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Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest

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Abstract

Variation in soil temperature can account for most of the seasonal and diel variation in soil CO_2 efflux, but the temperature effect is not always consistent, and other factors such as soil water content are known to influence soil respiration. The objectives of this research were to study the spatial and temporal variation in soil respiration in a temperate forested landscape and to evaluate temperature and soil water functions as predictors of soil respiration. Soil CO_2 fluxes were measured with chambers throughout an annual cycle in six study areas at the Harvard Forest in central Massachusetts that include soil drainage classes from well drained to very poorly drained. The mean annual estimate of soil CO_2 efflux was 7.2 Mg ha^{-1}, but ranged from 5.3 in the swamp site to 8.5 in a well-drained site, indicating that landscape heterogeneity is related to soil drainage class. An exponential function relating CO_2 fluxes to soil temperature accounted for 80% of the seasonal variation in fluxes across all sites ($Q_{10} = 3.9$), but the Q_{10} ranged from 3.4 to 5.6 for the individual study sites. A significant drought in 1995 caused rapid declines in soil respiration rates in August and September in five of the six sites (a swamp site was the exception). This decline in CO_2 fluxes correlated exponentially with decreasing soil matric potential, indicating a mechanistic effect of drought stress. At moderate to high water contents, however, soil water content was negatively correlated with soil temperature, which precluded distinguishing between the effects of these two confounded factors on CO_2 flux. Occurrence of high Q_{10} values and variation in Q_{10} values among sites may be related to: (i) confounding effects of high soil water content; (ii) seasonal and diel patterns in root respiration and turnover of fine roots that are linked to above ground phenology and metabolism; and (iii) variation in the depth where CO_2 is produced. The Q_{10} function can yield reasonably good predictions of annual fluxes of CO_2, but it is a simplification that masks responses of root and microbial processes to variation in temperature and water content throughout the soil.

Keywords: carbon dioxide, Harvard Forest, Massachusetts, microbial respiration, root respiration, soil organic matter

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Introduction

The advent of micrometeorological methods for measuring net ecosystem exchange (NEE) of CO_2 has permitted the quantitative partitioning of forest metabolism into the individual components of photosynthesis, above-ground respiration, and below-ground respiration. At the Harvard Forest in central Massachusetts, the above-ground processes have been successfully simulated with sophisticated, mechanistically based canopy process models that account for the effects of variation in light, water vapour, foliar nitrogen content, and other factors on photosynthesis and canopy respiration (Amthor *et al*. 1994; Waring *et al*. 1995; Aber *et al*. 1996; Williams *et al*. 1996). Below-ground respiration is the other major

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component of NEE, and it has been estimated to comprise 60–80% of total ecosystem respiration of this mixed hardwood forest (Wofsy *et al*. 1993; Amthor *et al*. 1994; Goulden *et al*. 1996a). This large soil component of NEE, however, has been related only to a simple exponential 'Q_{10}' function of soil temperature. Although soil temperature often does account for a large fraction of seasonal and diel variation in soil CO_2 fluxes, we know from laboratory and field studies that other factors, such as soil water content (Linn & Doran 1984), rates of C inputs to soils (Trumbore *et al*. 1995), and diffusivity (Davidson & Trumbore 1995) also affect CO_2 efflux from soils. Because the soil is a complex medium of an organo-mineral matrix of variable depth and supporting a broad array of plants, animals, and microorganisms, reductionist approaches to modelling individual components of soil processes that are comparable to canopy physiology models are extremely difficult, and simplifications, such as temperature dependent Q_{10} functions, are appealing. Moreover, large spatial heterogeneity of root and microbial activity within the landscape and covariation of potentially important factors, such as temperature and water content, create additional challenges to developing mechanistically based models that account for spatial and temporal variation in soil respiration.

Interest in the factors that control soil respiration is growing because of the potential for changing climate, including temperature and precipitation, to affect net ecosystem productivity and exchange of C between terrestrial ecosystems and the atmosphere (Jenkinson *et al*. 1991; Raich & Schlesinger 1992; Davidson 1994; Schimel *et al*. 1994; Goulden *et al*. 1996a). Trumbore *et al*. (1996) found a relatively high Q_{10} value of 3.8 for the temperature dependence of turnover of fast cycling low density soil organic matter along elevational and latitudinal gradients, and they argue that soil responses to interannual variation in temperature could account for much of the interannual variation in the atmospheric CO_2 anomaly. The use of Q_{10} functions for modelling soil respiration is common, although Townsend *et al*. (1992) and Holland *et al*. (1995) have shown that estimates of global soil respiration are very sensitive to the selected Q_{10} value for various biomes. Lloyd & Taylor (1994), Kirschbaum (1995), and Schleser (1982) argue that the Q_{10} value, itself, is temperature dependent, with higher values typically found in colder climates, and these authors also note that Q_{10} values are often affected by soil moisture conditions. The CENTURY model (Parton *et al*. 1987) and the Rothamsted model (Jenkinson & Rayner 1977) use temperature functions for decomposition of soil organic matter that account for greater temperature sensitivity at lower temperatures. Given the recognized uncertainties associated with assigning the appropriate Q_{10} value to the appropriate place and season, better understanding is clearly needed of the temperature dependence of soil processes and the factors that interact with or are confounded with temperature.

Several examples exist of empirical relationships that have been established between field measurements of soil respiration and soil temperature and water content (Bunnell *et al*. 1977; Kiefer & Amey 1992; Oberbauer *et al*. 1992; Hanson *et al*. 1993; Howard & Howard 1993; Raich & Potter 1995). Most of these relationships tend to be site specific, and no widely accepted and commonly used model has emerged. The only common theme to these various approaches to modelling soil respiration is that they all include an empirically derived Q_{10} function, although the range of reported Q_{10} values is large.

