting-induced soil carbon release could be made. During the growing season of 2006, estimated soil carbon loss due to field irrigation with the center pivot irrigation system at site 2 was 0.02 t C ha^{-1}.

While the magnitudes of soil respiration and wetting-induced enhancement were comparable at the two soybean sites, variations in flux enhancement depended on site-specific factors. Flux enhancement at site 2 was affected mainly by baseline CO_2 flux, pre-wetting soil moisture, and moisture increment in surface layer. At site 3, baseline CO_2 flux

and moisture increment showed moderate or weak correlations to flux enhancement, while pre-rain moisture appeared to have positive correlation with enhancement until it reached 20% (vol), though larger sample size would be necessary to verify and explain the trend. In general, soil temperature did not play an important role in determining variation in flux enhancement. The negative correlations between flux enhancement and moisture increment at the soybean sites suggest that unlike great Mountain Forest, oxygen, instead of water, is the limiting factor for soil respiration at the Nebraska soybean sites.

With the controlled, consistent and standardized experiment approach, we could quantify wetting-induced flux enhancement across ecosystems, and provide effective comparison. Comparisons were drawn based on ecosystem types, soil moisture regimes, and organic matter contents. Our results shed lights in the complexities of moisture dependence of wetting-induced pulses on agricultural soils, and the differences in behaviors and enhancement magnitudes of wetting-induced pulses between forest and agricultural ecosystems.

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Chapter 4

Incubation Experiments on Litter Decomposition and Moisture Level

ABSTRACT

Incubation experiments were devised to determine real-time CO_2 evolution of litter samples with a continuous flow incubator, including a 300-ml Teflon flask, a micro-pump and a gas analyzer. Red maple leaves, white pine needles, mixed forest litter and mineral soil samples were collected from Great Mountain Forest, CT, in 2002.

Litter decomposition increased with temperature, moisture and water potential, but the relationships were species-specific. At a given water content, mineral soil had the highest water potential, and red maple leaves the lowest. Under constant temperature, CO_2 evolution rate of litter samples increased with moisture: at lower water content, white pine litter showed higher CO_2 evolution rate and greater rate of increase than red maple litter or mixed forest floor litter. However, CO_2 evolution rate of white pine litter peaked at ~ 0.003 μmol g^{-1} s^{-1} when water content was only ~ 1.2 g g^{-1}, while CO_2 evolution rate of red maple peaked at ~ 0.005 μmol g^{-1} s^{-1} when water content was ~ 4 g g^{-1}. Decomposition of white pine litter was more drought-tolerant than red maple, and could sustain even when water potential was below the suggested critical threshold of -1.5 MPa.

CO_2 evolution of red maple at 50% moisture level and white pine at 25% moisture level showed dramatic increase at higher temperature, but in general litter with higher moisture level did not show higher temperature sensitivity in our study. The soil respiration model developed by Lloyd and Taylor in 1994 appeared to more accurately predict our measurements of CO_2 evolution rate than fitting with a simple exponential form. The constant in the Lloyd-Taylor model, denoted as A, changes with environmental and physiological variables, and was highest for red maple leaf litter. Constant A increased with moisture level of white pine needle and mixed forest floor litter, but no such trend was

observed for red maple. Substrate availability of red maple was unknown due to the confounding effect from loss of moisture during experiment. But substrate availability proved to not be a limiting factor in the 370-hour incubation of white pine litter, as long as moisture content was sufficient.

4.1. INTRODUCTION

Enhanced soil CO_2 emission following wetting was first characterized by H.F. Birch through laboratory observations while he was working in East Africa in 1950s and 1960s (e.g., Birch 1958a, b, Griffiths and Birch 1961). This phenomenon, now known as the Birch effect (Jarvis et al. 2007), has been widely recognized and studied in various aspects since Birch's time. Wetting-induced response patterns and magnitudes of soil respiration can vary among species and ecosystems. Wetting pluses are associated with enhanced soil microbial activity (Bottner 1985, Schnürer et al. 1986, Van Gestel et al. 1993), changes in soil structure and thus enhanced soil organic matter availability (Seneviratne and Wild 1985, Denef et al. 2001), and mineralization of cytoplasmic solute from living microbial cells in response to the water potential shock from wetting (Fierer and Schimel 2003). Wetting-induced soil carbon pulses increased with wetting intensity (Orchard and Cook 1983). Repeated drying and wetting can lead to substrate decline (Clein and Schimel 1994), shift in soil microbial carbon dynamics and community structure (Fierer and Schimel 2002, Fierer et al. 2003), and enhanced loss of soil carbon (Miller et al. 2005, Schimel et al. 2007, Yuste et al. 2005).

The Birch effect has received increasing interest after its significance at the ecosystem level was unveiled by eddy covariance techniques during natural rain events (e.g., Xu and Baldocchi 2004, Lee et al. 2004,). Given its immediate relevance to ecosystem carbon balance, the Birch effect introduces large uncertainties to interannual variations in carbon sequestration, especially under the potential impacts of increasing precipitation variability due to climate change (IPCC, 2001).

While stand-scale eddy covariance measurements and plot-scale observations reveal wetting-induced soil respiration response patterns *in situ*, controlled laboratory experiments

help clarify underlying mechanisms and assess effects of environmental variables. Advances in technology since Birch's time has allowed us to capture the immediate responses of soil respiration following wetting in the laboratory (e.g., Borken et al. 2003, Lee et al. 2004). To obtain further information complementing our rain simulation field experiments in Great Mountain Forest, Connecticut (see chapter 2), we performed laboratory incubation experiments on litter samples collected from the site. In this study, we explored how environmental variables affect CO_2 evolution of litter from forest floor. We focused on the effects of moisture and temperature gradients, water potential, plant species and substrate availability. The experiment set-up was devised to measure soil CO_2 evolution rate in real-time, with minimal confounding effects from unintended factors.

4.2. METHODS

Litter samples were collected from the study site at Great Mountain Forest during the field season in 2002. Glacial till is the parent material of the soils at Great Mountain Forest. Soils at the site are Inceptisols - young soils at the beginning of soil profile development; therefore, they are not thick and display no well-defined profile characteristics. The soils are in general well-drained because of their sandy-loam to sandy texture. Samples were collected from the upper 10-15 cm of forest floor, including red maple leaf litter, white pine needle litter, mixed forest floor litter, and mineral soils.

The experimental set-up was devised to determine real-time CO_2 evolution of litter samples with a continuous flow incubator, including a 300-ml Teflon flask, a micro-pump and a gas analyzer (model 6262, LI-COR, Inc.). Thermocouple wires were inserted to the flask so that the temperature of litter samples could be detected by the thermocouple. CO_2

evolution rates were measured by placing one sample a time into the flask, and flushing the system with ambient air for 30-60 seconds at a flow rate of 2.5 L min^{-1}. Then, the system was switched to a closed loop at the same flow rate, and CO_2 concentration was recorded every second for 60 seconds. CO_2 evolution rate was computed from the rate of change of the concentration with time. Before each experiment started, we ran a blank test with no sample in the flask to assure that there was no leakage. A schematic diagram of the incubator set-up is shown in Figure 4.1, and the image can be seen in the appendices (Fig. A8).

To study the response of CO_2 evolution to moisture and water potential gradients, samples of red maple leaf litter, white pine needle litter, and mixed forest floor litter were wetted with distilled water to saturation and left sealed in dishes for 8 to 12 hours before actual measurement. Each litter type had four replicates. After CO_2 evolution rate was measured from all four replicates, the litter samples were air-dried or fan-dried until they were ready for the next round of measurement. The measurement/drying cycle was repeated until the water potential of the litter samples was lowered to approximately -50 MPa, which usually happened within 24 hours. Temperature was maintained at 21°C. Gravimetric water content was measured before each measurement. Water potential was obtained from pre-established water retention curves (moisture response curves of water potential versus gravimetric water content) for each litter type, since direct measurement of water potential would cost more time and involve change of sample dishes, which could disturb samples and enhance water loss. Water potential measurements for the water retention curves were made with a dewpoint potential meter (WP4, Decagon Devices, Inc., WA).

A second set of experiments were performed to determine whether moisture content has an impact on the respiration-temperature relationship. Samples of each litter type were

wetted to four moisture levels. 100% moisture level represents a moisture content corresponding to the maximum respiration rate of the respective litter type, which was already determined by the experiments described in the previous paragraph. The other three moisture levels were roughly 75%, 50%, and 25% of the known optimum moisture content. The flask enclosing the sample dish was placed in a Styrofoam container. Temperature manipulation was achieved by first adding ice cubes into the Styrofoam container to bring sample temperature down to nearly 0°C, and then progressively adding room-temperature or warm water until the temperature reached 35°C. Total experiment time for one sample was about 6-7 hours. CO_2 evolution rate was measured at every 2°C of temperature increase. To prevent moisture loss from the samples over the course of incubation, air was moistened by being pumped through a large jar of water when circulated in closed loop.

The third set of experiments were conducted to identify the effects of substrate availability on litter CO_2 evolution. Red maple leaf litter and white pine needle litter samples were wetted only once to various levels of water content. To prevent the samples from moisture loss, they were usually covered up, and during measurement, moist air was circulated in the system. However, some minor moisture loss was inevitable. A measurement of CO_2 evolution rate was taken using the above-mentioned set-up within 1 min after wetting, followed by periodic measurements for days until the CO_2 evolution rates became very low.

4.3. RESULTS AND DISCUSSION

Water potential is difficult to measure in the field, and therefore water retention curves were developed to help determining water potential of litter samples from the site with

known water content. Figure 4.2 shows water potential measured by a dewpoint potential meter (WP4, Decagon Devices, Inc.), which measures the sum of matric and osmotic potentials in a sample. Mineral soils have higher water potential than organic litters under the same water content (Fig. 4.2). That is because soils bind water mainly through matric forces, and mineral soils have greater adsorptive forces binding water to a matrix than porous leaf litter.

