Drying and Wetting Effects on Carbon Dioxide Release from Organic Horizons

W. Borken,* E. A. Davidson, K. Savage, J. Gaudinski, and S. E. Trumbore

ABSTRACT

Drying and wetting cycles of O horizon in forest soils have not received much attention, partly due to methodological limitations for nondestructive monitoring of the O horizon water content. The objective of this study was to determine the importance of moisture limitations in the O horizon of a temperate forest on summertime soil respiration. We measured soil respiration in three replicated plots in a mixed deciduous forest at Harvard Forest, Massachusetts, weekly from May to October 2001. Direct Current (DC) half-bridge sensors that had been calibrated using destructive samples of the Oi and Oe/Oa horizons were placed in the Oi and Oe/Oa horizons to record hourly changes of gravimetric water contents. Soil temperature explained 47% of the variation in soil respiration using the Arrhenius equation. The residuals of the temperature model were linearly correlated with gravimetric water content of the Oi horizon ($r^2 = 0.72$, $P < 0.0001$) and Oe/Oa horizon ($r^2 = 0.56$, $P < 0.001$), indicating that temporal variation in soil respiration can be partly explained by water content of the O horizon. Additionally, a laboratory study was performed to evaluate drying/wetting cycles of the O horizon at constant temperature. Even small simulated rainfall amounts of 0.5 mm significantly increase CO_2 flux from dry O horizon within a few minutes. The duration of CO_2 pulses increased with the amount of applied water, lasting from a few hours to days. A strong correlation between CO_2 release and water content of the O horizons demonstrates a clear regulatory role of litter water content on decomposition within the O horizons.

THE O HORIZON of many temperate and boreal forests stores a large amount of soil organic matter that is not physically protected against microbial decomposition. It is thought that the turnover time of soil organic matter is mainly a result of litter quality, soil fertility, mineralogy, soil texture, temperature, and soil moisture (Davidson et al., 2000). In general, the storage of soil organic matter increases at high water contents and decreasing temperature, resulting in thicker O horizons with increasing latitude (Trumbore, 2000). In undisturbed, mature forests, the amount of soil organic matter is usually near steady state, with similar rates of decomposition and C inputs on decadal time scales. However, variation in temperature and soil moisture may alter rates of decomposition and litter production on seasonal and annual time scales. Hence, soil respiration, which is the largest flux of CO_2 from the terrestrial biosphere to the atmosphere (Schimel, 1995), is likely to respond to climatic drivers seasonally and interannually, thus contributing to interannual variations in forest C balances (Barford et al., 2001).

In terms of global warming, the effect of temperature on decomposition of soil organic matter and soil respiration has been intensively investigated in laboratory and field studies. By contrast, little is known about how temperate and boreal forest soils respond to short-term and long-term changes in soil moisture. The response to changes in soil moisture may vary from site to site. Within the same study area, Davidson et al. (1998) reported decreased soil respiration of well-drained soils and increased soil respiration of poorly drained soils during dry summer, while opposite results were found for wet summers. An increase or decrease in precipitation as well as changes in frequency and distribution of precipitation due to large-scale natural climatic or interannual variability could affect soil respiration and the storage of soil organic matter.

According to the model of Bunnell and Tait (1974), soil moisture has no or little effect on microbial activity within a certain optimum range, but is important at higher or lower water contents. Moreover, the range of optimum soil moisture values decreases with increasing temperature, so that variation in soil moisture potentially becomes more important at higher temperatures. Low water contents can limit the growth rate and activity of soil microorganisms as well as the diffusion of nutrients and C substrates in water films, whereas high water contents can restrict the oxygen supply of microorganisms (Skopp et al., 1990; Howard and Howard, 1993). In many temperate and boreal regions, O horizons are subjected to rapid changes in water content during the growing season. Despite the importance of the O horizon as an organic C reservoir, most drying/wetting studies have focused on mineral soils. From laboratory studies it is well known that wetting of dry mineral soils causes a pulse of CO_2 for a few days (Birch, 1958; Orchard and Cook, 1983; Kieft et al., 1987). The CO_2 pulse has been attributed to improved C availability from killed microbial biomass and increased availability of soil organic C (SOC) due to increased exposure of organic surfaces during drying (Birch, 1958; Orchard and Cook, 1983, van Gestel et al., 1991). The response to wetting may vary with soil texture, quality and quantity of soil organic matter, temperature, frequency of drying and wetting cycles, and the amount of added water. Franzluebbers et al. (2000) suggested the use of the CO_2 pulse following wetting of dry soil as an indicator for biological soil quality, because they found that the CO_2 pulse was strongly correlated with soil microbial biomass and net N mineralization. Borken et al. (1999) reported that the temperature during wetting events

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Abbreviations: DC, direct current; IRGA, infrared gas analyzer; SOC, soil organic carbon; TDR, Time domain reflectometry.

had a strong effect on the intensity of CO_2 pulses in a temperate spruce forest. When the spruce soil was gradually wetted in summer at high soil temperature, soil respiration increased by 144% compared with the control, while wetting in autumn at low soil temperature had no significant effect on soil respiration. Conversely, in arid climates it has been demonstrated that the temperature sensitivity of soil respiration is expressed only when the soil is adequately moist (Wildung et al., 1975; Xu and Qi, 2001).

The response of soil respiration following wetting of dry soils has rarely been reported from forests, although this is a frequent phenomenon. Wetting events have been attributed to increases in soil moisture of the mineral soil (Borken et al., 2002) since no reliable technique has been developed to continuously record the moisture conditions of O horizons. However, small rain events may wet up only the O horizons or parts of it while the covered mineral soil remains unaffected. Such small wetting events may last only for a few hours and are difficult to measure by weekly or biweekly measurements. Moreover, partial wetting of the O horizon might cause only small CO_2 pulses compared with overall soil respiration.