In laboratory studies where roots are excluded and temperatures are controlled, the effects of varying soil water content on microbial respiration have been mechanistically attributed to limitation of diffusion of substrate in water films, to desiccation stress at low water contents (Orchard & Cook 1983; Linn & Doran 1984; Skopp *et al*. 1990), and to limitation of diffusion of oxygen in pore spaces at high water contents (Linn & Doran 1984; Skopp *et al*. 1990). Applying this laboratory-based mechanistic understanding of the effects of soil water content on soil respiration to a field setting has not been fully achieved.

We have taken advantage of an unusual drought in New England during the summer of 1995 to investigate the effects of low water content on soil respiration measured in the field using a dynamic chamber technique. The first objective of our work is to demonstrate how low water content can be represented in an algorithm for estimating soil respiration that may be sufficiently mechanistic to be applicable elsewhere. A second objective is to begin to investigate how and why empirically derived Q_{10} functions tend to vary. A third objective is to evaluate spatial heterogeneity in soil respiration rates and soil drainage patterns within the probable 'footprint' area of the tower-based micrometeorological measurements that are ongoing at this research site (Wofsy *et al*. 1993; Goulden *et al*. 1996a).

Methods

Site description

The study area is on the Prospect Hill tract of the Harvard Forest, near Petersham, Massachusetts (42 32′N, 72 11′W) at 340 m elevation. Most of the area was used for grazing in the late 19th century, which was abandoned by the early 20th century (Foster 1992). The wetter areas, including the swamp site in this study, were not grazed, but were repeatedly harvested for wood. A hurricane levelled most of the regrowing forest in 1938. The mixed hardwood forest is now about 60 years old and is dominated by

Table 1 The six study areas near the environmental monitoring station tower at the Harvard Forest

Direction & Distance (m) from Tower	Soil Series	Drainage class	Dominant vegetation	Annual CO_2 Flux (Mg C ha^{-1})			
				Interpolated	Temp. Fn	Temp. & Matric Pot. Fn	Q_{10} value (± 95% C.I.)
NW 20	Canton fsl	well	mixed hardwood	7.1	7.1	6.7	3.5 ± 1.5
NW 150	Scituate fsl	mod. well	hemlock	6.7	7.5	7.3	5.6 ± 1.3
NW 250	Swamp (peat)	very poorly	maple/sphagnum	5.3	5.6	5.6	4.5 ± 1.3
SW 20	Whitman fsl	poorly	hemlock/hardwood	8.4	8.8	8.1	4.0 ± 1.4
SW 100	Scituate fsl	mod. well	mixed hardwood	7.2	7.3	7.1	4.1 ± 1.4
SW 200	Canton fsl	well	mixed hardwood	8.5	8.9	8.3	3.4 ± 1.4
Mean				7.2	7.5	7.2	*3.9 ± 1.2

*This Q_{10} value is not a mean of the other Q_{10} values, but rather is calculated by lumping together data from all sites and fitting a single exponential function.

red oak and red maple, with some stands of hemlock, white pine, and red pine. This study was conducted in the same area as the ongoing, tower-based, continuous, eddy flux correlation measurements reported by Wofsy *et al.* (1993) and Goulden *et al.* (1996a). Six study areas were identified within 300 m from the tower to the north-west and south-west, which are the dominant wind directions from which the tower instruments sample. Soil drainage class and dominant vegetation vary at this scale (Table 1).

CO_2 *flux measurements*

In each of the six study areas, six PVC rings, 10 cm tall and 25 cm diameter, were driven through the forest floor layer and inserted about 1 cm into the soil. Once inserted, rings were left in place in the field throughout the year. Fluxes of CO_2 were measured by circulating air with a battery operated pump at 0.5 L min^{-1} between a vented, 10 cm-tall chamber placed over the PVC ring and a battery operated LiCor infrared gas analyser mounted on a backpack (Davidson & Trumbore 1995). Concentrations were logged with a laptop computer at 12 s intervals for 5 min The increase in CO_2 concentration within the chamber headspace was calculated by linear regression of a linear portion of the tracing, usually between 1 and 3 min after putting the chamber in place. Fluxes were calculated from the following formula

$$\frac{dCO_2}{dt} \times \frac{PV}{ART}$$

where P is the atmospheric pressure, V is the volume of the headspace gas within the chamber, A is the area of soil enclosed by the chamber, R is the gas constant, and T is the air temperature (K).

Flux measurements were made between 09.00 and 13.00 hours at each of the 36 chamber sites. During the summer, measurements were made once per week. During the autumn and spring, measurements were made once every two or three weeks. We attempted to make measurements through the winter snowpack, but do not believe we were successful, probably because most of the soil CO_2 was effluxing through ablation rings around trees where we could not fit our chambers (Winston *et al.* 1995).

Temperature and water measurements

Soil temperature was measured adjacent to each PVC chamber ring at the time of the flux measurement. Temperature was measured at 10 cm below the top of the forest litter layer, which is about 4–8 cm below the surface of the mineral soil, depending on local variation in the thickness of the litter layer.