Decomposition rate increased with soil moisture and water potential, but the relationships were species-specific (Fig. 4.3). Under constant temperature, decomposition increased with sample water content (Fig. 4.3). At lower water content, white pine litter showed a higher CO_2 evolution rate and greater rate of increase than red maple or mixed forest floor litter (Fig. 4.3). However, CO_2 evolution rate of white pine litter peaked at ~ 0.003 μmol g^{-1} s^{-1}, when water content was ~ 1.2 g g^{-1}. In contrast, for red maple litter, peak CO_2 evolution rate occurred at ~ 0.005 μmol g^{-1} s^{-1}, when water content was ~ 4 g g^{-1} (Fig. 4.3). The peak-point water contents were later used as a measure of "100% moisture level", which refers *not* to field capacity, but instead to the moisture content corresponding to maximum CO_2 evolution rate. The peak CO_2 evolution rate of mixed forest floor litter, although not identified by the data presented here, was determined by another incubation experiment to be ~ 2 g g^{-1}. Variations in samples may be due to different compositions of contributing plant species, including red maple, oak, white pine, beech, birch, witch hazel, hemlock, etc. However, even with litter samples taken from the same site at the same time, rewetted with the same amount of water, CO_2 evolution rates were often different from experiment to experiment. Figures 4.4 and 4.5 show the relationships between litter decomposition and water potential as well as logarithmic water potential. Decomposition of

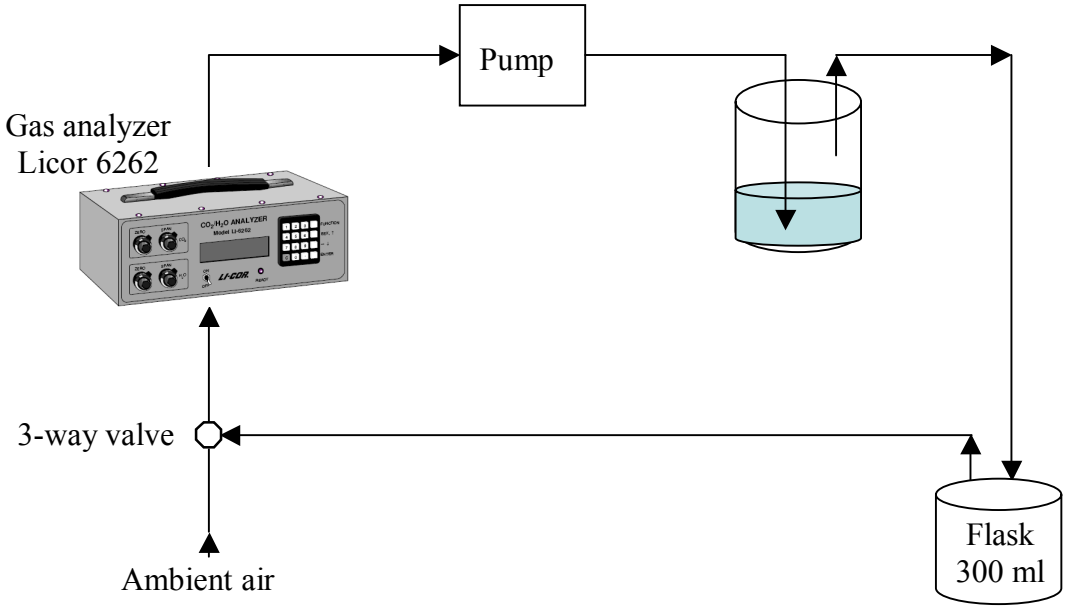

Figure 4.1. Schematic diagram of incubator set-up. The 3-way valve allowed ambient air to circulate in the system in an open loop initially, and blocked the entry of ambient air when the system was subsequently switched to closed loop circulation.

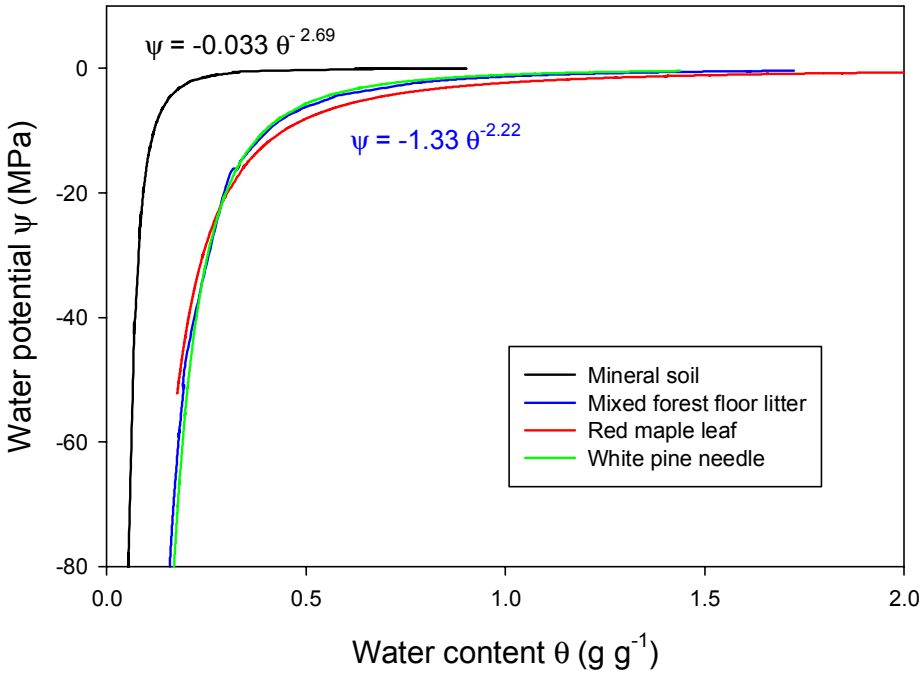

Figure 4.2. Water retention curves of mineral soil, mixed forest floor litter, red maple litter and white pine litter samples taken from Great Mountain Forest.

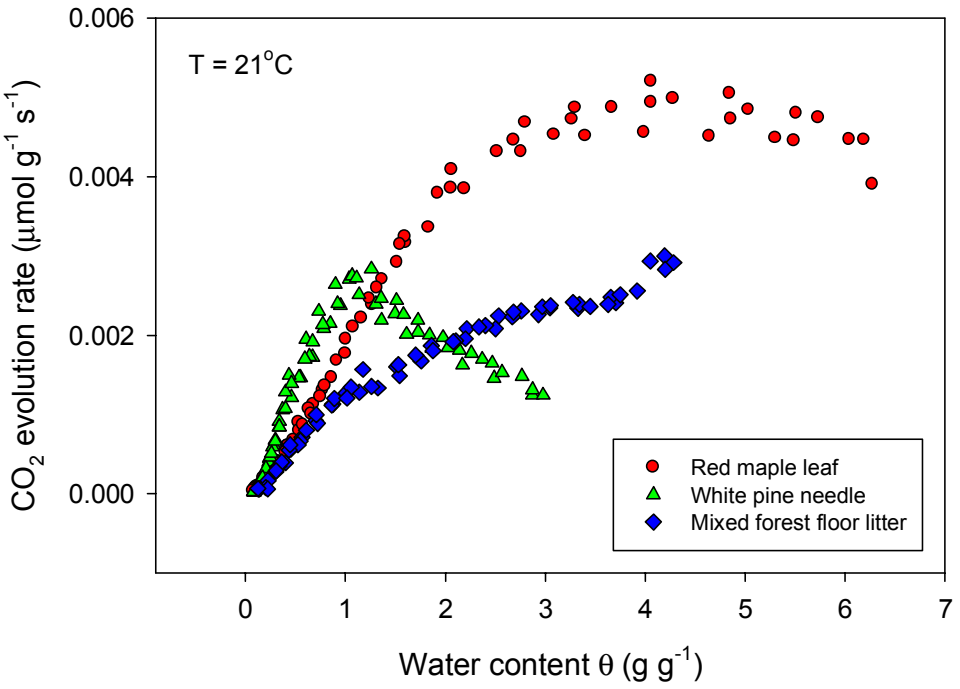

Figure 4.3. CO_2 evolution rate vs. water content of red maple litter, white pine litter, and mixed forest floor litter samples from Great Mountain Forest.

white pine litter appeared to be more drought-tolerant than red maple litter, and could maintain some level of CO_2 evolution rate even when water potential was below the suggested critical threshold of -1.5 MPa (Griffin 1981). Red maple litter increased in a sharper way with water potential than white pine litter, and while CO_2 evolution rate of white pine litter dropped at higher water potential, that of red maple litter continued to increase until approaching maximum water potential – 0.

CO_2 evolution rate from decomposing litter increased with temperature, and was best explained by an exponential function. Samples with different moisture levels were prepared based on the known 100% moisture level for each kind of litter, as mentioned above. The four moisture levels were targeted, to the best of our abilities, to be 100%, 75%, 50%, and 25%, although it was impossible to be exact. The general pattern recorded was similar for red maple litter, white pine litter, and mixed forest floor litter. However, for a given moisture level (note that this does not mean the same water content), red maple litter generally had higher CO_2 evolution rate than the other two (Fig. 4.6, 4.7, 4.8). Within each litter type, under the same temperature, samples with higher moisture levels usually had higher CO_2 evolution rate, but there were some exceptions for red maple litter (Fig. 4.6, 4.7, 4.8). To offset the effect of the different moisture levels, measurements of CO_2 evolution rate at all moisture levels were normalized by the value of evolution rate when temperature is 10^oC, derived from their respective best fitted exponential functions. For all three kinds of litter, the values of the normalized evolution rate were quite similar when temperature was lower, while large variations appeared at higher temperature. Normalized red maple CO_2 evolution rate with 50% moisture level ($\theta = 2.1$ g g^{-1}) increased more rapidly and deviated further from those with other moisture levels when temperature was over 30°C (Fig. 4.9). Normalized