Time domain reflectometry (TDR) and frequency domain reflectometry (FDR) sensors have been successfully used to record volumetric soil water content of mineral soils (Roth et al., 1990; Veldkamp and O'Brien, 2000). However, the probes of these sensors require complete contact with the surrounding soil matrix and therefore are problematic for O horizons. The total pore space of the O horizon might vary with water content due to shrinking and swelling processes. Destructive samples are generally taken to determine the gravimetric water content of O horizons. One important disadvantage of destructive sampling is that short-term events on an hourly or daily basis are usually missed. Recently, DC half-bridge sensors were developed for continuous measurement of litter water content of the Oi/Oe horizons in a temperate deciduous forest (Hanson et al., 2003). This approach is based on the electrical impedance grids for recording wetness of leaves (Gillespie and Kidd, 1978) and monitors the resistance or voltage across an intact dead oak (*Quercus prinus* L.) leaf as a function of litter water content (Hanson et al., 2003).

The objective of this study was to evaluate drying and wetting effects of the O horizon on soil respiration of a temperate deciduous forest at Harvard Forest. The approach of Hanson et al. (2003) using DC half-bridge sensors was modified by (i) using basswood pieces instead of intact oak leaves, (ii) installing DC half-bridge sensors separately in the Oi and Oe/Oa horizons and (iii) calibrating the volt signals of DC half-bridge sensors using gravimetric water content from destructive samples of the Oi and Oe/Oa horizons. In addition to field measurements of soil respiration and water content, the effect of repeated drying and wetting events on heterotrophic respiration of the O horizon from Harvard Forest was investigated in the laboratory at constant temperature.

MATERIALS AND METHODS

The study was conducted on three 5 by 5 m plots in a mixed deciduous forest at the Prospect Hill tract of the Harvard Forest (42° 32′ N lat., 72° 11′ W lat.) in Petersham (340 m elevation), MA. The forest developed after a hurricane in 1938 and is dominated by red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.). Before the hurricane, a mixed deciduous forest had developed on pastures abandoned since the late 19th century (Foster, 1992). As a result of 19th century agricultural use, the upper mineral soil is partly disturbed as indicated by varying depths of the A horizons from 2 cm down to 15 cm. The thickness of the mineral soil varies from 40 to 65 cm and has rock contents up to 40% of soil volume. The soil, a fine sandy loam, is well aerated and has been classified as a well-drained Typic Dystrochrept. The O horizon is 3 to 8 cm thick, stores about 7 kg m^{-2} of organic matter, and consists of Oi, Oe, and Oa horizons. An average maximum water-holding capacity of 19 L m^{-2} was measured for the total O horizon. Mean annual air temperature is 8.5°C and mean annual precipitation is 1050 mm.

Soil moisture of the O horizon was measured directly by gravimetric water content and indirectly with DC half-bridge sensors. Gravimetric water content was measured on 17 sampling days from June to October 2001 by taking five random samples of 100 cm^2 area outside the study plots. The O horizon was separated into Oi and Oe/Oa horizons from which the coarse roots >2 mm in diameter were removed. The water content of the Oa horizon was not separately measured because its thickness was usually <1 cm and did not allow the installation of DC half-bridge sensors. Fresh samples were weighed, and then dried at 60°C for 1 wk.

Relative changes in water content of the Oi and Oe/Oa horizon were continuously measured on hourly basis from June throughout October 2002 using DC half-bridge sensors (Fig. 1). This method, described by Hanson et al. (2003), was modified by using one 1.59 mm thick and 9 cm^2 basswood (*Tilia americana* L.) piece (cut out from 1/16″ by 4″ by 24″ basswood, Midwest Products CO., Inc., Hobart, IN) per sensor instead of a dead oak leaf. Two stainless steel alligator clips, connected to 15 to 25 m lengths of six conductor 22 AWG cables, were attached to each basswood piece with a spacing of 2 cm between the paired clips. At hourly intervals a data logger (CR10X, Campbell Scientific, Logan, UT) supplied a constant 2.5 V signal across the wood and logged the voltage. The electronic setup of DC half-bridge sensors followed the AM416 Relay Multiplexer instructions by Campbell Scientific Inc. (1996) for half-bridge measurements. The voltage reading on the data logger can be described by the following equation:

$$V_1 = Vx - Vx \times [Rs/(Rs + Rf)],$$

where V_1 is the data logger voltage reading in V, Vx is 2.5 V, Rf is the resistance of the fixed resistor (390 kΩ), and Rs is the resistance of basswood (Fig. 1). A DC voltage of 2.5 V (Vx) is applied across the half-bridge circuit and the return signal (V_1) is related to the resistance of basswood (Rs). As moisture increases in the O horizon, the basswood quickly equilibrates and its resistance decreases, thereby causing an
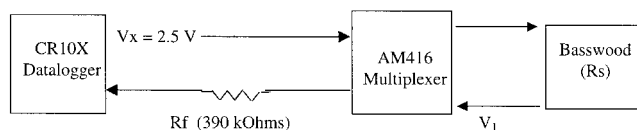

Fig. 1. General description of the direct current half-bridge sensor. The data logger and multiplexer are used to monitor the change in resistance of a piece of basswood placed in the O horizon as a function of water content.

increase in V_1. Different resistors with known resistance (10 kΩ, 413 kΩ, 835 kΩ, 1MΩ) were put in place of the basswood to test the half-bridge set up. In each of the three plots, four and eight DC half-bridge sensors were installed in the Oi and Oe/Oa horizons, respectively. The installation depth in the Oe/Oa horizon was 2 to 6 cm, varying with the thickness of the O horizon.

Calibration curves were obtained for DC half-bridge sensors by performing linear regressions across dates between the mean voltage signal of the 12 (Oi) or 24 (Oe/Oa) sensors and mean gravimetric soil water contents of five destructive samples of each horizon taken randomly from the study area.