Nonlinear curve fitting was performed on JMP-SAS software for the Macintosh computer. The temperature functions were fitted to the following formula:

$$\text{Flux} = \beta_0 \, e^{\beta_1 T},$$

where 'Flux' is the measured CO_2 flux and T is measured soil temperature. The Q_{10} values were calculated as:

$$Q_{10} = e^{10\beta 1.}$$

Soil water content was measured by time domain reflectometry (TDR). Three-rod unbalanced probes (Zegelin *et al.* 1989; Heimovaara 1993) that are 15 cm long were placed vertically through the forest floor and into the mineral soil. The design is identical to that used by the Marine Biological Laboratory (MBL) Ecosystems Centre group at a nearby soil warming study site at the Harvard Forest (Peterjohn *et al.* 1994). We also used the MBL calibration curve (Kathy Newkirk, pers. comm.) to convert soil dielectric measurements to estimates of volumetric water content. The MBL calibrations were conducted on well-drained soils of the same series as our well drained sites. The calibrations may not be accurate for our very poorly drained swamp site that contains sphagnum moss on top of a deep organic layer. On the other hand, the TDR estimates for this site appear reasonable, as they demonstrate a clear seasonal pattern ranging from saturation in the spring to relatively dry conditions in the late summer. While the accuracy of any single measurement at this swamp site is not known, the relative seasonal patterns are probably reliable. Each of the six study areas has 3 or 4 TDR probes.

Estimates of volumetric water content of mineral soils were converted to matric potential by using published values of soil texture of the A horizons for these soil series (Natural Resource Conservation Service profile descriptions) and the equations published by Saxton *et al.* (1986) for converting volumetric water content to matric potential based on sand and clay content.

Results

Soil respiration increased during June 1995, and peaked in July (Figs 1,2,3; data from only three of the study areas are shown; the others followed very similar patterns). By mid-August (day-of-year 227), the effects of the summer drought became apparent, as soil water content fell below 0.12 cm^3 H_2O cm^{-3} soil in the well drained sites (Fig. 1), and respiration rates declined rapidly through the remainder of August and the first half of September. Similar rapid declines in both water content and respiration rates were observed in the poorly drained site to the south-west of the tower (Fig. 2), but decreases in respiration were more modest in the very poorly drained swamp site to the north-west of the tower (Fig. 3).

Rain in mid-September (day-of-year 255) caused soil water contents and soil respiration rates to increase at all sites, although not to predrought levels (Figs 1,2,3). By mid-September, soil temperatures had declined to 13 °C, which presumably precluded higher respiration rates. As expected, respiration rates declined as temperatures decreased and as soil water content increased in the autumn and winter. Increasing temperatures were accompanied by increasing soil respiration rates in the spring of 1996.

Combining the data from all dates and all sites, an exponential model based on soil temperature accounts for 80% of the variation in CO_2 fluxes (Fig. 4). The fitted Q_{10} value is 3.9 ± 1.1 (95% confidence interval). Fitting the data for each of the 6 study areas independently, the Q_{10} values range from 3.4 ± 1.4–5.6 ± 1.3, with the well drained sites having the lowest Q_{10} values (Table 1). The highest Q_{10} value of 5.6 ± 1.3 occurred in the thickly shaded Hemlock stand, which was significantly cooler (mean annual soil temperature at 10 cm depth = 7.1°C) than the other five sites (7.8 °C to 8.1 °C).

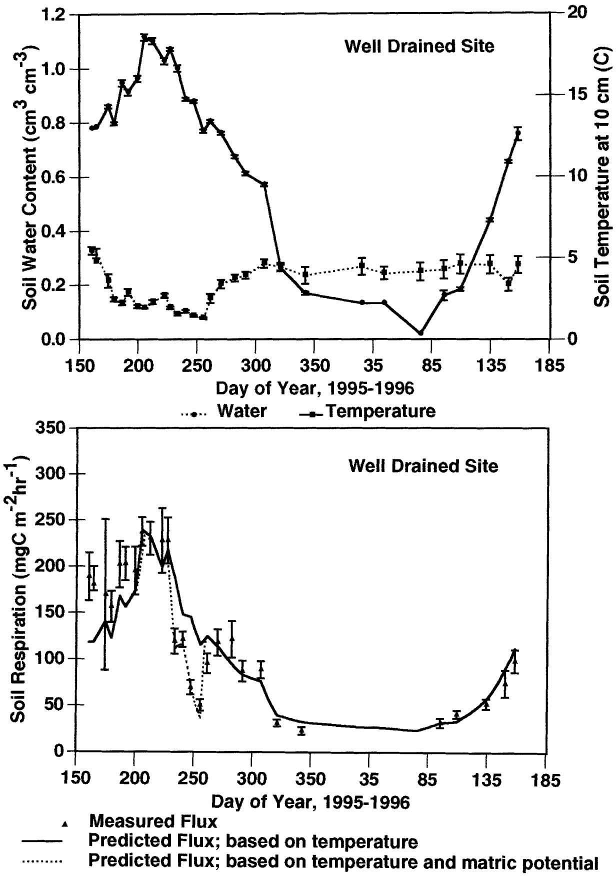

Fig. 1 Seasonal variation in soil respiration, soil temperature, and volumetric soil water content at the well-drained site about 20 m to the north-west of the tower. Each estimate of water content is a mean of 3 or 4 TDR measurements. Each temperature estimate is a mean of six measurements. Error bars represent standard errors of the mean. Each CO_2 flux estimate is a mean of six flux measurements. The solid line shows predicted soil respiration rates based on the fitted Q_{10} value shown in **Table 1** The dashed line shows the predicted respiration when the matric potential algorithm (see text) is added to the temperature function.

The Q_{10} calculated for diel variation in soil respiration in August 1994, at both well drained and poorly drained sites was 4.2 ± 1.5 (Fig. 5). The temperature range is smaller for diel variation, resulting in a smaller 'signal-to-noise' ratio and a smaller R^2 value of 0.33 (N = 95; significant at = 0.01).