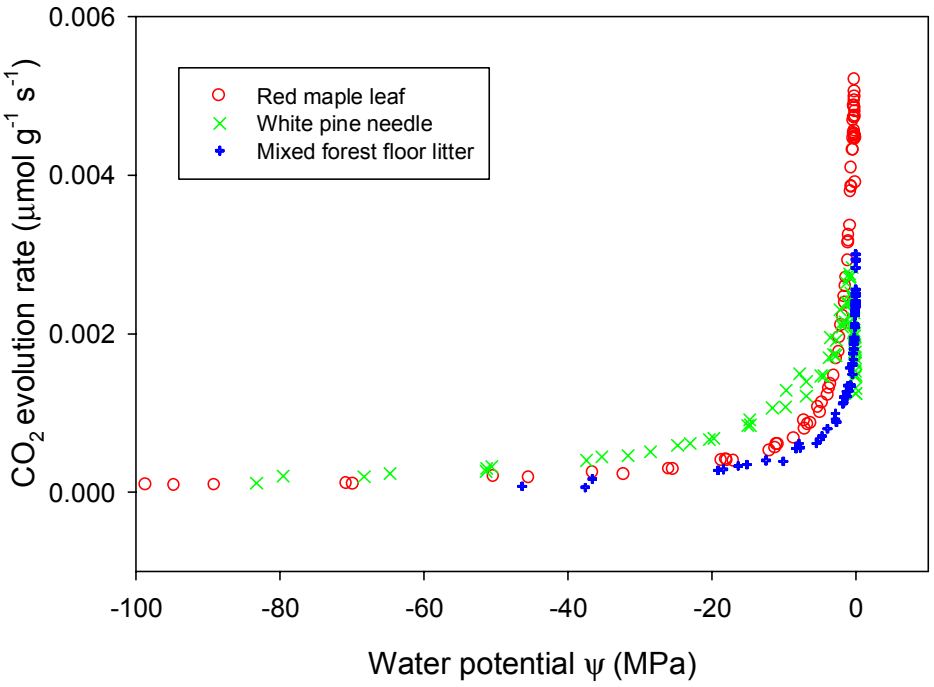

Figure 4.4. CO_2 evolution rate vs. water potential of red maple litter, white pine litter, and mixed forest floor litter samples from Great Mountain Forest.

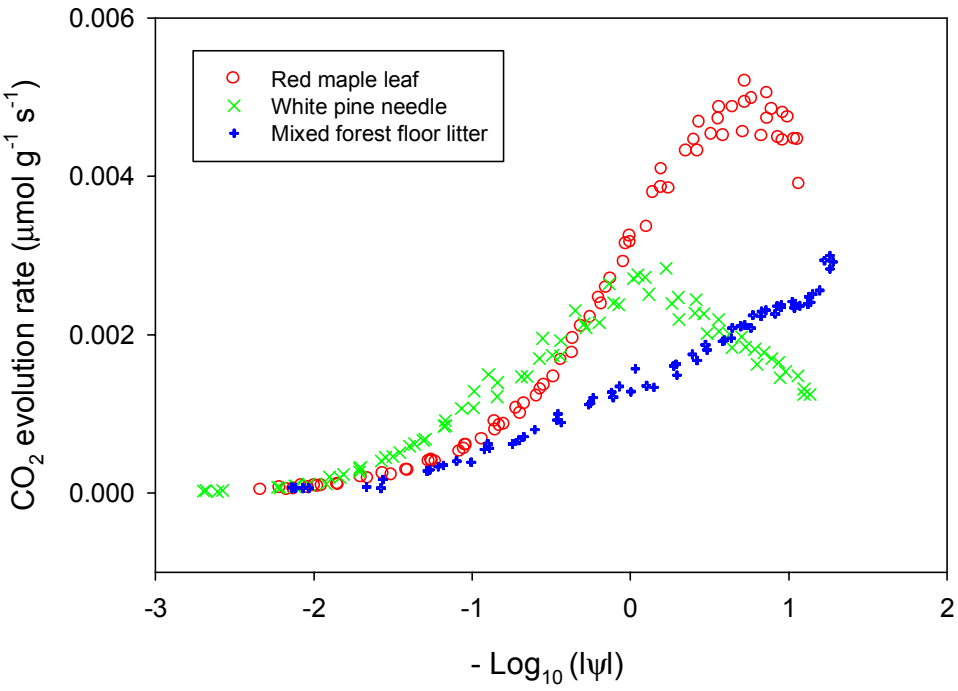

Figure 4.5. CO_2 evolution rate vs. logarithmic water potential of red maple litter, white pine litter, and mixed forest floor litter samples from Great Mountain Forest.

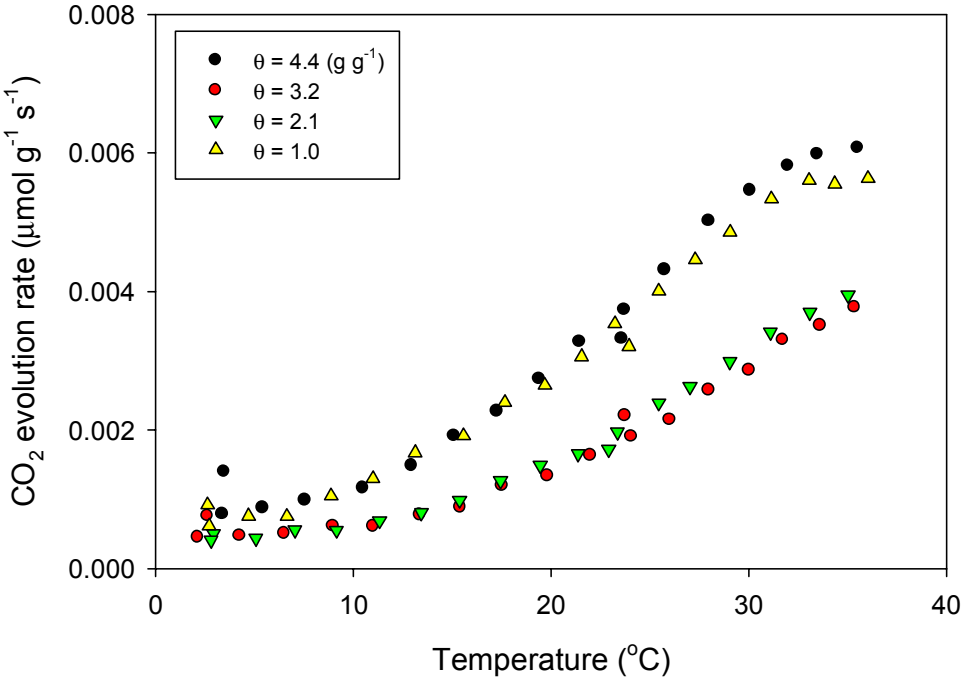

Figure 4.6. CO_2 evolution rate vs. temperature of red maple litter samples with different water contents.

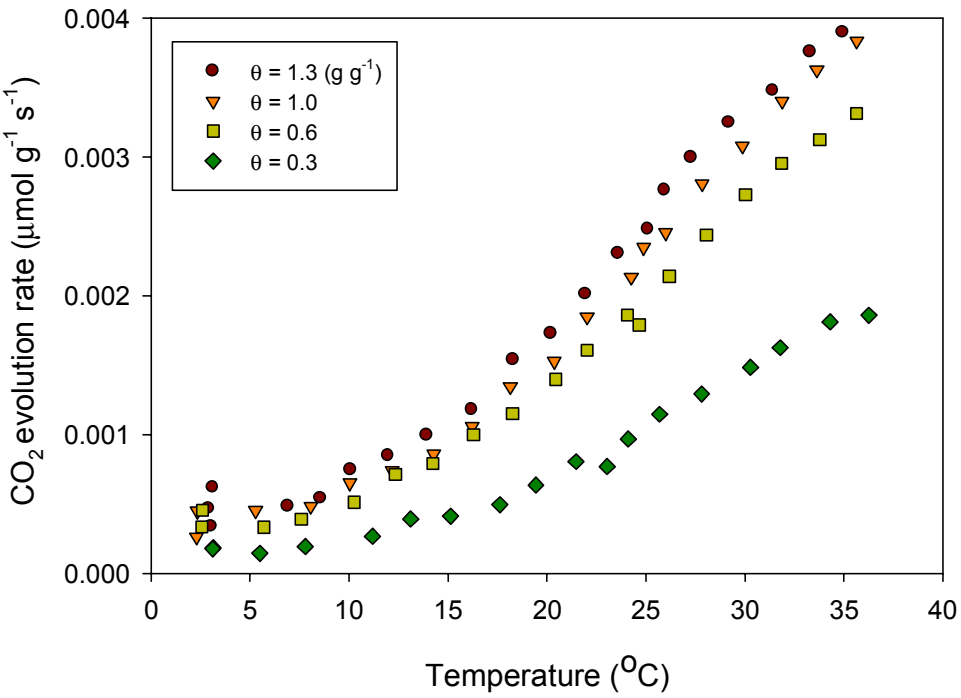

Figure 4.7. CO_2 evolution rate vs. temperature of white pine needle litter with different water contents.

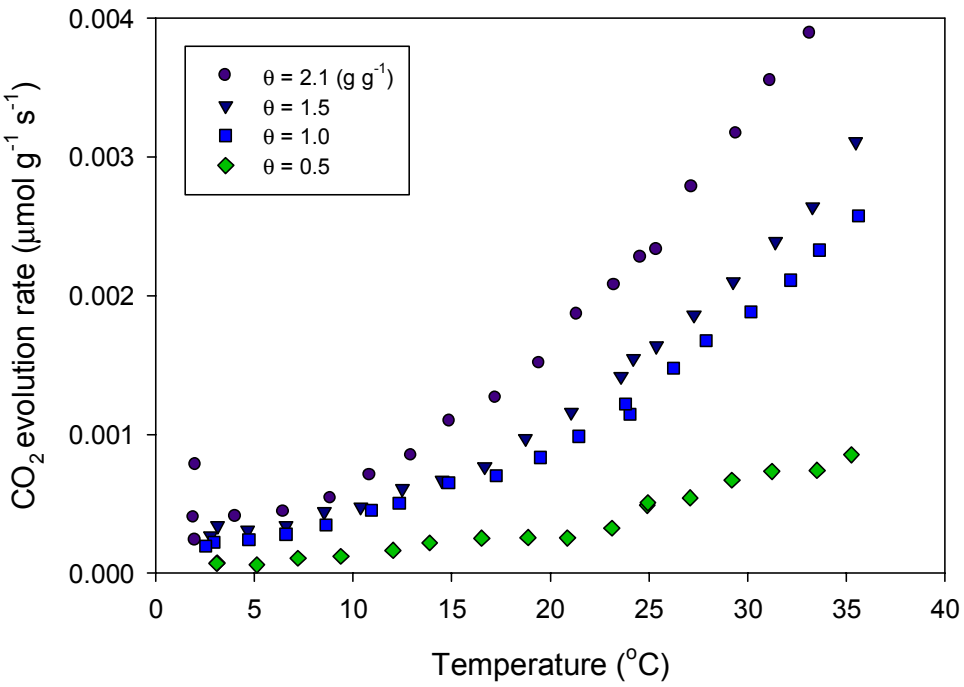

Figure 4.8. CO_2 evolution rate vs. temperature of mixed forest floor litter samples with different water contents.

