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Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia

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Abstract. The effect of soil water content on efflux of CO_2 from soils has been described by linear, logarithmic, quadratic, and parabolic functions of soil water expressed as matric potential, gravimetric and volumetric water content, water holding capacity, water-filled pore space, precipitation indices, and depth to water table. The effects of temperature and water content are often statistically confounded. The objectives of this study are: (1) to analyze seasonal variation in soil water content and soil respiration in the eastern Amazon Basin where seasonal temperature variation is minor; and (2) to examine differences in soil CO_2 emissions among primary forests, secondary forests, active cattle pastures, and degraded cattle pastures. Rates of soil respiration decreased from wet to dry seasons in all land uses. Grasses in the active cattle pasture were productive in the wet season and senescent in the dry season, resulting in the largest seasonal amplitude of CO_2 emissions, whereas deep-rooted forests maintained substantial soil respiration during the dry season. Annual emissions were 2.0, 1.8, 1.5, and 1.0 kg C m^{-2} yr^{-1} for primary forest, secondary forest, active pasture, and degraded pasture, respectively. Emissions of CO_2 were correlated with the logarithm of matric potential and with the cube of volumetric water content, which are mechanistically appropriate functions for relating soil respiration at below-optimal water contents. The parameterization of these empirical functions was not consistent with those for a temperate forest. Relating rates of soil respiration to water and temperature measurements made at some arbitrarily chosen depth of the surface horizons is simplistic. Further progress in defining temperature and moisture functions may require measurements of temperature, water content and CO_2 production for each soil horizon.

Introduction

Soil temperature and water content are the factors most commonly related to temporal variation in CO_2 efflux from soils. The temperature effect is nearly always described as an exponential function, although there is discussion of which exponential formulation is best (Lloyd & Taylor 1994; Kirchbaum, this issue). The effect of soil water content, in contrast, has been described by numerous equations, including linear, logarithmic, quadratic, and parabolic functions of soil water expressed as matric potential, gravimetric water content, volumetric water content, fractions of water holding capacity, water-filled pore space, precipitation indices, and depth to water table (Table 1).

It is clear from the studies cited in Table 1, that low water contents can inhibit CO_2 production in soils. In laboratory incubations of mixed soil samples, where the effects of temperature and spatial heterogeneity are controlled, CO_2 production declines as water content falls below field capacity (Doran et al. 1991; Orchard & Cook 1983). In a field study in arid central Washington state, Wildung et al. (1975) found that a temperature-water interaction term explained seasonal variation in CO_2 efflux, which they attributed to the temperature effect being manifest only when there was sufficient soil moisture to permit significant root and microbial CO_2 production (hereafter referred to collectively as soil respiration).

Soil water content can also exceed optimal conditions for soil respiration. In the Arctic tundra, Oberbauer et al. (1992) found that soil respiration generally increased as the water table dropped, leaving the surface horizon better aerated. Although the quadratic and parabolic functions included in Table 1 are based on various expressions of water content, they demonstrate that the optimum for soil respiration is frequently found at intermediate water contents, with decreases in respiration at water contents both above and below the optimum. Linn and Doran (1984) explained this phenomenon mechanistically for microbial respiration as limitation of O_2 diffusion through pore spaces in very wet soils and limitation of soluble organic-C substrates in water films in very dry soils. Oxygen is needed for aerobic respiration, and soluble organic substrates are used as energy sources by heterotrophic microorganisms. The optimum water content is usually somewhere near field capacity, where the macropore spaces are mostly air-filled, thus facilitating O_2 diffusion, and the micropore spaces are mostly water-filled, thus facilitating diffusion of soluble substrates. Papendick and Campbell (1981) show that diffusion of soluble substrates in soil water films is a function of the cube of the volumetric water content, and this function has been applied to studies of nitrification (Davidson et al. 1990), but we are unaware of its application to studies of soil respiration. Water content also affects the rate of diffusion of CO_2 within the soil profile (Davidson & Trumbore 1995).

Laboratory studies have demonstrated clearly the importance of water content as a factor influencing soil respiration. In field studies, however,

Table 1. Selected functions relating CO_2 production in soils to soil water content. For units and values of fitted parameters, readers are referred to the original publications.