Temperature and volumetric water content were correlated across seasons (Fig. 6). In general, the summer months were warm and dry, and the autumn, winter, and spring months were cool and wet. The poorly and very poorly drained sites were consistently wetter than the other sites, but they showed the same negative

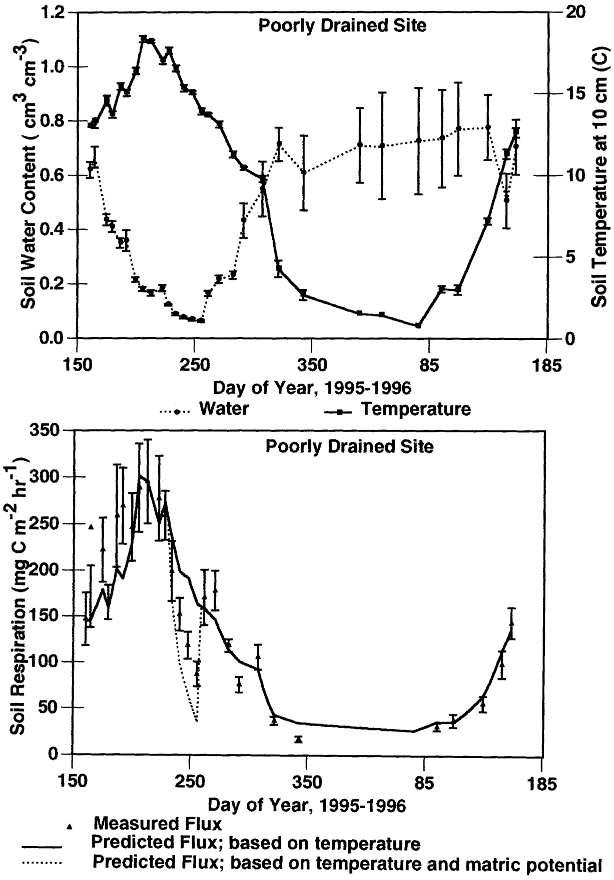

Fig. 2 Seasonal variation in soil respiration, soil temperature, and volumetric soil water content at the poorly drained site about 20 m to the south-west of the tower. See Fig. 1 caption for explanation of means and lines.

correlation between temperature and volumetric water content.

Ignoring the effects of temperature, a plot of volumetric water content vs. soil respiration reveals a bimodal relation. Throughout most of the year, the correlation is negative, i.e high respiration rates during the dry summer and low respiration during wet autumn, winter, and spring months (Fig. 7). During the peak of the drought in August and September, however, a positive correlation with a steep slope exists, with respiration rates falling sharply as soil water content fell below 0.12 cm^3 H_2O cm^{-3} soil.

In order to characterize the drought effect in each study area, the August and September respiration data were normalized to predrought levels for each of the five sites where a drought effect was observed. In other words, the mean respiration rate observed at each study area in early August, before the rapid decline in respiration rates, was given a value of unity. Subsequent mean respiration rates for each study area were normalized to the early August values, so that each value during the drought was < 1. These normalized respiration rates between 0 and 1 were then fitted to a nonlinear function of matric potential of the soil (Fig. 8). An exponential model was

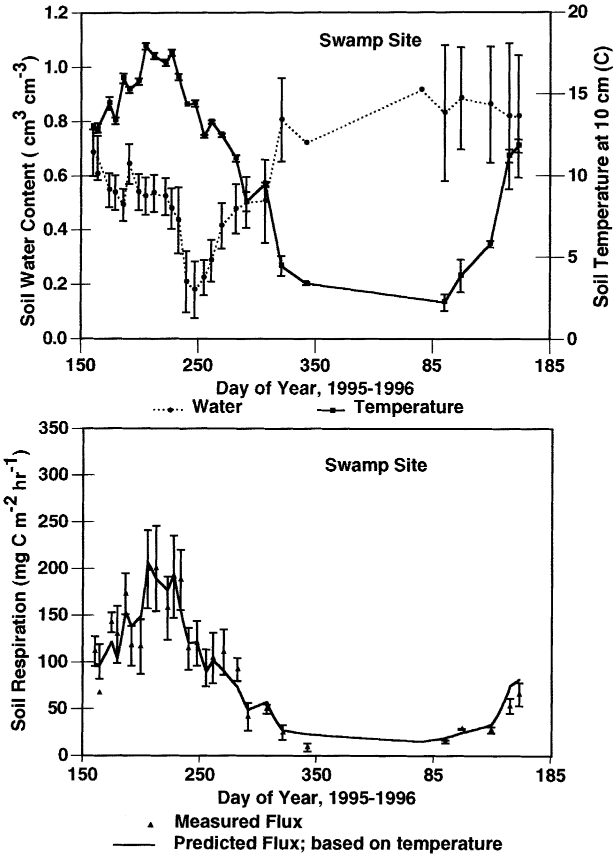

Fig. 3 Seasonal variation in soil respiration, soil temperature, and volumetric soil water content at the very poorly drained swamp site about 250 m to the north-west of the tower. See Fig. 1 caption for explanation of means and lines.