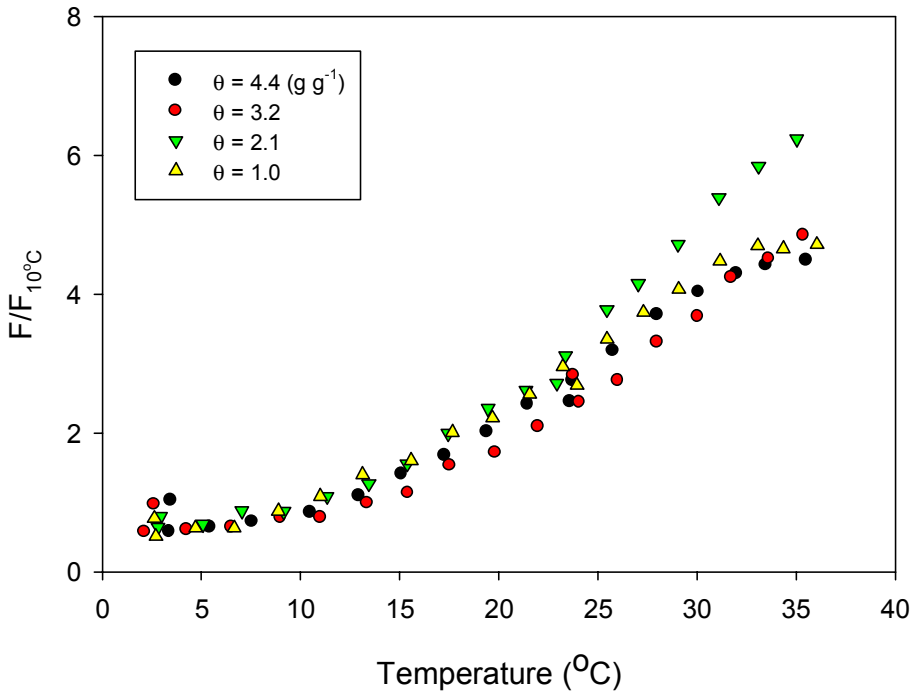

Figure 4.9. Normalized CO_2 evolution rate of red maple litter samples with different water contents. CO_2 evolution rate is normalized by the value at 10°C.

white pine CO_2 evolution rate with 25% moisture level ($\theta = 0.3$ g g^{-1}) increased with temperature greatly after temperature went above 20°C (Fig. 4.10). On the other hand, for the mixed forest floor litter, normalized CO_2 evolution rate followed the same trend against temperature at all moisture levels (Fig. 4.11). Therefore, unlike some studies suggested (Lloyd and Taylor 1994, Kirschbaum 1995, Xu and Qi 2001), litter with higher moisture levels was not seen to show higher temperature sensitivity in our study.

At higher temperatures, CO_2 evolution rates tended to fall below values predicted by an exponential function. Rate of increase of CO_2 evolution rate started to decrease, probably due to destruction of protein by high temperature. This is evident when examining the residuals of CO_2 evolution rate (measured value – predicted value), which are often negative at higher temperatures (Figures 4.12, 4.13, 4.14).

Figures 4.12, 4.13 and 4.14 also compare the residuals from fitting using an exponential function versus fits based on the soil respiration model developed by Lloyd and Taylor (1994):

$$F = A \times e^{-308.56 / (Tk-227.13)} \quad (4.1)$$

where F is CO_2 evolution rate, A is a constant that changes with environmental and physiological variables, and T_k is sample temperature in degrees Kelvin. With few exceptions, the Lloyd-Taylor model provides better prediction of our measurements. Although both the exponential function and the Lloyd-Taylor model deviate from the measured CO_2 evolution rates when temperatures exceeded 30°C, the latter form still provides the better fit to the measured value, especially in cases where the exponential fit overshot the measured values strongly (Fig. 4.13 b, Fig. 4.13 c, and Fig. 4.14 a).

Based on our measured CO_2 evolution rates and known sample temperature, we were

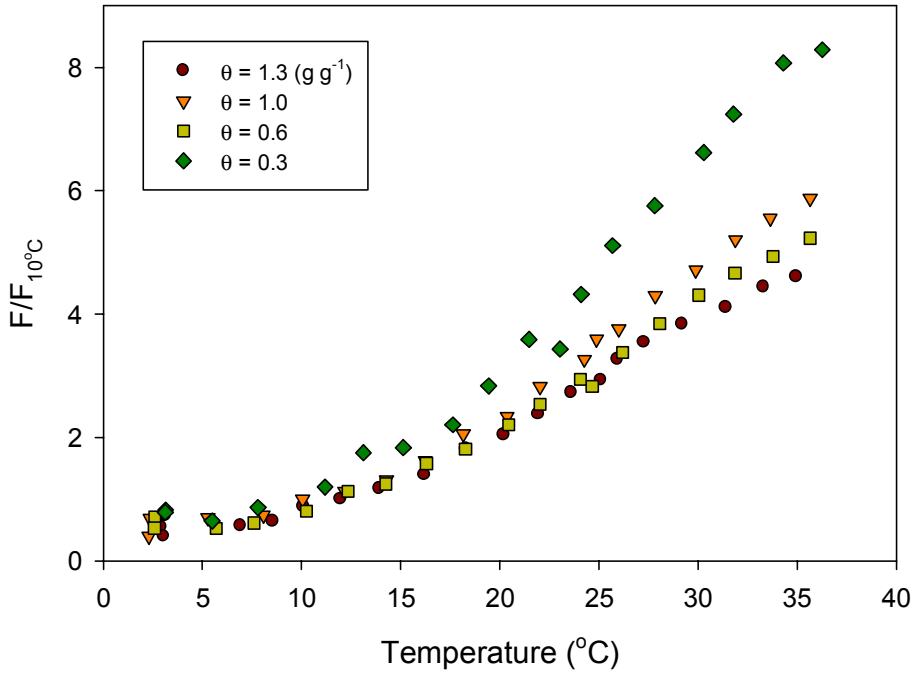

Figure 4.10. Normalized CO_2 evolution rate of white pine needle litter with different water content. CO_2 evolution rate is normalized by the value at 10°C.

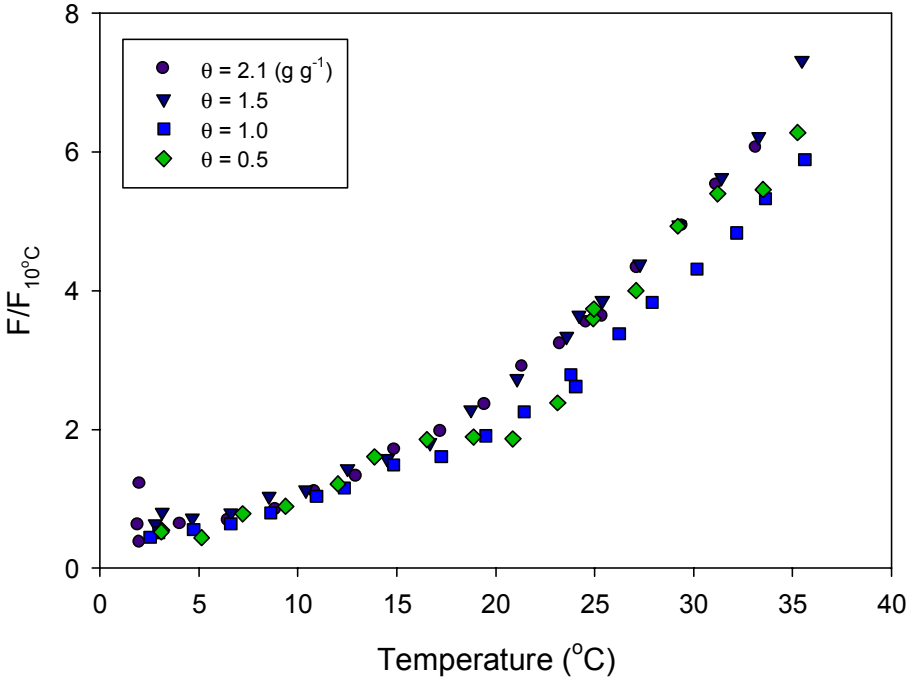

Figure 4.11. Normalized CO_2 evolution rate of mixed forest floor litter samples with different water content. CO_2 evolution rate is normalized by the value at 10°C.