In each of the three plots, four PVC collars, 10 cm tall and 25 cm in diameter, were installed approximately 4 cm into the soil for the duration of the experiment. Soil respiration was measured weekly from June to October 2001 between 0900 and 1200 h using a vented chamber with a volume of 5.2 L that was placed over a collar and connected to a portable infrared gas analyzer (IRGA, Licor 6252, LI-COR, Lincoln, NE). Air was circulated in this closed system by a pump with a constant rate of 0.5 L min^{-1}, and the increase in CO_2 concentration was recorded every 12 s for a 5 min period. Linear regressions were performed to calculate the CO_2 flux rates, which were corrected by air pressure and air temperature within the headspace. A certified standard of 523 μL CO_2 L^{-1} (±2%) was used to calibrate the IRGA each sampling day. More details about this method are given by Davidson et al. (1998; 2002). Soil temperature at the 10-cm depth was manually measured next to each collar using a temperature probe. Volumetric water content of the mineral soil at the 5-cm depth was determined hourly using one horizontally installed TDR sensor (CS615 Water Content Reflectometer, Campbell Scientific, Logan, UT) per plot. The TDR sensors were connected to the data logger (CR10X, Campbell Scientific, Logan, UT).

To study the response of repeated drying and wetting on heterotrophic respiration, three intact O horizon samples, each of 700 cm^2, were taken from the same mixed hardwood stand in the summer of 2000. The O horizon had a thickness of 6.3 to 6.7 cm and dry weights of 800 to 1050 g. The samples were placed in plastic boxes (hereafter, "microcosm") and dried at ambient air temperature for 4 mo. In each microcosm, three DC half-bridge sensors were permanently installed at depths of 0.5, 2, and 5 cm to measure gravimetric water content. The field calibration curves for the Oi horizon (Fig. 2a) were used to convert voltage signals of the DC half-bridges in the leaf litter into gravimetric water contents. Voltage signals from the 2- and 5-cm depth were converted into gravimetric water contents using the field calibration of the Oe/Oa horizon (Fig. 2b). Each microcosm had a sealable lid that could be closed for measurements of CO_2 production.

The O horizon was allowed to dry at room temperature before the wetting experiment began and between each of the water additions in the first experiment. Each of the three replicate microcosms received the same sequence of water additions over a 79-d period in the following order: 0.5, 1, 2, 4, 8, and 0.5 mm. At least 1 wk of drying was permitted between water additions and until the CO_2 flux decreased below 7 mg C m^{-2} h^{-1}, when the next wetting treatment was then applied. The water was sprayed onto the surface in <5 min, except in the case of the 8.0 mm wetting treatment, which required a gradual addition of water sprayed over a 1-h period. Incubation temperature (17 ± 1°C) was adjusted 24 h before CO_2 measurements were performed.

In a second experiment, a sequential, stepwise wetting with 2, 2, 4, 4, and 8 mm d^{-1} was performed within 5 d to measure the short-term increase in CO_2 flux from dry to water saturated O horizon. In total, an amount of 20 mm water was added to
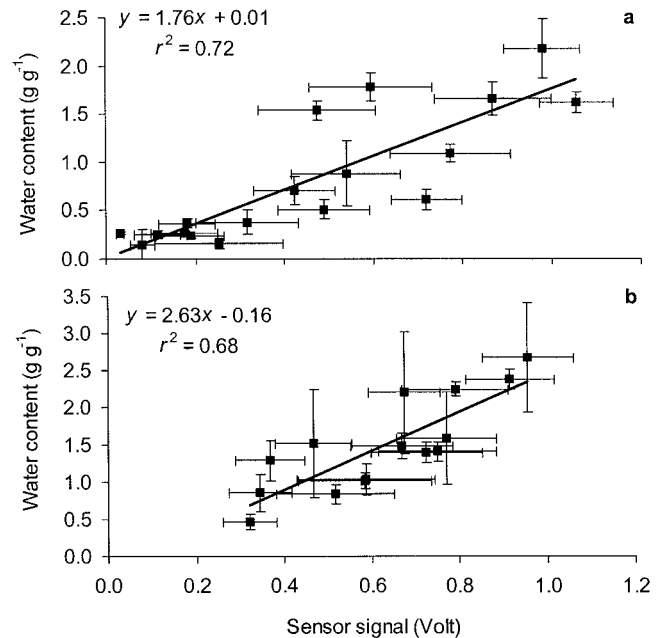

Fig. 2. Relationship between gravimetric water content ($n = 5$) and volt signal from direct current half-bridge sensors installed in the (2a; $n = 12$) Oi horizon and (2b; $n = 24$) Oe/Oa horizon. Error bars represent the standard error of the mean.

each microcosm, which is 1 mm more than average maximum water-holding capacity of the O horizon at our study site. All O horizons were water saturated after 5 d, and drained water was removed from microcosms to avoid anaerobic conditions. Microcosms were continuously incubated at 17 ± 1°C during this experiment. Carbon dioxide fluxes of the dry and wetted O horizon were measured in the same way as in the forest, except that the microcosms were sealed with a lid fitted with sampling ports similar to the chamber used for respiration measurements in the field.

Soil respiration rates, soil temperatures, and DC half-bridge signals from the field study were means of three replicate plots. Linear and nonlinear regressions were performed (Systat Software, 2001) (i) to evaluate the relationships of DC half-bridge signals and gravimetric water contents of the Oi and Oe/Oa horizon, (ii) to model the temperature dependency of soil respiration using the Arrhenius function, and (iii) to evaluate the relationship between residuals of the temperature model and gravimetric soil water content of the Oi and Oe/Oa horizon. Multiple linear regressions were performed to analyze the combined effects of soil temperature and soil water content of the Oi, Oe/Oa and A horizons on soil respiration.

RESULTS

Field Measurements

The DC half-bridge sensors were calibrated using gravimetric water contents of samples from the Oi and Oe/Oa horizons. Voltage signals of DC half-bridge sensors were linearly correlated ($r^2 = 0.72$, $P < 0.001$) to gravimetric water content of the Oi horizon (Fig. 2a). The correlation between gravimetric water content and the voltage signal of the Oe/Oa horizon was weaker ($r^2 = 0.68$, $P < 0.001$) than for the Oi horizon (Fig. 2b).