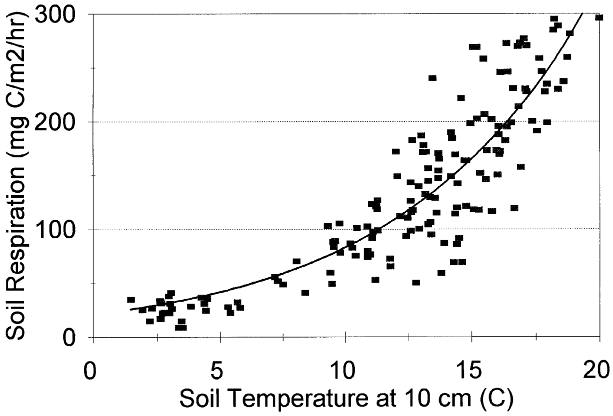

Fig. 4 Seasonal temperature dependence of soil respiration. Each square is a mean of six flux and temperature measurements made at one of the study areas at one date. The fitted function is:. Flux = 21.13 × $e^{(0.1371 \times \text{temp})}$. $R^2 = 0.80$, which is significant at $\alpha = 0.01$ (d.f. = 154).

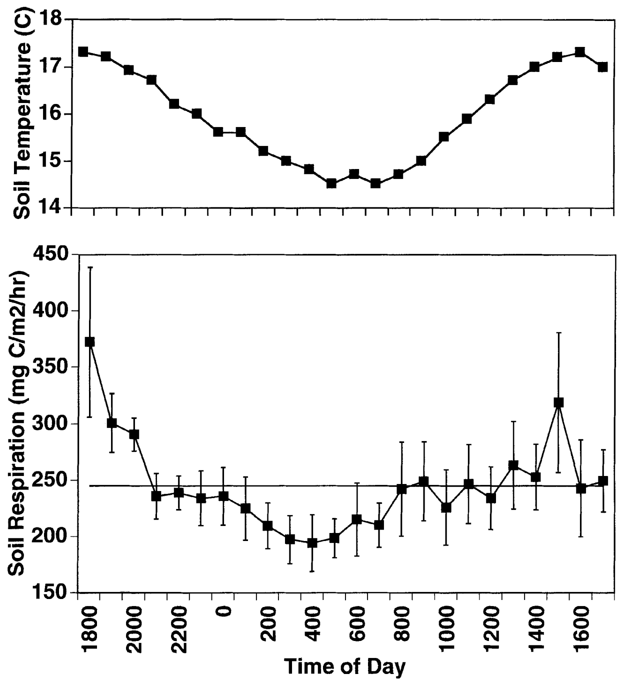

Fig. 5 Diel temperature variation in soil respiration and temperature on 6–7 August 1994. Each flux estimate is a mean of four flux and temperature measurements made within an hour, two at the well drained site 20 m to the north-west of the tower and two at the poorly drained site 20 m to the south-west of the tower. Error bars are standard errors of the mean. The horizonal line shows the mean for the day. Unlike all other soil temperature measurements, these were made at 5 cm depth. For the correlation between temperature and CO_2 efflux, $R^2 = 0.33$, which is significant at $\alpha = 0.01$ (d.f. = 93).

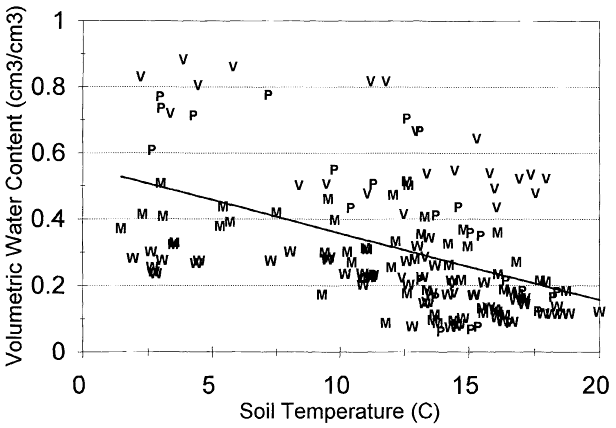

Fig. 6 Covariation of soil temperature with volumetric water content. The plotting symbols indicate the drainage class of the study site (V = very poorly drained, P = poorly drained, M = moderately well drained, W = well drained; see Table 1). Each datum is a mean of six temperature measurements and 3 or 4 TDR soil water measurements at a study area on a given date. The fitted linear regression is: water content $\alpha = 0.56 - (0.02 \times \text{temperature})$; $R^2 = 0.23$, which is significant at $\alpha = 0.01$ (d.f. = 154).

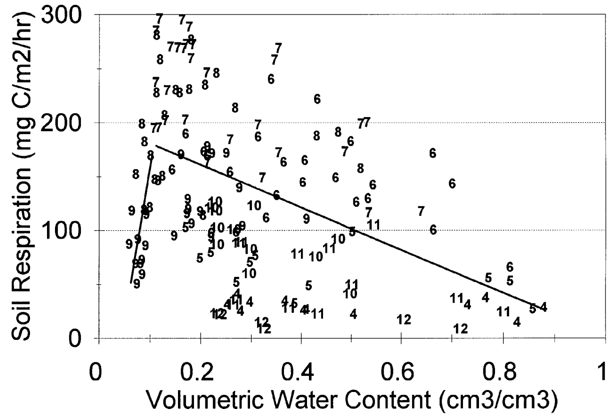

Fig. 7 Correlations of volumetric water content and soil respiration. The plotting symbol represents the month of the year that the measurements were made. Each datum is a mean of 3 or 4 TDR water content measurements and 6 flux measurements for a study area on a given date. The August (8) and September (9) data where water content was < 0.12 cm^3 cm^{-3} were fitted to the linear regression: flux $\alpha = -128 + (2852 \times \text{water content})$; $R^2 = 0.48$, which is significant at $\alpha = 0.05$ (d.f. = 21). The data from the rest of the year where water content was > 0.12 cm^3 cm^{-3} were fitted to the linear regression: flux = $201 - (198 \times \text{water content})$; $R^2 = 0.22$, which is significant at $\alpha = 0.01$ (d.f. = 131).