Orchard & Cook (1983). Lab incubations.
$CO_2 = -0.167 \ln(-\Psi) + 0.95$ Ψ = water potential

Wildung et al. (1975). Field fluxes in central Washington state.
$CO_2 = 0.88 \pm 0.013\,(w)\,(t)$ w =% gravimetric water content t = temperature

Howard & Howard (1993). Lab incubations.
$\text{Ln}\,CO_2 = \alpha + \beta_1 (T - T^*) + \beta_2 (T - T^*)^2 + Y_1 (M - M^*) + Y_2 (M - M^*)^2$
M = % of water holding capacity M* = mean of M T = temperature T* = mean of T

Doran et al. (1991). Lab incubations.
$CO_2 = (a \times WFPS) + (b \times WFPS^2) + c$ WFPS = water-filled pore space

Raich & Potter (1995). Analysis of published field fluxes of CO_2.
$CO_2 = F \times e^{Q \times T} \times (P/K{+}P)$ P = mean monthly precipitation T = mean monthly air temperature Q = Q_{10} factor K = half saturation coefficient of precipitation F = flux when temperature is zero and moisture is not limiting

Hanson et al. (1993). Field fluxes at Walker Branch mixed hardwood forest, Tennessee.
$CO_2 = (R_b Q^{(Ts/10)})\,(1 - Cf/100)$ $R_b = (KW_s R_{max})/((KW_s) + R_{max})$ W_s = volumetric water content Cf = % coarse fraction T = temperature R_{max} = maximum flux when W_s = 100% K and Q are fitted constants

Oberbauer et al. (1992). Field CO_2 fluxes in Alaskan tundra.
$CO_2 = C \cdot e^{(-E/R \cdot T_k)} \cdot e^{(Swt)}$ T = temperature R = gas constant E = apparent activation energy $Swt = A \cdot W_t/(W_t + B)$ W_t = depth to water table A and B are fitted parameters

Schlentner & Van Cleve (1985). Field CO_2 fluxes in Alaskan forests.
$CO_2 = [M/(a_1 + M)] \times [a_2/(a_2 + M)] \times a_3 \times a_4^{[(T-10)/10]}$ M = gravimetric water content of organic soil T = temperature

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the temperature effect is often more pronounced than the water effect, especially in temperate and boreal regions. Davidson et al. (1998) noted that the effects of temperature and water content were confounded in the soils of their New England temperate forest study site, where the summers are warm with dry periods and the winters are cool and wet. Rates of soil respiration may increase between winter and summer not only because the soils become warm, but also because water contents decline from saturated conditions in the winter to near optimal water contents in the early summer. Nevertheless, a simple Q_{10} temperature function statistically accounted for this seasonal variation as well as did a more complicated function that included water effects, such as that of Schlentner and Van Cleve (1985; see Table 1), but either model could be mechanistically correct. A late summer drought at this site, on the other hand, revealed an inhibitory effect of very low water contents that agreed with the matric potential formulation by Orchard and Cook (1983; see Table 1).

One way to study the effects of soil water content in a field setting without the confounding effect of temperature is to choose a field site where temperature is nearly uniform throughout the year. The first objective of this study is to describe the effects of seasonal variation in soil water content on soil respiration in a tropical forest of the eastern Amazon Basin where seasonal variation in temperature is small relative to variation in precipitation. This portion of the Brazilian Amazon forest has undergone extensive land-use change (Nepstad et al. 1991), and a second objective is to examine differences in soil CO_2 emissions among primary forests, secondary forests, active cattle pastures, and degraded cattle pastures.

Methods

Site description

The study was conducted at the Fazenda Vitória, located 6.5 km northwest of the town of Paragominas, Pará State, Brazil, in eastern Amazonia (2° 59′ S, 47° 31′ W). Paragominas has been a center of cattle ranching and logging since the 1960's (Nepstad et al. 1991). Average annual rainfall is 1800 mm and is highly seasonal, with $<$250 mm falling from July to November (Jipp et al. 1998). The forest maintains an evergreen canopy throughout the dry season by extracting water from deep in the soil profile, where roots have been observed at 18 m depth (Nepstad et al. 1994). In contrast, pasture grasses turn brown during the dry season, and root biomass below 2 m soil depth is 10–100 times lower in pasture soils than forest soils (Nepstad et al. 1994). The deeply weathered soils in this region are developed on Pleistocene terraces cut into the Belterra clay and Tertiary Barreiras formations (Clapperton 1993; Sombroek 1966). The soils were classified by Sombroek (1966) as Kaolinitic Yellow Latosols (Haplustox, according to USDA Soil Taxonomy). Oxisols cover about 40% of the Amazon Basin (Richter & Babbar 1991) and are most common in eastern and southern Amazonia, coincident with much of the "arc of deforestation" (Nepstad et al. 1991) and with highly seasonal precipitation patterns (Nepstad et al. 1994).