Soil respiration varied from 65 to 266 mg C m^{-2} h^{-1} during the growing season, mainly following the tempo-
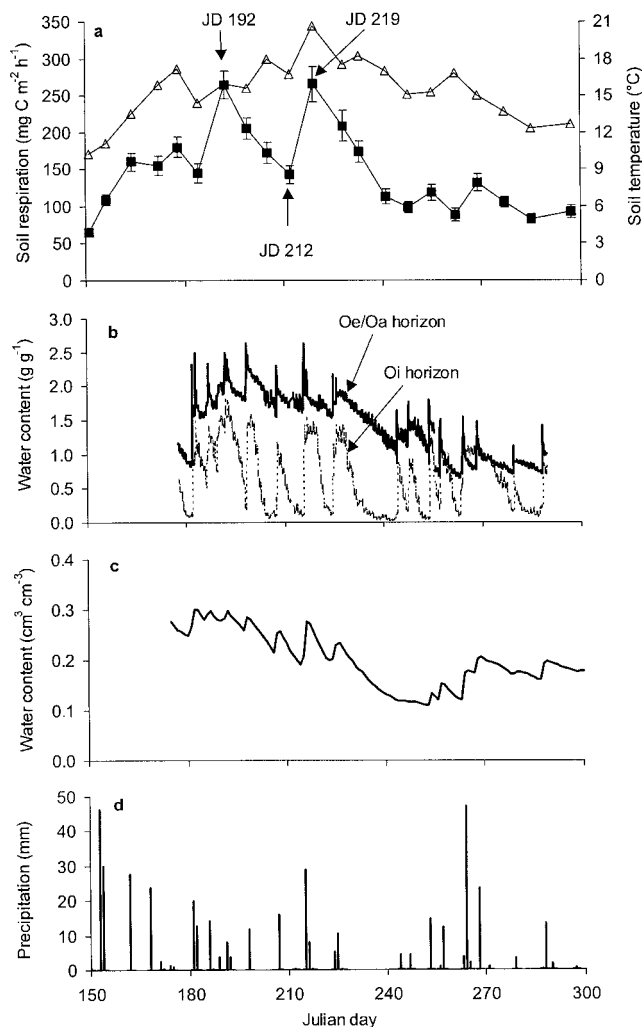
Fig. 3. (a) Mean soil respiration (squares) and mean soil temperature at the 10-cm depth (triangles) **(b)** predicted gravimetric water contents in the Oi and Oe/Oa horizons, **(c)** volumetric soil water content at the 5-cm mineral soil depth, and **(d)** daily precipitation of a mixed deciduous forest at Harvard Forest from June to October 2001. Error bars represent the standard error of mean soil respiration rate ($n = 3$).

Fig. 4. Relationship between soil respiration and soil temperature at the 10-cm depth using the Arrhenius equation ($n = 21$). Symbols A, E, R, T of the Arrhenius equation stand for Arrhenius constant (dimensionless), apparent activation energy (kJ mol^{-1}), gas constant (kJ mol^{-1} K^{-1}), and soil temperature (K), respectively.

ral course in soil temperature (Fig. 3a). The first maximum soil respiration rate of 265 mg C m^{-2} h^{-1} occurred on Julian day 192, corresponding with high water contents in the Oi and Oe/Oa horizon (Fig. 3b) and top mineral soil (Fig. 3c), following precipitation of 11.5 mm on Julian day 191 and 192 (Fig. 3d). Subsequently, soil respiration dropped continuously to 143 mg C m^{-2} h^{-1} until Julian day 212 although soil temperature increased by 0.8°C, suggesting that low soil moisture reduced soil respiration on these four sampling days. During this 20-d period, two rainfall events of 11.7 and 16.0 mm on Julian days 198 and 207, respectively, wetted the Oi and Oe/Oa horizon and mineral soil (Fig. 3b and 3c). However, the water content of the Oi and Oe/Oa horizon dropped again to the previous level within 4 d. The second maximum soil respiration rate of 266 mg C m^{-2} h^{-1} on Julian day 219 corresponds with the seasonal maximum soil temperature of 20.6°C as well as to previous rainfall of 37.4 mm on Julian days 215 to 217. During
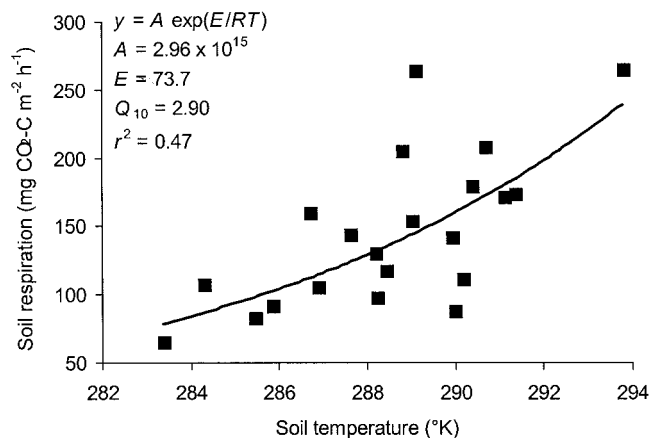
the following 22 d soil respiration dropped again continuously to 112 mg C m^{-2} h^{-1}, accompanied by a 3.6°C soil temperature decrease and declining soil moisture in the O horizon and top mineral soil.