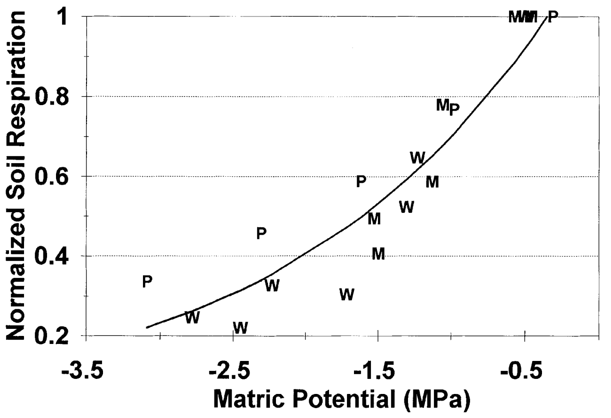

Fig. 8 Effect of soil matric potential estimated from volumetric water content on normalized soil respiration during the summer drought, where fluxes prior to the rapid drought induced drop in respiration rates were assigned values of unity. The plotting symbols refer to the site drainage classes (see Fig. 6 caption). The fitted function is:
normalized respiration = $1.21 \times e^{(0.553 \times \text{matric potential})}$. $R^2 = 0.83$, which is significant at $\alpha = 0.01$ (d.f. = 17).

fitted to all of the normalized respiration values of the five sites throughout the remainder of the drought ($R^2 = 0.83$; Fig. 8). The matric potential prior to the decline in respiration rates (i.e. when the normalized respiration rate was defined as unity) was calculated to be about –0.5 MPa. At – 1.5 MPa, the normalized respiration rates were about 0.5. The normalized respiration rates fell as low as 0.2 before the drought ended and the calculated matric potentials fell as low as – 3.0 MPa.

Discussion

Effects of low water content

When soil water contents are sufficiently low that desiccation stress of roots or microorganisms is suspected, matric potential is a more appropriate expression of water content than is either volumetric or gravimetric water content. Using only soils from the Harvard Forest, we could have obtained a good correlation between gravimetric water content and soil respiration, but the correlation parameter estimates would not be applicable to soils from other sites with greater clay content. Matric potential provides an expression of water available to the organisms, and it is applicable to all soil textures.

In a laboratory study of sieved soils from which roots had been removed, Orchard & Cook (1983) found a similar exponential function relating matric potential to microbial respiration. Unlike our results, they found a decrease in microbial respiration when the matric potential fell below –0.01 MPa, which they attributed to a decline in bacterial activity. They suggest that fungi can tolerate greater water stress than can bacteria, which may explain why respiration rates declined only after the matric potential had fallen below –0.5 MPa in the Harvard Forest soils where fungal activity is presumably important (Fig. 8). Assuming that most roots are able to obtain water to at least – 1.5 MPa, root respiration may have also contributed to a delayed response to the summer drought. As in our study, Orchard & Cook (1993) found that respiration dropped by about 50% between –0.5 and – 1.5 MPa. In a field study in an arid grassland, soil respiration declined when soil water content fell below about – 1.3 MPa (Wildung *et al*. 1975).

Soils that have different compositions of bacterial, fungal, and root respiration may not conform to the same matric potential curve shown in Fig. 8. There may also be some error introduced in our conversion of volumetric water content to matric potential. Partitioning the sources of CO_2 into O, A, and B horizons may be necessary to further refine the relation between matric potential in each of these horizons and the measured CO_2 efflux. Nevertheless, the approach demonstrated here using matric potential shows a promising start for providing a mechanistic basis for broadly applicable models of soil respiration.

When the algorithm for matric potential in dry soils (when $MP < -0.34$ MPa) shown in Fig. 8 is added to the empirically fit Q_{10} temperature (T) effect for each study site:

$$\text{Flux} = (\beta_0 e^{\beta_1 T}\})\ (1.21e^{0.553\text{MP}}).$$

the predicted respiration rates are in reasonably good agreement with observed values for all sites (Figs 1,2). For most of the year, the Q_{10} algorithm alone is sufficient for good predictions. Only in late August and early September (day-of-year 227–255) of this drought year is the matric potential algorithm necessary to improve the agreement between predicted and observed rates.

Confounding of temperature and water content

Because soil water content and temperature covary across seasons (Fig. 6), it is possible that the empirically derived Q_{10} temperature function is confounded with an effect of soil water content in addition to the drought related matric potential effect already described. In other words, the Q_{10} effect may include within it and may mask a negative correlation between water content and soil respiration at high water contents. We know from laboratory studies and from theory (Doran 1984; Doran *et al.* 1990; Linn & Skopp *et al.* 1990) that high water content can impede diffusion of O_2, which impedes decomposition and CO_2 production. Although there is a great deal of scatter in the relation between soil water content and respiration rates (Fig. 7), presumably the result of a temperature effect, the bimodal correlation with water content is consistent with the theoretical predictions of Skopp *et al.* (1990).

Statistically, it is very difficult, and perhaps impossible, to distinguish between the effect of declining temperature and increasing water content on soil respiration as the soils become colder and wetter in the autumn and winter. In an arid grassland, soil respiration was significantly correlated with the temperature–water interaction effect and not with the main effects in a multiple regression analysis (Wildung *et al.* 1975). When combined in a nonlinear model such as that of Bunnell *et al.* (1977), the solutions for the best fit of the temperature and water functions are not unique. We were able to obtain similarly good fits for our data either by letting the fitting program find a high Q_{10} value for the temperature function that accounted for most of the variation, in which case the nonlinear water content functions contributed little to the reduction in sums of squares, or by forcing a lower Q_{10} value of 2.4 and letting the nonlinear fitting program assign parameters to the water content function that compensated for the poorer Q_{10} fit.