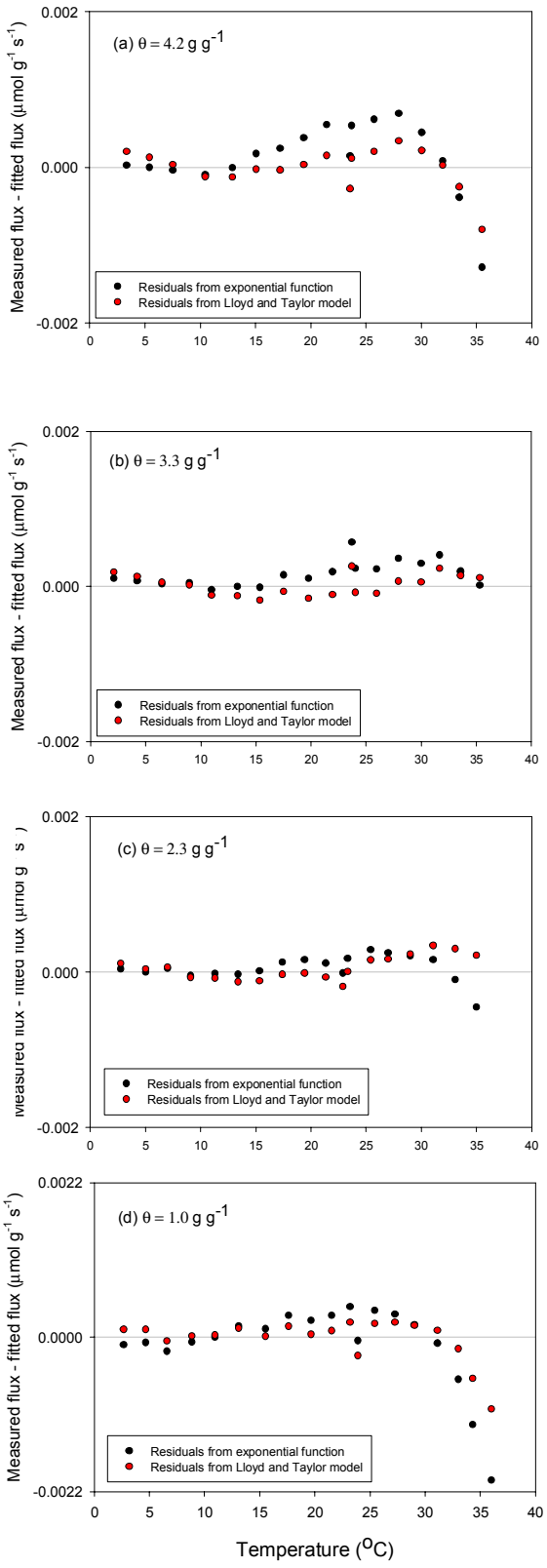

Figure 4.12. Residuals (measured value – predicted value) from exponential function and the Taylor-Lloyd model for red maple leaf litter with different water contents.

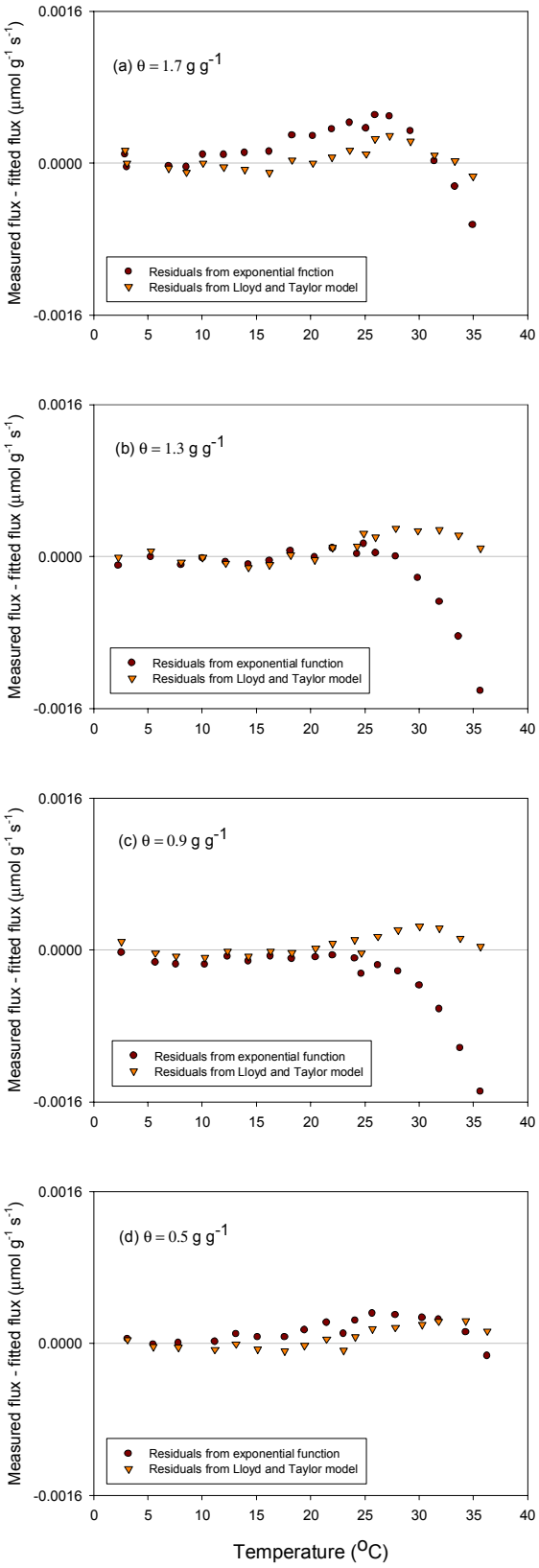

Figure 4.13. Residuals (measured value – fitted value) from exponential function and the Lloyd-Taylor model for white pine needle litter with different water contents.

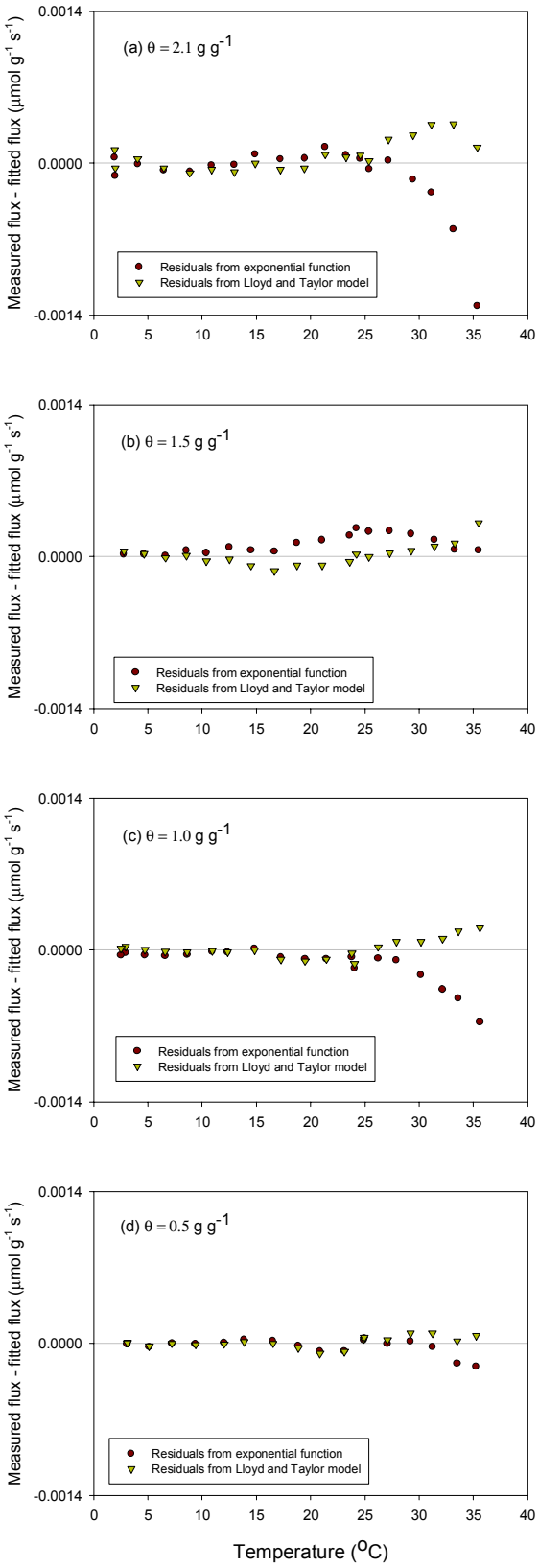

Figure 4.14. Residuals (measured value – fitted value) from exponential function and the Lloyd-Taylor model for mixed forest floor litter with different water contents.

able to compute the values of constant A in the Lloyd-Taylor model for the three litter species. A varied with litter species and moisture content. A was in general greater with red maple litter than with white pine litter or mixed forest floor litter. This means higher CO_2 evolution rate for red maple litter overall. A increased with moisture levels of white pine litter and mixed forest floor litter, but no such trend was observed for A of red maple litter (Table 4.1).

One-time wetting was performed on red maple and white pine samples to reach four moisture levels. Measurement started within one minute of wetting, followed with periodic measurements for days until CO_2 evolution rates became too low to measure. CO_2 evolution rate of red maple at all moisture levels started at a maximum value, and decayed to lower values over the course of 76 hrs (Fig. 4.15). In contrast, CO_2 evolution rate of white pine litter initially increased over time after wetting and depending on moisture level, peaked between 50 and 75 hours since wetting (Fig. 4.16). The only exception was CO_2 evolution rate of white pine at 25% moisture level, which peaked and then declined within only 2 hours after wetting, most likely due to the low water content. Although we tried to maintain constant sample water content, there was still some loss of moisture over the course of experiment. The decrease in red maple CO_2 evolution rate coincided with decrease in moisture (Fig. 4.17), and therefore loss of moisture was confounded with the effect of substrate availability. However, in the case of white pine litter, despite decreasing moisture content, CO_2 evolution rate initially increased with time (Fig. 4.18). And 370 hours later, decomposition was still in process, evidenced by the slightly higher CO_2 evolution rate of 100% and 75% samples than when first wetted, although moisture content was much lower than when first wetted. O'Connell (1990) found that litter moisture content and temperature could explain 93–94% of the variation in rates of CO_2 production; respiration was relatively

Table 4.1. Constant A from the Lloyd-Taylor model:
$F = A \times e^{-308.56 / (Tk-227.13)}$
where T_k is temperature in degree Kelvin, and A is the constant that changes with litter type and moisture.