The large fluctuation of water content in the Oi horizon between 0.03 and 1.81 g g^{-1} shows this horizon is subjected to frequent and extreme drying and wetting cycles (Fig. 3b). Direct current half-bridge sensors responded within a few hours to precipitation events, depending on the previous moisture level and the amount of precipitation. In total, the Oi horizon showed 10 pronounced wetting events from Julian day 177 to 289. The water content of the Oe/Oa horizon ranged between 0.65 and 2.64 g g^{-1}; however, the fluctuation in water content was less pronounced than in the Oi horizon (Fig. 3b). Direct current half-bridge sensors appeared to overestimate the minimum water content of 0.65 g g^{-1} (equivalent to 0.31 V) in the Oe/Oa horizon, whereas destructive samples revealed a water content of 0.47 g g^{-1} (Fig. 2b).

Volumetric water content of the mineral soil as measured by TDR ranged between 0.11 and 0.30 cm^3 cm^{-3} (Fig. 3c). In contrast to the O horizon, the mineral soil did not respond to precipitation events of 4.3 mm on Julian day 244 and 247, indicating that the mineral soil is less subjected to wetting events. Despite the precipitation of 105 mm between Julian day 253 and 268, the volumetric water content of the top mineral soil remained below 0.21 cm^3 cm^{-3}.

Relationship between Soil Respiration, Temperature, and Water Content

Using the Arrhenius equation, soil temperature measured at the 10-cm depth explained 47% ($P < 0.001$) of the variation in soil respiration and revealed a Q_{10} value of 2.90 for the temperature range between 10.5 and 20.5°C (Fig. 4). The residuals of the Arrhenius model were best explained by gravimetric water content of the Oi horizon ($r^2 = 0.72$, $P < 0.0001$) obtained from
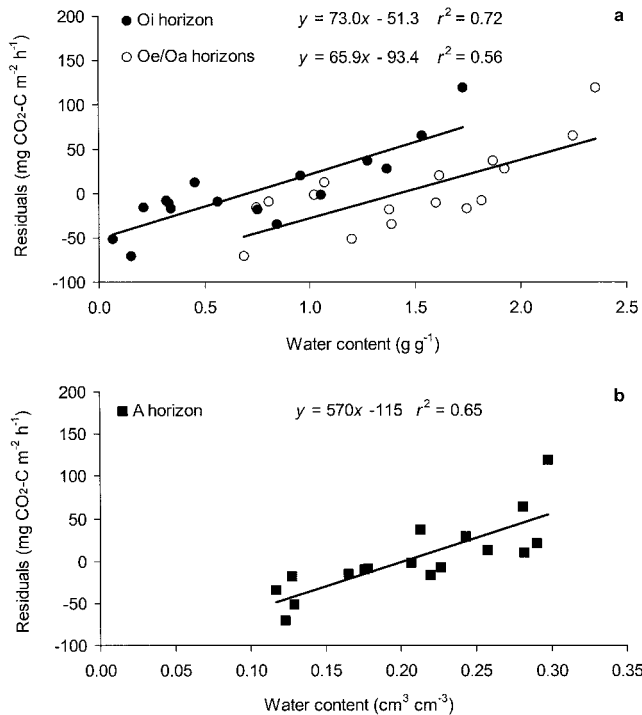
Fig. 5. Residuals of the Arrhenius equation versus (a) gravimetric water contents predicted by direct current half-bridge sensors in the Oi and Oe/Oa horizons and (b) volumetric water content of the mineral soil at the 5-cm depth measured with time domain reflectometry sensors. Positive residuals indicate an underestimation of soil respiration by the temperature function when water contents are high and negative residuals indicate an overestimation of soil respiration by the temperature function when water contents are low. Data were obtained from field measurements at the Harvard Forest.
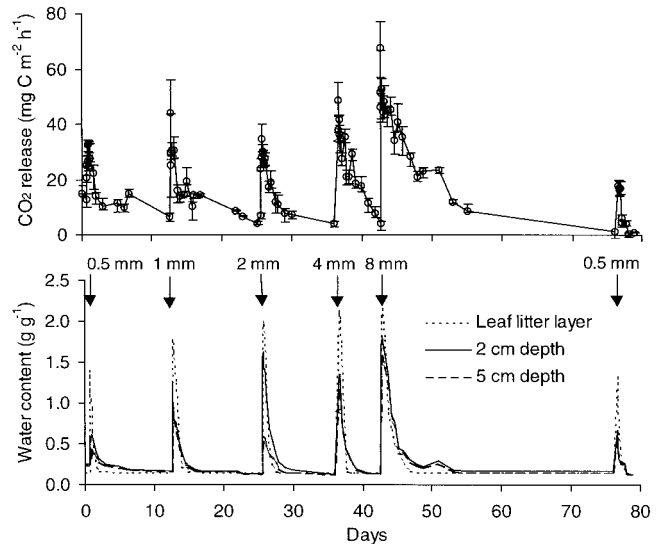

Fig. 6. Carbon dioxide release of O horizon, and water contents of leaf litter layer, the 2- and 5-cm depth during drying and wetting cycles. The O horizon material was initially air-dry. Stepwise additions of 0.5, 1, 2, 4, 8, and 0.5 mm of water were applied sequentially over 79 d in laboratory microcosm experiments. Error bars represent the standard error of the mean of three replicate microcosms ($n = 3$).

DC half-bridge measurements (Fig. 5a). The gravimetric water content of the Oe/Oa horizon determined by DC half-bridge sensors explained 56% ($P < 0.001$) of the residuals (Fig. 5a). The linear relationship between residuals and volumetric water content of the mineral soil at the 5-cm depth (Fig. 5b; $r^2 = 0.65$, $P < 0.001$) indicates that responses of either or both the O horizon and the top mineral soil could contribute to variation in soil respiration during drying and wetting events.

Another approach for analyzing the combined effects of temperature and water content on soil respiration is multiple linear regression. The temperature response is nearly fitted equally well by linear ($r^2 = 0.45$) and exponential functions ($r^2 = 0.47$), and so a linear function was used to simplify multiple linear regression. Temperature and water content were not correlated, so these factors are independent in the multilinear regression analysis. Combining a linear temperature term with a linear moisture term explained 80% ($y = 16.2 \times$ Temp $+ 73.6 \times$ Water $- 161$, $P < 0.0001$), 72% ($y = 9.33 \times$ Temp $+ 76.4 \times$ Water $- 107$, $P < 0.0001$), and 74% ($y = 15.5 \times$ Temp $+ 572 \times$ Water $- 213$, $P < 0.0001$), of the variation in soil respiration using the water contents of the Oi, Oe/Oa or A horizons, respectively.