If a water content effect is masked by the fitted Q_{10} function, then the Q_{10} fit might vary among wet and dry years and among wet and dry sites. In a multiyear study of a grassland and a beech-spruce forest in Germany, Dörr & Münnich (1987) found that Q_{10} values fitted for each year's data varied from 1.4 to 3.1, with the low values mostly in the wet years and the high values mostly in the dry years. On the other hand, we find that comparing the Q_{10} values calculated for each site within the single year of 1995, that the lowest Q_{10} values were for the well-drained sites, with higher values for the wetter sites, and the highest value for the cooler, well-shaded Hemlock stand (Table 1).

Several mechanisms could explain varying Q_{10} values among wet and dry years and among wet and dry sites. In wet years when soil water content remains high throughout much of the summer, high water content could impede O_2 diffusion, thereby reducing rates of decomposition and microbial production of CO_2. In this case, the CO_2 efflux would be less responsive to temperature (i.e. have a lower Q_{10} value) during wet years than during dry years. A different sort of mechanism could account for how a normally wet site responds to seasonal drying within a single year. If a wet site dries substantially during a dry summer, as did our study sites in 1995, then a large release of CO_2 and an enhancement of microbial and root respiration may occur at intermediate water contents that effectively inflates the fitted Q_{10} function.

Other factors affecting Q_{10} functions

Our reported Q_{10} values (Table 1) are above the median of 2.4 reported in a literature review of soil respiration studies (Raich & Schlesinger 1992), although our values are within the range of reported values (Schleser 1982; Kirchbaum 1995). Many of the values reported in the older literature are based on soda lime measurements of soil respiration, which probably underestimated high fluxes (Ewel *et al*. 1987; Boone, unpubl. data) and would underestimate Q_{10} values.

Another complication in interpreting Q_{10} values for soil respiration is the possible differential response of microbial and root respiration to temperature. McClaugherty *et al*. (1982) reported that root growth occurred primarily in April and May at the Harvard Forest. Our relatively high Q_{10} values (3.4 and higher) probably reflect the importance of spring and summer root respiration in this forest. At a different study area on the Harvard Forest, the observed Q_{10} for trenched plots that are presumably nearly void of roots was only 2.5, whereas the control plot had a Q_{10} of 3.5 (Boone, unpubl. data). The difference between the control and root-free respiration rates was related to soil temperature with a Q_{10} value of 4.6. This high estimate of the sensitivity of root respiration to soil temperature may include both direct physiological effects of temperature on roots and the indirect effects related to phenology of photosynthesis and C allocation to roots.

Our reported Q_{10} values are also higher than the 2.1-value reported by Goulden *et al*. (1996b) using their tower-based nocturnal eddy flux correlation measurements at the same study site (daytime data cannot be used because photosynthesis affects NEE measured at the tower; nocturnal measurements estimate respiration only). These above canopy measurements include all forest respiration, but if the soil emits most of the total CO_2 (60–80%), then better agreement in temperature sensitivities between their results and our chamber based soil respiration measurements might be expected. This expectation assumes, however, that root and microbial respiration are equally active in both day and night. In a study in a hardwood forest of Vermont, Eric Sundquist and coworkers (USGS, Woods Hole, MA, pers. comm.) have shown that diel variation in soil respiration appears to be linked to diel patterns in solar radiation. On clear days, they have measured a higher Q_{10} value for soil respiration than on cloudy days. They deduce that root respiration is linked to photosynthesis, thereby causing a larger increase in daytime soil respiration on clear days than on cloudy days. We also observed a relatively large Q_{10} value for total soil respiration on a clear day in August 1994, at our study site (Fig. 5). The tower-based Q_{10} estimate using only nocturnal data may underestimate the temperature response of total respiration, and may be indicating a temperature response that is dominated by soil microbial respiration, which is consistent with a Q_{10} value of about 2.

Also at the same study site, Moore *et al*. (1996) have measured below-canopy NEE using eddy flux correlation instruments mounted at 11 m height on the tower. Because there is little understorey photosynthesis, they were able to use daytime measures of NEE at this height to estimate respiration and its response to temperature. Although they used a linear function to characterize the dependence of measured respiration on soil temperature, which does not yield a Q_{10} value *per se*, they show that daytime CO_2 fluxes when the soil was 20 C were 3.6 times higher than when the soil was 10 C. Using their night-time measurements, this ratio is only 2.7, which is consistent with greater root activity during the day that elevates the fitted Q_{10} value.

Goulden *et al*. (1996b) also conducted soil respiration measurements over diel cycles in 1992 on this site using an open chamber design, and they report a Q_{10} value of only 2.2. They also note that chamber based estimates of ecosystem respiration (including chamber measurements on leaves and stems) yielded significantly higher values than did the nocturnal tower-based micrometeorological measurements, and they were unable to explain this difference. Our mid- to late-morning chamber measurements are also about 50% higher on average than the tower-based nocturnal respiration measurements for the summer of 1995 (data not shown). Concern about methodological errors in chamber based flux measurements have focused primarily on the potential for underestimating fluxes because accumulation of CO_2 within the chamber headspace reduces the concentration gradient and thereby reduces the measured flux (Livingston & Hutchinson 1995; Nay *et al*. 1994). We can think of no plausible explanation for why chambers would overestimate fluxes. If, however, the diel variation in soil temperature is sufficiently large, and particularly if root respiration varies more than microbial respiration over diel cycles, then the measured differences in fluxes could be real rather than an error of one or both of the measurement technologies. As Goulden *et al*. (1996b) also point out, both sets of measurements could be correct if the tower-based measurements integrate over a different area than does the design of chamber deployment.