Within the ranch, we located two study areas for each of four land uses: primary forest, secondary forest, degraded cattle pasture, and active cattle pasture. All of the sites, with the exception of the primary forest, were cleared in 1969 and planted in *Panicum maximum* and *Brachiaria humidicola* for use as cattle pasture. The secondary forest site was abandoned in 1976 and secondary succession was allowed to proceed. During our study in 1995 and 1996, it had a closed canopy forest with above-ground biomass of about 50 mg ha^{-1} (Nepstad et al. 1995, D. Nepstad, pers. comm.). The degraded cattle pasture was heavily grazed in the 1970's, but was invaded with weeds and grazed only intermittently in the 1980's and 1990's. Accidental fires enter this site nearly every year, which has retarded secondary succession. The vegetation is a mixture of grasses, herbs, shrubs, and islands of small trees. The active pasture had a similar history as the degraded pasture, but it was "reformed" in 1987, which consisted of disking, fertilizing with phosphorus, and replanting with *Brachiaria brizantha.* Grazing is controlled at about one head per hectare, fire has only occasionally entered the pasture, weeds are a relatively minor component of the vegetation, and grass productivity has remained high. Reforming pastures in this manner is becoming increasingly common in the eastern portion of the Brazilian Amazon Basin, although degraded pastures still cover a large area.

This ranch has been the site of recent studies on soil carbon dynamics (Davidson & Trumbore 1995; Trumbore et al. 1995), nitrogen oxide emissions from soils (Verchot et al. 1999), soil water use (Jipp et al. 1998; Nepstad et al. 1994), root distributions (Carvalheiro & Nepstad 1996), and secondary succession (Nepstad et al 1996).

Measurement of CO_2 flux from the soil surface

Flux measurements were made by circulating air between a LiCor infrared gas analyzer and a flux chamber consisting of a PVC ring (20 cm diameter × 10 cm height) and a vented PVC cover (10 cm height). The rings were inserted 1 to 2 cm into the soil. The chamber was vented to the atmosphere through a stainless steel tube (10 cm long × 3.2 mm OD) to keep pressure within the chamber equal to the atmosphere. A battery-operated pump maintained a flow of 0.5 liters min^{-1} to and from the chamber and the LiCor. Varying the flow rate from 0.4 to 1.2 liters min^{-1} had no detectable effect on measured flux rates. The LiCor readout was recorded on a 5 second interval with a datalogger and the CO_2 flux was calculated from linear regression of the increasing CO_2 concentrations within the chamber, usually between 1 and 3 minutes after placing the cover over the ring. The LiCor was calibrated in the field by allowing the pump to draw air from a vented tube through which a standard of CO_2 in air was flowing. Eight chamber flux measurements were taken per site and date. Coefficients of variation among the chamber measurements within a site at each date were typically about 30% and ranged from 14% to 75%. Measurements were made once per month from February, 1995, through May, 1996, although a few months were missed due to equipment failure. We also measured diel variation in CO_2 fluxes once at the end of the dry season by repeating measurements four times during a 24-hour period on the same 8 chambers within each of three sites.

Measurement of soil temperature and moisture

Soil temperature was measured at 10 cm depth with a portable temperature probe at the same time that flux measurements were made. Two sets of time domain reflectometry (TDR) probes were permanently installed vertically into the soil surface between 0 and 30 cm depth at each study site. Readings were taken at each flux measurement date. The TDR measurements were converted to volumetric water content using calibration curves derived from laboratory analysis of intact soil cores (Jipp et al. 1998). The volumetric water content was then converted to matric potential using water retention curves generated from pressure plate analyses of intact soil cores. Volumetric water contents (θ in cm^3 H_2O cm^{-3}) were measured at 0, 0.2, 6, 10, 30, 50, 100, and 1500 kPa tension (Ψ), and the following exponential functions were fitted to these data (Papendick & Campbell 1981):

forest soils: $\Psi = -1.34 \times 10^{-4} \times \theta^{-11.52}$
pasture soils: $\Psi = -0.648 \times 10^{-4} \times \theta^{-12.75}$

Results and discussion

Comparisons of fluxes among land uses

Monthly precipitation and volumetric soil water content measurements reveal a strong dry season from June to December (Figure 1). In all land uses, rates of soil respiration were relatively high during the rainy season of 1995, declined during the dry season, and increased with the onset of the rainy season in January, 1996 (Figure 1). During the wet season, the primary forest and the active pasture had the highest emissions. During the dry season, the primary and secondary forests had higher emissions than the active and degraded pastures. The active pasture showed the greatest difference between wet and dry seasons. The degraded pasture had the lowest emissions in both seasons. We estimated annual emissions by extrapolating each monthly measurement to a 30-day period and summing for a year. For February through May, when we had data for both 1995 and 1996, a mean was calculated