Laboratory Incubation: Drying and Wetting Effects on Heterotrophic Respiration of O Horizon

The CO_2 release from the dry O horizon of the microcosms was <8 mg C m^{-2} h^{-1} before wetting. A postwetting pulse of CO_2 release peaked <5 min after the water was added to the dry O horizon (Fig. 6). Peak CO_2 fluxes of similar magnitude were observed at water additions of 0.5 (32 mg C m^{-2} h^{-1}), 1.0 (44 mg C m^{-2} h^{-1}), and 2.0 mm (35 mg C m^{-2} h^{-1}). Larger peak CO_2 fluxes were observed at 4 (50 mg C m^{-2} h^{-1}) and 8 mm (68 mg C m^{-2} h^{-1}) water additions. The rate of CO_2 release dropped as soils dried to prewetting levels in 1 to 10 d, with the slowest decline occurring after the largest water additions. These pulses of 30 to 50 mg C m^{-2} h^{-1} following laboratory wetting are smaller than the CO_2 pulses of about 125 mg C m^{-2} h^{-1} measured in the field (Fig. 3a), but clearly are large enough to contribute significantly to post-wetting pulses in situ. In the microcosm experiment, we repeated the 0.5-mm addition at the end of the experiment, after the O horizon had dried again. The first and last CO_2 pulses following addition of 0.5 mm water were similar, although the CO_2 flux of dry O horizon was higher at the beginning of the experiment than after 77 d (Fig. 6).

In the second microcosm experiment, the stepwise wetting of the O horizon to water saturation by adding 20 mm within 5 d increased the CO_2 release to a maximum of 67 mg C m^{-2} h^{-1} (Fig. 7). Each water addition caused a CO_2 pulse that was probably related to wetting of previously dried organic matter. After the last water addition, the CO_2 release and the water contents of the gradually drying O horizon were measured during the following 20 d. During these incubations at constant temperature, the gravimetric water contents of the leaf
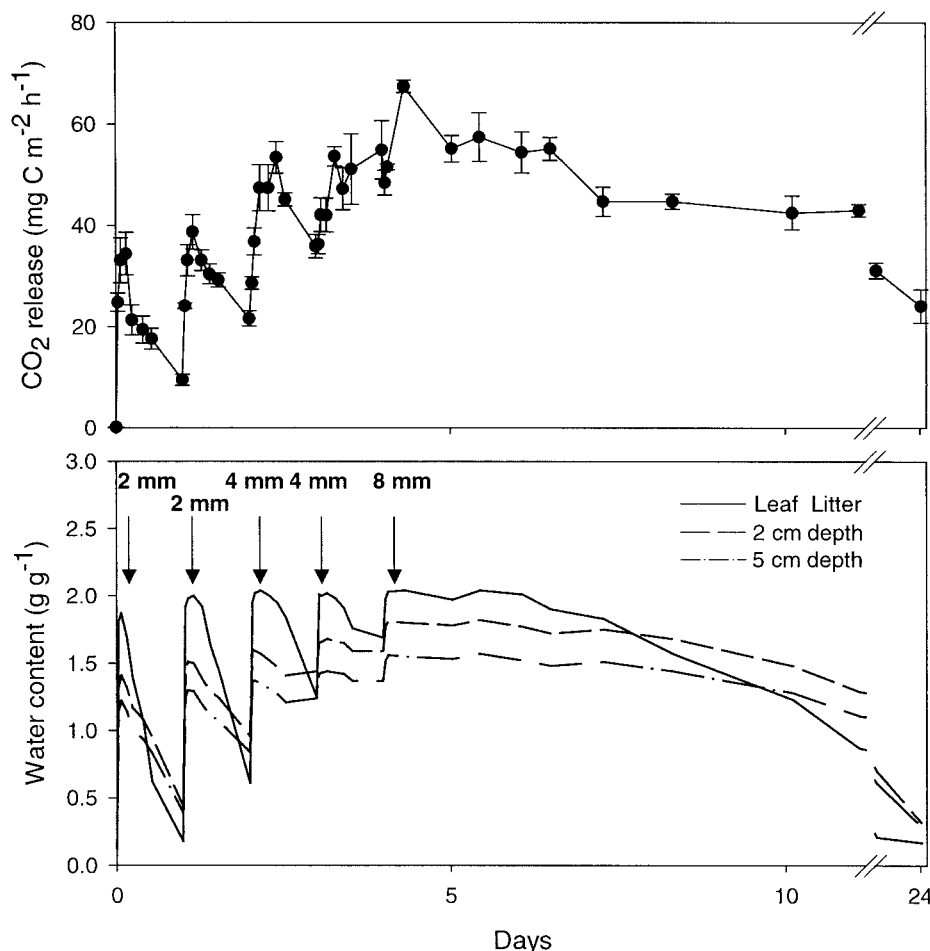
Fig. 7. Carbon dioxide release from the O horizon and water contents in the leaf litter layer, and at the 2- and 5-cm depths in a second laboratory microcosm experiment. O horizon material was initially air-dried. Stepwise additions of 2, 2, 4, 4, and 8 mm of water were applied sequentially over 5 d. Error bars represent the standard error of the mean of three replicate microcosms (n = 3).

litter layer, the 2- and 5-cm depth explained 60 ($P <$ 0.001), 71 ($P <$ 0.001), and 73% ($P <$ 0.001), of the variation in CO_2 fluxes, respectively (Fig. 8a–c). The maximum water content decreased from 2.15 g g^{-1} in the leaf litter layer to 1.57 g g^{-1} at the 5-cm depth, whereas the minimum water contents of 0.15 to 0.13 g g^{-1} were consistent for all three depths. Due to the limitation of DC half-bridge sensors at low water contents <0.15 g g^{-1}, the relationships between CO_2 release and low water contents were weak (Fig. 8a–c).