Finally, another source of variation in Q_{10} estimates among studies is the depth at which soil temperatures were measured. Larger temperature variation occurs near the soil surface than at depth, both seasonally and diurnally, which will result in lower apparent sensitivity of CO_2 efflux to soil temperature when based on superficial soil temperatures than when based on deeper soil temperatures. Goulden *et al*. (1996b) measured soil temperature at 2 cm below the mineral soil surface, Moore *et al*. (1996) measured temperature at 5 cm below the mineral soil surface, and we measured temperatures at 10 cm below the surface of the litter layer, which varied from 2 to 6 cm thick. Hence, the lower Q_{10} values of Goulden *et al*. (1996b), the middle range values of Moore *et al*. (1996) and our higher Q_{10} values might be partially explained by this inconsistency in soil depths for temperature measurements. Perhaps some variation in reported Q_{10} values in the literature is attributable to this simple effect of inconsistent depth of measurement of soil temperatures. Even if soil temperatures were measured consistently at an arbitrarily chosen soil depth, the soil depth at which CO_2 is predominantly produced may vary among sites and among seasons within a site (Winston *et al*. 1995). Ideally, the temperature dependence of CO_2 production would be determined, both in field measurements and in models, for each soil horizon, rather than relating total soil CO_2 efflux to the temperature of some arbitrarily chosen depth.

Annual estimates of soil CO_2 efflux and spatial variation

Our soil respiration measurements were made between 09.00 and 12.00 hours, which is when the average flux of the diel cycle occurs (Fig. 5). We did not attempt to make a correction for diel variation when extrapolating to daily estimates, assuming that morning measurements are reasonable estimates of the daily mean. To estimate annual fluxes, we interpolated between sampling dates to estimate the mean flux for each site each day of the year and then computed the sum for the year. Interpolating between the last autumn chamber measurement and the first spring chamber measurement (Figs 1,2,3) yields winter flux estimates that are in reasonable agreement with tower-based measurements in the winter (Goulden *et al*. 1996a).

The annual interpolated estimates vary from a low of 5.3 Mg C ha^{-1} in the swamp to a high of 8.5 Mg C ha^{-1} in one of the well drained sites (Table 1). Assuming that 60–80% of total ecosystem respiration is from the soil (Amthor *et al*. 1994; Goulden *et al*. 1996b; Wofsy *et al*. 1993), the mean soil respiration rate of 7.2 Mg C ha^{-1} (Table 1) agrees with the 5-year average of tower-based total ecosystem respiration of 9.6 Mg C ha^{-1} (Goulden *et al*. 1996a). With the exception of the swamp, differences among sites are probably within uncertainty levels of the measurements and interpolations. Winds are commonly from the north-west, but it is not known how strongly the swamp study area 300 m to the north-west of the tower influences the tower measurements. If the relative contribution of this swamp site to the tower measurements varies significantly with wind direction and speed, then this spatial heterogeneity in the landscape may be confounded with temporal variation in tower measurements.

The lower CO_2 efflux from the swamp site is probably influenced not only by wetness and its effect on diffusion of O_2 into the peat, but also presumably by lower C inputs to the soil. Trees are sparse, sphagnum moss is common, and rates of net primary productivity are presumably lower in the swamp than in the other study sites. In contrast, the poorly drained site on the Whitman soil series to the south-west of the tower (Table 1) also has periods of seasonal soil saturation, but a mineral soil is present below a deep (18 cm) organic horizon, sphagnum is rare, and tree density is similar in this site relative to the nearby well drained sites. The estimate of annual CO_2 efflux from the poorly drained soil is similar to the annual efflux from the well drained sites (Table 1). Hence, the vegetation appears to be adapted to the seasonal saturation of this site, and C inputs to the soil must be sufficient to produce CO_2 efflux rates similar to the well drained areas. In this case, the difference between classifications of 'poorly drained' and 'very poorly drained' for these two wet sites appears to be important.

Estimates of the annual CO_2 efflux have also been calculated for each of the six study sites using interpolations of data on soil temperature and soil water content as inputs to the simple Q_{10} algorithms for temperature, with and without the addition of the algorithm for matric potential (Table 1). Using temperature data alone, the annual estimates are somewhat higher than the estimates based on direct interpolation of the flux data. When the matric potential effect is added to the model, the annual estimates are lowered to about the levels of the interpolated flux data. The differences between these annual estimates are very small relative to errors in measurements and interpolation. Hence, if our only objective were to estimate annual CO_2 efflux from the soil, a simple Q_{10} function empirically derived for each site would remain sufficient. If, however, accuracy of estimates is needed for brief periods of drought, such as August and September 1995, then the matric potential effect is crucial (Figs 1,2). Moreover, it appears that the Q_{10} functions are variable from site to site and may be variable from year to year, probably because the Q_{10} temperature function masks several processes, including effects of high water content on microbial decomposition and perhaps depth dependent responses of root and microbial respiration to seasonally varying soil conditions.

Further progress in mechanistic understanding of spatial and temporal patterns of soil respiration will require investigation of the factors that affect root and microbial processes and that appear to be masked by the empirically fit temperature functions. Spatial heterogeneity in soil respiration rates within the landscape is related to soil drainage class, but the effects of drainage on soil microbial activity may be confounded with differences in net primary productivity and C inputs to the soil among the study areas. Complete soil C budgets and models that differentiate between root and microbial processes and that include the effects of C inputs, temperature, water content, and gaseous transport are needed to refine our current understanding of soil respiration.

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