Moisture level	Red maple	White pine	Mixed forest floor litter
~ 100%	0.3	0.18	0.17
~ 75%	0.16	0.17	0.12
~ 50%	0.17	0.14	0.1
~ 25%	0.29	0.07	0.03

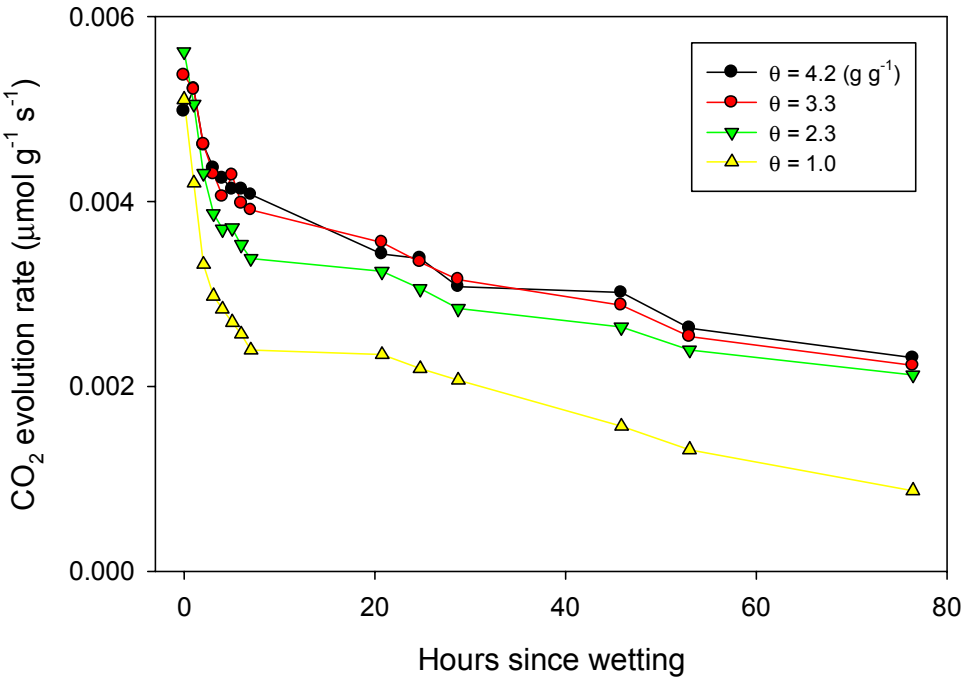

Figure 4.15. CO_2 evolution rates of red maple litter samples over 76-hr incubation. Four different water contents of red maple litter samples are shown above.

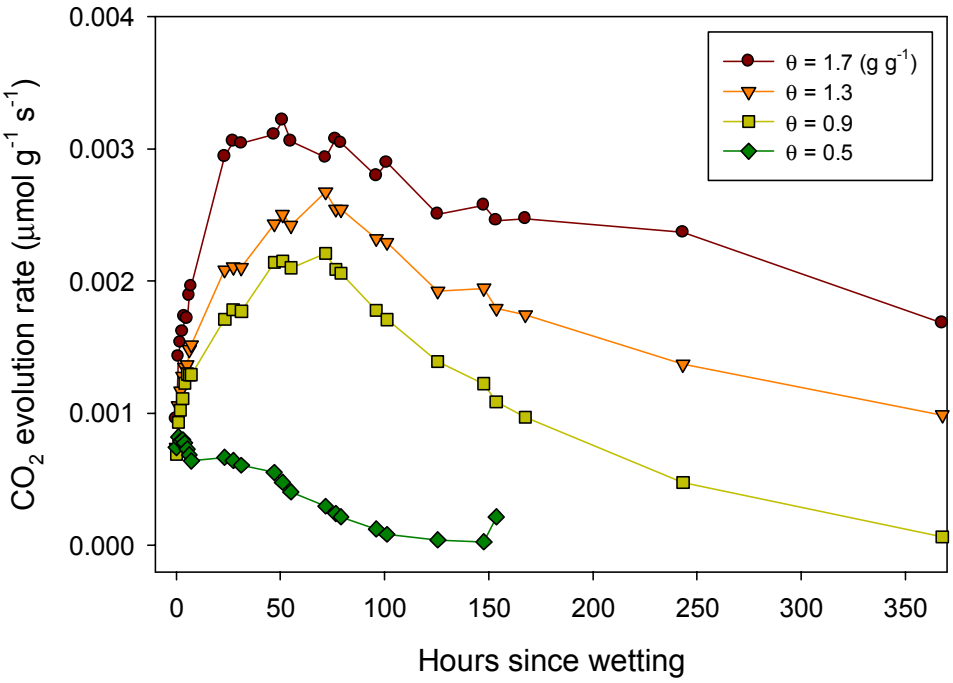

Figure 4.16. CO_2 evolution rates of white pine needle litter over 370-hr incubation. Four different water contents of white pine litter are shown here.

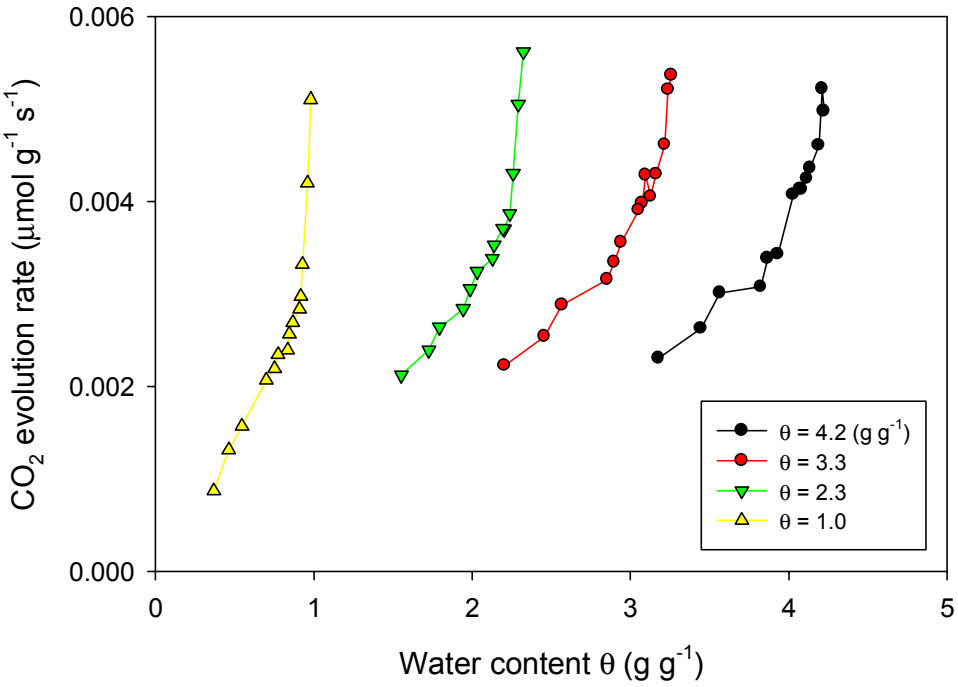

Figure 4.17. CO_2 evolution rate vs. water content over 76-hr incubation for red maple litter samples with different water contents. Water content gradually decreased after wetting.

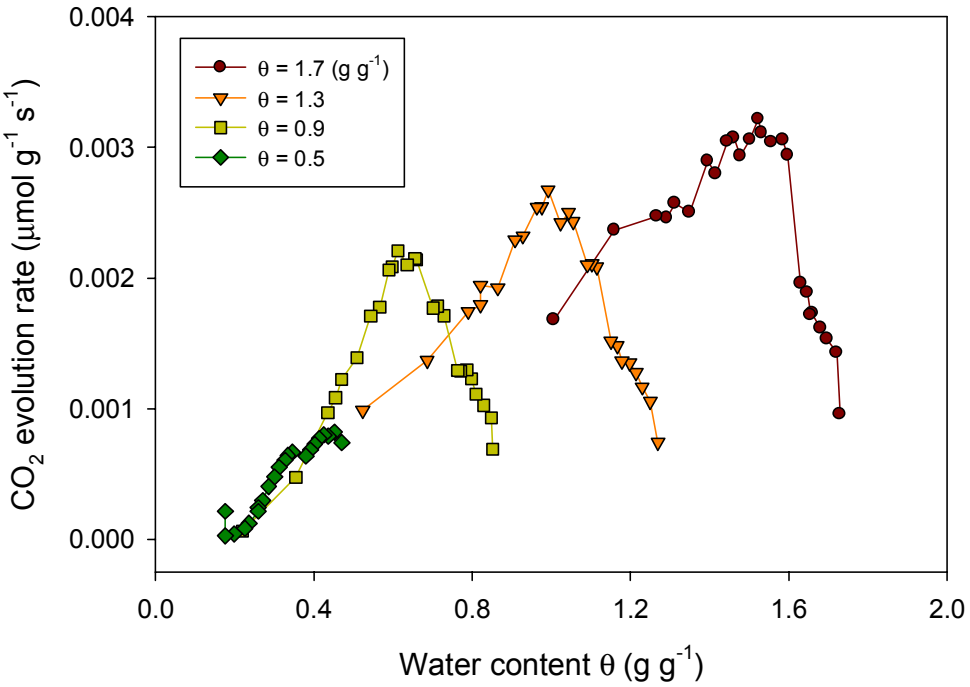

Figure 4.18. CO_2 evolution rate vs. water content over 370-hr incubation for white pine needle litter with different water contents.

constant at moisture contents > 100% ODW (oven dried weight), but decreased markedly when moisture <80% ODW. It may be safe to say that that substrate availability was not a limiting factor for the white pine litter, as long as sample moisture was sufficient.

4.4. CONCLUSIONS

Litter decomposition increased with temperature, moisture and water potential, but the relationship also depends on litter species. Decomposition of white pine litter was more drought-tolerant, and could be sustained under conditions with lower water content and water potential. Within each litter type, under the same temperature, samples with higher moisture levels usually had higher CO_2 evolution rate, but there were some exceptions for red maple litter. The effect of different moisture levels was normalized, and while samples of 50% moisture level red maple litter and 25% moisture level white pine litter showed dramatic increase at higher temperature, litter with higher moisture level did not show much sensitivity to change in temperature in our study. Through comparison of residuals, the Lloyd-Taylor model was found to more accurately predict our measures of CO_2 evolution rate than fitting with a simple exponential form. Constant A from the Lloyd-Taylor model was highest for red maple leaf litter. The values of A increased with moisture level of white pine and mixed forest floor litter, but no such trend was observed for red maple. Substrate availability of red maple was unknown due to the confounding effect from loss of moisture. But substrate availability was not a limiting factor in our 370-hour incubation of white pine litter, as long as moisture content was sufficient.