DISCUSSION

Direct Current Half-Bridge Sensors

Determination of gravimetric water content of the O horizon is often limited by destructive sampling and by small plot areas, resulting in the lack of information for studying drying/wetting cycles in forests. Except at very low water contents, DC half-bridge sensors equipped with basswood represent an inexpensive and reasonably reliable technique to continuously measure the water content of the Oi and Oe/Oa horizon without disturbing the O horizon. Our field calibration showed intercepts of 0.01 g g^{-1} for the Oi horizon and −0.16 g g^{-1} for the Oe/Oa horizon. Because the lowest gravimetrically

measured water contents were 0.15 g g^{-1} for the Oi horizon and 0.47 g g^{-1} Oe/Oa horizon, the DC half-bridge calibration is less certain for lower water contents.

The sensors responded immediately to drying and wetting events, indicating rapid equilibration with the surrounding organic matter. However, our results show that due to the large heterogeneity in the thickness and composition of O horizon, many DC half-bridge sensors are required to obtain an accurate estimate of the water content on a 25-m^2 scale. The calibration curve for the Oe/Oa horizon (Fig. 2b) was rather weak (r^2 = 0.68) although twice as many DC half-bridge sensors were installed in this horizon compared with the Oi horizon. One explanation is that the spatial and vertical variation in gravimetric water content of the Oe/Oa horizon is higher than that of the Oi horizon, as indicated by larger error bars (Fig. 3a and 3b). In fact, the water-holding capacity of the O horizon decreases with increasing depth as a result of degree of decomposition and decreasing organic matter content.

In contrast to our approach, Hanson et al. (2003) installed intact leaves from *Q. prinus* for DC half-bridge sensors and obtained a linear calibration (r^2 = 0.87) for the Oi horizon by collecting separate *Q. prinus* leaves at varying water contents over time. It is not known
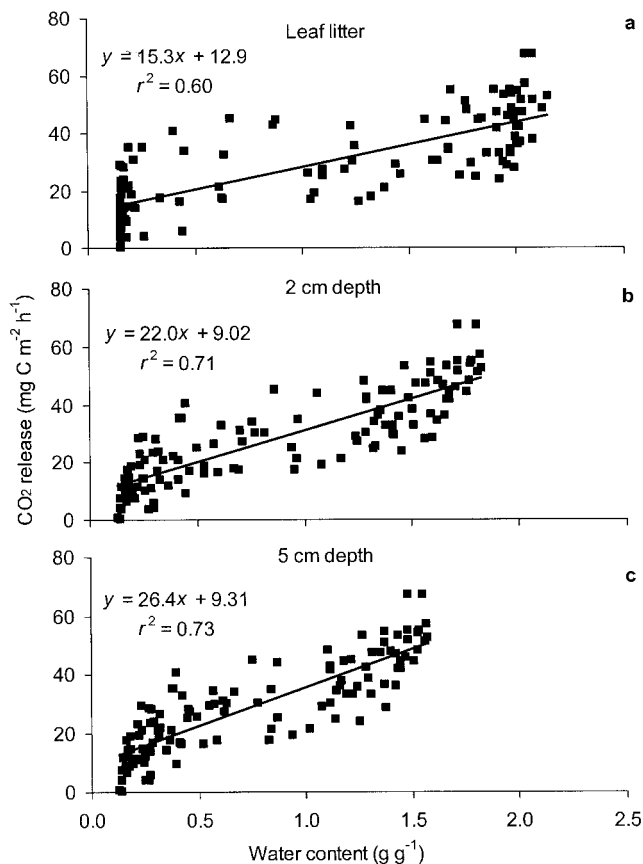
Fig. 8. Relationship between CO_2 release and water content of (a) leaf litter layer, (b) the 2- and (c) 5-cm depth of O horizon from Harvard Forest in laboratory microcosm drying and wetting experiments. This figure includes all data from Fig. 6 and 7.

how well a calibration based on intact leaves of a single species or one based on commercially available basswood sticks accurately reflects the water content of O horizon material that is comprised of litter from several species at varying degrees of decay. However, our calibration using basswood sticks relates the stick wetness to an integrated measure of the gravimetric water content of each sampled horizon. This approach allows monitoring of the water content of different layers in the O horizon and might also be applicable in coniferous forests. The disadvantage of using either basswood or *Q. prinus* leaves is that both materials may change their water-holding capacity during microbial decomposition over time. Hanson et al. (2003) observed only a small shift in the calibration with decomposition of oak leaves throughout the summer. The basswood was visually not decomposed during the growing season at Harvard Forest. Nevertheless, we recommend replacement of the basswood at the beginning of each growing season or more often if decomposition of basswood is observed. Moreover, a specific calibration curve may be required for each site because the water-holding capacity of O horizons may vary from forest to forest.

Effect of Drying and Wetting on Soil Respiration and Heterotrophic Respiration

Soil respiration at our study site was correlated with soil temperature ($r^2 = 0.47$), resulting in a Q_{10} value of

2.90 for the temperature range between 10.5 and 20.5°C. This is lower than the Q_{10} values of 3.4 and 3.5 reported by Davidson et al. (1998) for adjacent well-drained soils at Harvard Forest calculated for a temperature range of 3 to 20°C in 1995 to 1996. Including soil respiration rates from additional years, Savage and Davidson (2001) explained the negative residuals of their temperature model by soil moisture of the mineral soil, indicating a linear decrease in soil respiration with decreasing mineral soil matric potential. However, positive residuals of the temperature model could not be explained by mineral soil matric potential. In European beech and conifer forests, Borken et al. (2002) found a linear trend between residuals from their temperature model and the relative change in soil matric potential. In other words, the relative change in soil matric potential from wet to dry soil or from dry to wet soil was used as an indicator of drying and wetting processes that covaried with CO_2 fluxes. This approach, however, explained only a small part of the residuals from the temperature model. By contrast, our results here reveal linear relationships between the residuals (both positive and negative residuals) from the temperature model and water content of the Oi horizon ($r^2 = 0.72$), Oe/Oa horizon ($r^2 = 0.56$) and top mineral soil ($r^2 = 0.65$), indicating that soil respiration was strongly affected by drying and wetting of the O horizon and/or the top mineral soil. Both microbial respiration and root respiration may have responded to drying and wetting cycles, and their relative contributions to soil respiration at very dry soil conditions and subsequent wetting is unknown. Although the correlation is stronger for the water content of the Oi horizon, pulses of CO_2 emissions from the mineral soil following wetting events may also contribute to variation in soil respiration. However, short drought periods as well as small amounts of rainfall are more likely to alter respiration of the O horizon, while respiration of the mineral soil may require larger precipitation events and longer drought periods to be affected.

Taking a maximum water-holding capacity of 19 L m^{-2} (the equivalent of 19 mm precipitation) for the O horizon into account, the water deficit of the O horizon varied between 0 and 13 L m^{-2} (13 mm precipitation) during the growing season. Because precipitation events are usually <20 mm and summertime evapotranspiration of the Harvard Forest is usually on the order of 3 to 4 mm d^{-1} (Greenland, 1996), it is not surprising that the water content of the O horizon is very dynamic. Precipitation and DC half-bridge sensors indicated 10 pronounced drying/wetting cycles in the Oi horizon and to a lesser extend in the Oe/Oa horizon. In only two of these 10 cases did our weekly schedule of soil respiration measurements happen to fall within 1 d after the wetting event. Assuming that each wetting of dry O horizon caused a pulse in soil respiration, weekly measurements may underestimate annual soil respiration fluxes. According to the model simulation by Hanson et al. (2003), inclusion of decomposition associated with the wetting dynamics of the surface litter layer increased estimated annual soil respiration by 23% in a upland oak forest in Tennessee.

Our laboratory study suggests that soil microorganisms have the ability to respond within a few minutes to wetting. This is consistent with the observation by Orchard and Cook (1983), whereby the duration of the post-wetting CO_2 pulse may depend on many factors such as the duration of drought and the amount of water added. Not only did the maximum CO_2 pulse increase with the intensity of wetting, but also the period of elevated CO_2 release increased with increasing wetting intensity. Similar CO_2 pulses were measured in the second laboratory experiment, where the O horizon was wetted daily to achieve saturation within 5 d. Pulses of CO_2 releases in the range of 30 to 70 mg C m^{-2} h^{-1} represent 11 to 26% of the maximum in situ soil respiration rate at our study site. These CO_2 pulses observed in the laboratory are in the range of most of the positive residuals from the temperature model used to analyze field data (Fig. 5), indicating that the increase in soil respiration following wetting in the field could plausibly have resulted from increased microbial respiration of the O horizon.

The CO_2 pulse following wetting of dried soil has been related to the amount of easily decomposable C due to the death of microorganisms or exposure of easily decomposable C on drying (van Gestel et al., 1991). It is unclear if the frequency of drying/wetting cycles affects CO_2 pulses and C mineralization of O horizons in the long-term. Degens and Sparling (1995) demonstrated that repeated wetting-drying cycles had no effect on the C mineralization of a sandy loam soil. By contrast, Fierer and Schimel (2002) reported that the total CO_2 loss of sieved mineral oak soil increased with the number of rewetting events during 2 mo. However, disturbance of soil by sieving or root cutting may increase the availability of the light C fraction, resulting in higher CO_2 fluxes.

Franzluebbers et al. (2000) found a strong relationship between the CO_2 pulse within the first 24 h after wetting of dry mineral soils and soil microbial biomass. Generally, microbial biomass decreases strongly from the leaf litter layer down the soil profile and thus, the importance of drying/wetting processes for microbial respiration may decrease with depth. Because of the relatively strong response at only 0.5 mm water addition, which wetted only the surface layer of intact leaf litter, it is likely that a significant part of the easily decomposable C that can potentially be mineralized after wetting resides in the leaf litter layer. Moreover, the laboratory experiments reported here demonstrated that the source of available C apparently was not exhausted even after 5 or 6 wetting and drying events. The supply of mineralizable C to microorganisms may be less limiting in the organic-rich O horizon than in mineral soils, resulting in a larger potential for repeated pulses of CO_2 production after numerous wetting and drying events.

CONCLUSIONS

We conclude that microbial respiration of the O horizon decreases strongly with decreasing water content, and, therefore, that microbial decomposition of soil organic matter is frequently limited by low summertime water content at our study site. The CO_2 pulse following repeated wetting of dry O horizon can be explained by water content only, indicating that easily decomposable C is abundant. Because of the demonstrated link between O horizon water content and soil respiration, interannual variability in precipitation could affect interannual variation in net ecosystem exchange of C. The O horizon is likely to act as a temporary sink for C in dry years and a temporary source of atmospheric C in wet years, which may help explain interannual variation in net ecosystem exchange of C measured by eddy covariance at our Harvard Forest study site (Barford et al., 2001). Long-term trends in climate related to total precipitation and the seasonality of precipitation could also affect the storage of soil organic matter over the long-term.

From our DC half-bridge measurements it may be deduced that many of the CO_2 pulses due to wetting were not captured by our weekly field measurements of soil respiration, resulting in underestimation of annual soil respiration rates. We are currently measuring soil respiration hourly with an automated system to quantify the possible underestimate caused by missing pulse events in a weekly manual sampling protocol (Savage and Davidson, 2003). Direct current half-bridge sensors can be used for continuous monitoring of water content in layers of the O horizon, allowing the modeling of short-term and long-term responses of biogeochemical processes to changes in water content.

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