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Chapter 5

Summary

This study investigated short-term effects of wetting on soil respiration, with focus on the dynamics of soil moisture, which is predicted to decrease in most regions on earth in this century (Meehl et al. 2007). Rain simulation experiments were carried out in two New England forests (Great Mountain Forest, CT, and Harvard Forest, MA), and on Nebraska soybean fields. The significance of rain-induced CO_2 emissions at ecosystem scale was first unveiled with eddy covariance techniques recently (Xu and Baldocchi 2004, Lee et al. 2004). Enhanced soil respiration has been suggested to be responsible for the observed wetting-induced carbon pulses based on results from drying and wetting experiments in laboratory environment (e.g., Birch 1958, Orchard and Cook 1983, Kieft et al. 1987, Clein and Schimel 1994, Borken et al. 2003). By *in-situ* flux measurements, our rain simulation experiments helped to verify that soil respiration is indeed the contributor to the enhanced ecosystem CO_2 efflux during wetting, and further explored the enhancement dynamics and the underlying mechanisms regulating such enhancement.

Manipulative field experiments on wetting-induced soil respiration have been rare, and field studies documenting the effects of wetting on soil CO_2 flux often relied on post-wetting measurements or laboratory data due to the technical difficulties to measure during wetting. Our short sampling intervals and the mobility of portable photosynthesis system allowed us to trace the change of CO_2 flux along the process of wetting with fine time resolution, which captured the immediate on-site response of soil respiration to wetting, Through the controlled, consistent and standardized experiment methods (i.e., identical site preparation and irrigation methods, predetermined duration and quantity of water addition, and consistent measurement intervals), we could effectively quantify and compare wetting-induced CO_2 flux enhancement within sites and across ecosystems.

A primary goal of this study is to detect the response patterns and magnitudes of wetting-induced soil respiration on various study sites, and to identify the main contributors to the enhanced CO_2 emission. It was found that, even without long-lasting drought at our study sites, mild to medium wetting was enough to trigger immediate increase in CO_2 flux. CO_2 level started to decline as soon as the 30-min wetting ended, along with declining soil moisture, and returned to the pre-wetting level within 90 min. Such pulse-like response pattern was shared by Great Mountain Forest, Harvard Forest and the Nebraska soybean fields. Based on pilot field experiments and laboratory incubation experiments, we found that loss of moisture, instead of substrate availability, was the main reason for the observed fast decline in post-wetting CO_2 flux. Therefore, it is not surprising to find that rain intensity had significant effect on flux enhancement.

Perhaps the most notable finding from the study is the observation that, wetting-induced flux enhancement and total soil carbon loss during the experiment time frame was greater at the Nebraska soybean fields than the New England forest sites. Flux enhancement ratios at Great Mountain Forest in 2002 (GMF02), Harvard Forest in 2004 and 2005 (HF04 and HF05) were 1.52, 1.41 and 1.45 respectively. The values are comparable with the enhancement magnitudes from natural rain events in other forest ecosystems (Kelliher et al.1999, Lee et al. 2002). At the Nebraska soybean fields, pre-wetting CO_2 flux was lower than that at the New England forest sites, but leaped to much higher level upon wetting, with an average enhancement ratio of 4.25 at sites 2 and 3.79 at site 3. The difference in enhancement magnitudes between the forest and soybean fields was probably due to the higher soil temperature at the soybean fields.

O horizon exclusion allowed us to detect the different behaviors between plots with

and without O horizon, and thus to determine that wetting-induced CO_2 pulses were mainly contributed by O horizon/crop residues. Mechanisms associated with such CO_2 pulses are: (1) reactivated microbial activities by water addition (Orchard and Cook 1983, Bottner 1985, Saetre and Stark 2005); (2) rapid increase in microbial biomass (Griffiths and Birch 1961, Orchard and Cook 1983, Schnürer et al. 1986, Lundiquist et al. 1999); and (3) increased substrate availability for microbial mineralization. As Borken and Matzner (2009) pointed out, the organic substrates that fueled the CO_2 pulses during wetting could derive from different sources produced, accumulated or exposed during the drying period, but wetting can induce further mechanisms that enhance the availability of organic substrates. It has been suggested that the labile substrate pool initially used by soil microbes upon wetting was mainly of microbial origin - cytoplasmic solutes released by living microbes in response to sudden change in water potential due to wetting (Fierer and Schimel 2003, Lovieno and Bååth 2008). Although our results could not provide direct, conclusive information as to the sources of substrate used for the observed CO_2 pulses, they nonetheless strongly support the abovementioned mechanism.

Another goal of this study was to determine the driving forces of the temporal and spatial variations in flux enhancement. In general, flux enhancement at all sites was negatively correlated with pre-wetting baseline CO_2 flux. But baseline CO_2 flux is virtually an approximate of soil organic matter content, temperature, moisture, and species effect of substrates. Soil temperature dictated seasonal fluctuation of soil respiration, and was negatively correlated with flux enhancement at the New England forest sites, but the trend was not as strong at the soybean sites. Soil moisture was the main factor we investigated, and we did find moisture dependence of wetting-induced flux enhancement. However, the

workings of soil moisture were different at the study sites. At Harvard Forest, flux enhancement decreased with increasing pre-wetting soil moisture; at Great Mountain Forest, CO_2 flux enhancement increased with soil moisture increment due to wetting; and on the Nebraska soybean fields, flux enhancement decreased with increasing moisture increment, which suggest that oxygen was probably the major limiting factor for flux enhancement on agricultural soils. The different aspects of moisture dependence were attributed to variations in site moisture conditions, organic matter contents, soil characteristics, and drainage level, which further shows that wetting-induced soil respiration relies on site-specific factors.

During our field experiment in New England forests and Nebraska soybean fields, due to the regular rain simulation, there was no long-lasting drought on our sites, and moisture content at lower soil profile was rarely below field capacity. In contrast, topsoils, where leaf litter and crop residues accumulated, were most often subjected to drying and severe moisture stress. The dynamics of O horizon contribution to total soil respiration was different between the forest sites and agricultural fields. At the soybean sites, baseline CO_2 flux was similar on plots with and without crop residues, and enhancement ratio upon wetting was slightly higher on plots with residues. This may suggest that belowground respiration usually dominated soil respiration on these soybean fields, but during wetting, a considerable portion of initial CO_2 pulses was contributed by surface crop residues. At the forest sites, O horizon contributed to 44% of soil respiration at Great Mountain forest during the growing season, and the contribution increased with pre-wetting soil moisture. At Harvard Forest, O horizon contribution was 26-29%, while decreased with increasing pre-wetting soil moisture. Upon wetting, since organic layer was the main contributor of elevated CO_2 emission, variations in flux enhancement showed similar relationships with soil

moisture as O horizon contribution did.

This study also intended to provide quantitative information to help estimating the amount of rain-induced carbon release at the ecosystem level. However, wetting-induced enhancement is often site-specific and experiment-specific. Even based on results from rain simulation or laboratory incubation experiments, the uncertainties remain, and it is difficult to effectively predict the absolute flux during natural rainfall, mainly because of variable site conditions, changeable/inconsistent rain intensity and duration, as well as accompanying meteorological factors such as stronger wind speed and lower temperature during rain. Moreover, wetting-induced CO_2 flush from laboratory incubation experiments may overestimate enhancement magnitude if directly applied to field conditions, likely due to disturbance in soil structure during sample preparation. For example, the enhancement ratio from field rain simulation at Great Mountain Forest was much smaller than the results from our laboratory incubation experiments on forest litter, which showed a 10-fold enhancement within 1 min (Lee et al. 2004). Therefore, while laboratory data can hint the direction of wetting effects, they may not be directly extrapolated to field conditions or to ecosystem scale. However, manipulative field experiments may still contribute to a better understanding of the processes involved and improve the knowledge about underlying mechanisms and variations, and to provide some quantitative information that can serve as base for site-specific model building.

Further research on wetting-induced soil respiration lies on various aspects, including long-term shift in microbial composition and diversity as a result of drying and wetting, plant ecophysiological responses, canopy structural dynamics, interaction between N and C pulses, and effect of hydrophobicity of dry soils on wetting-induced carbon release.

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Appendix I

Additional Data -

Continuous CO_2 flux measurements with automated system

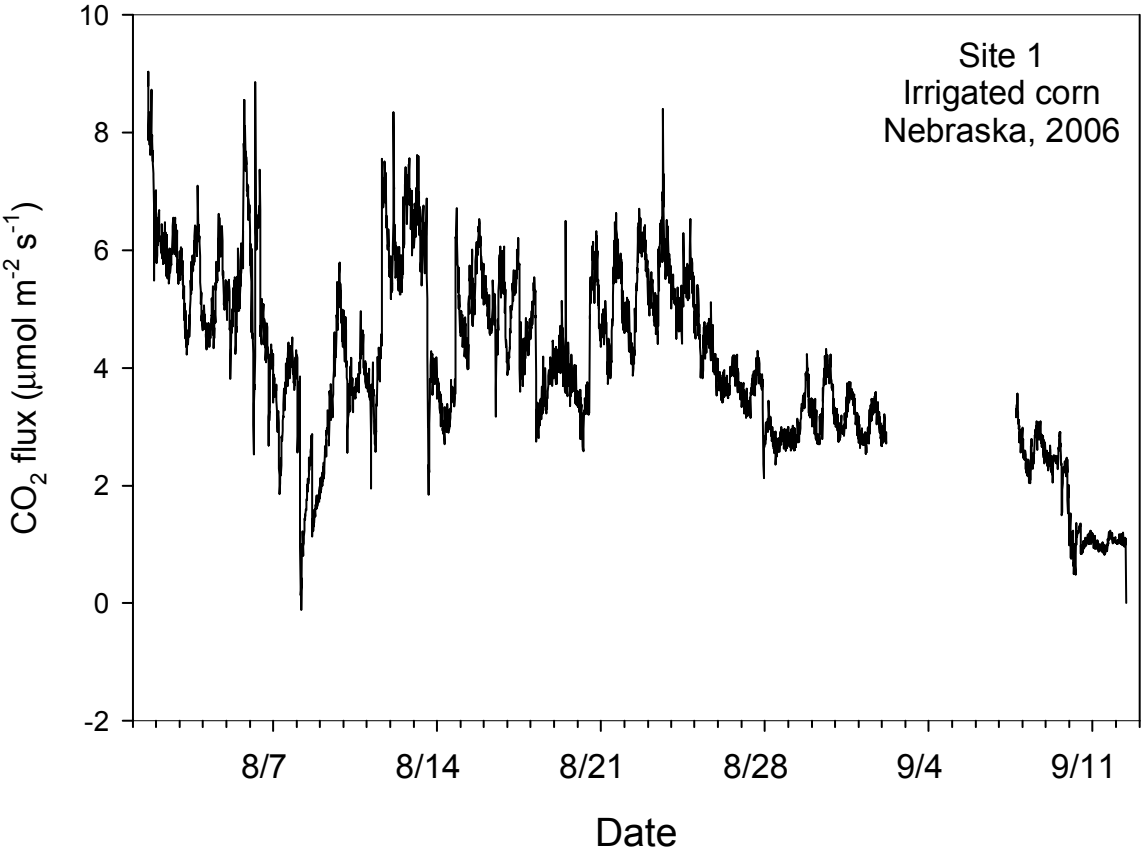

Figure A1. Automated long-term measurements of CO_2 flux with LI-8100 automated soil CO_2 flux system. The system, powered with two marine batteries, was set up in the irrigated corn field (site 1) at the Agricultural Research and Development Center (ARDC), Univ. of Nebraska at Lincoln, Nebraska, 2006. The use of LI-8100 system was by courtesy of LI-LOR Inc. Data collection started from Aug. 1 and ended on Sep. 12. Measurement interval was 15 min. The data gap in early September was due to out of battery. The data presented here was not included or analyzed in the study, because I had no control and information about the timing, intensity and quantity of irrigation (done by center-pivot irrigation system), and often could not distinguish the effects of irrigation from those of natural rain events. However, there is still some information that could be deciphered from the data. For example, the sharp decreases in flux on Aug. 6, 8, and 14 were probably due to rain events. Due to regular irrigation, site 1 always had higher soil moisture, and muddy soils and surface accumulation of water was commonly seen. Therefore, occurrence of rain often led to temporary suppression of soil respiration.

Appendix II

Photos of Field and Laboratory Experiment Set-up

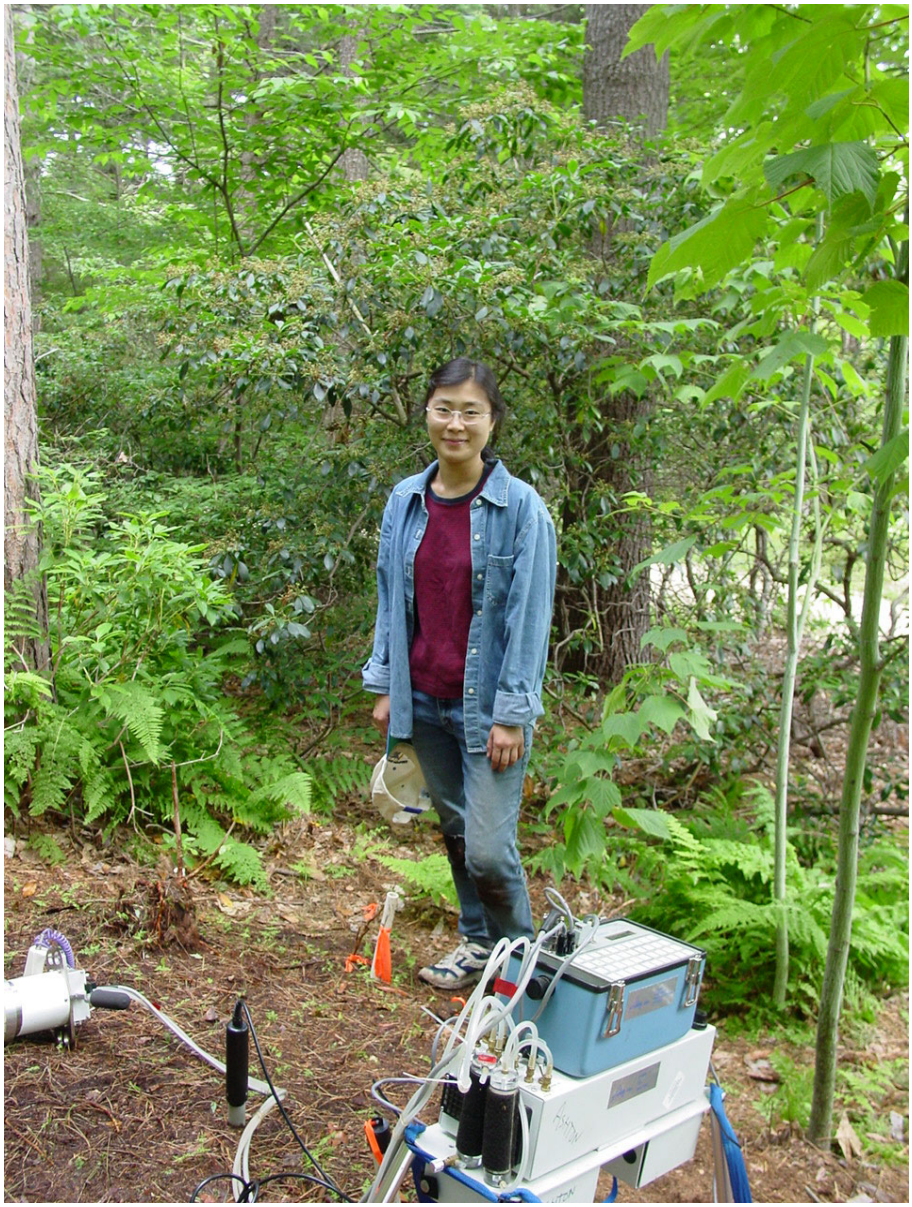

Figure A2. Field set-up at Great Mountain Forest, 2002. LI-6200 was used for CO_2 flux measurements. The plot shown here is a bare plot on a gentle slope.

Figure A3. Field set-up and flux measurement at Harvard Forest, 2004. LI-6200 was used for CO_2 flux measurement here. Flux measurement was being made on a forest floor plot, while soil moisture probe was already set to prepare for measuring soil moisture on a nearby bare plot at the next time step.

Figure A4. Field set-up and rain simulation at Harvard Forest, 2005. LI-6400 was used for CO_2 flux measurement here.

Figure A5. Field set-up at Nebraska soybean site 2, 2006. LI-6400 was used for CO_2 flux measurement here. Plots were placed between rows of soybean plants. The picture was taken at the beginning of the growing season (June 20).

Figure A6. Plot with intact crop residues and plot with residues removed on the Nebraska soybean site. Aboveground residues were corn stalks from previous year.

Figure A7. LI-8100 automated soil CO_2 flux system set up in the irrigated corn field site 1 (courtesy of LI-COR, Inc.) in ARDC, Univ. of Lincoln, Nebraska, 2006. The system consisted of an analyzer control unit and a long-term chamber (model 8100-101), collecting soil CO_2 data continuously for over a month (as presented in Fig. A1).

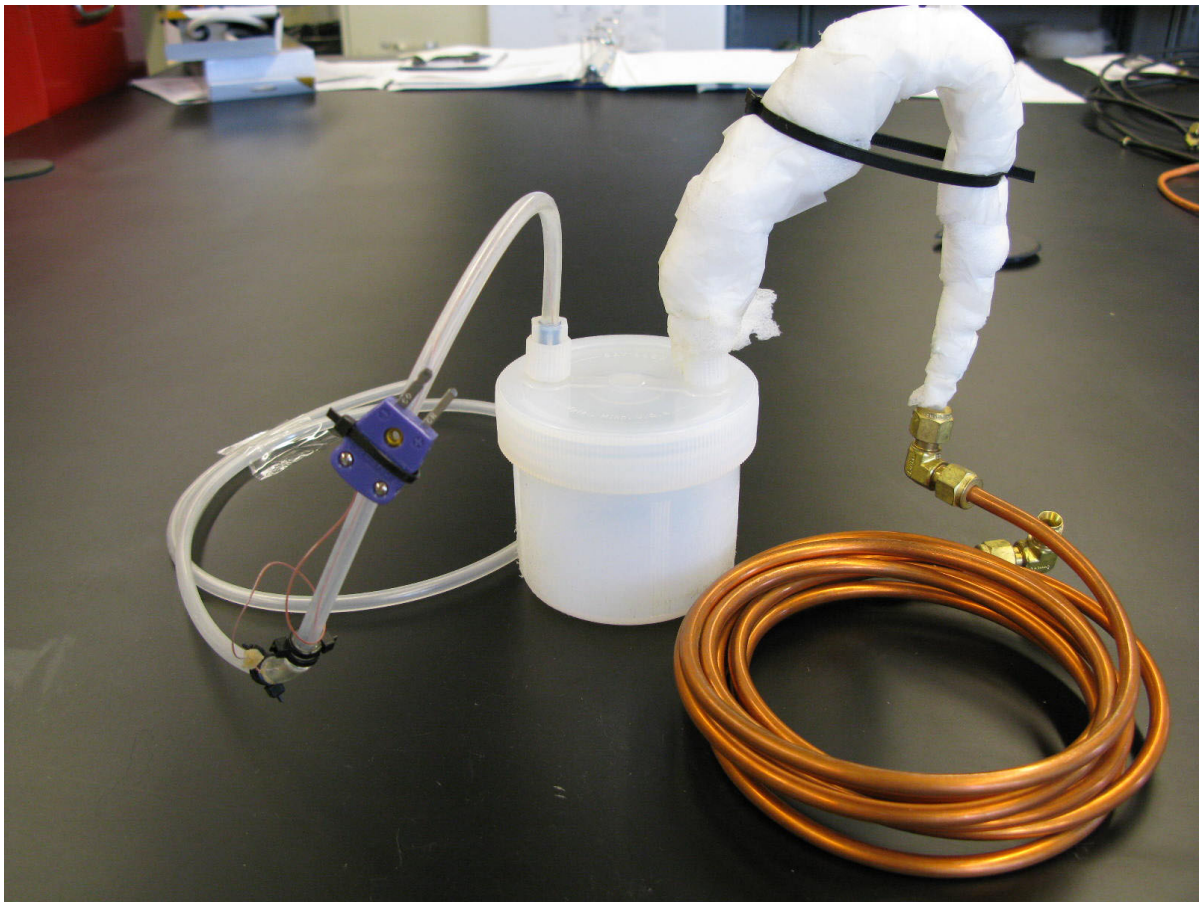

Figure A8. Parts of incubator for litter incubation experiments, as represented in Fig. 4.1.