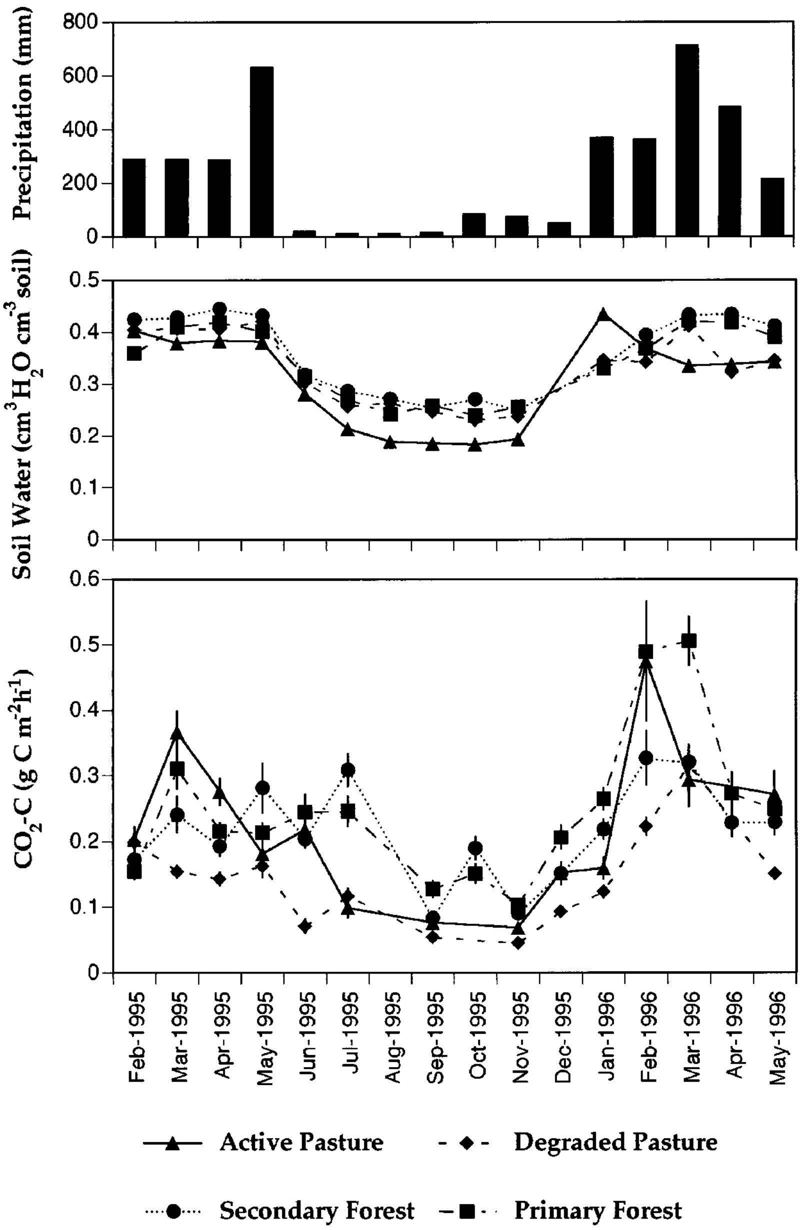

Figure 1. Monthly precipitation, volumetric water content, and emissions of CO_2 from soils of four land uses. For CO_2 fluxes, each symbol is a mean of 16 chamber measurements for that land use, and standard errors of the mean are plotted as error bars.

for each month. Where there were missing data due to equipment failure, the average of the preceding and following months was used. The calculated annual estimates are 2.0, 1.8, 1.5, and 1.0 kg C m^{-2} yr^{-1} for primary forest, secondary forest, active pasture, and degraded pasture, respectively.

Efflux of CO_2 from the soil is a good indicator of total below-ground allocation of carbon and of ecosystem productivity (Raich & Nadelhoffer 1989). The evergreen primary forest maintains productivity year round, including water uptake by deep roots during the dry season, so it is not surprising that it is the most productive ecosystem of those we studied and has the highest rates of soil respiration. The active pasture is also very productive during the rainy season, but the grasses become brown and dormant during the dry season, so that annual CO_2 emissions are lower than those of the primary forest. The degraded pasture has sparse vegetation and low CO_2 emissions throughout the year. The secondary forest, which was also once a degraded pasture, has regained much of its productivity, but its rates of soil respiration are not yet as high as the primary forest.

The soil CO_2 efflux rate of 2.0 kg C m^{-2} yr^{-1} reported here for the primary forest is among the highest reported in the literature (Raich & Schlesinger 1992). Most published studies of tropical forests have used soda lime techniques for measuring CO_2 emissions, which have been shown to underestimate actual emissions when emissions are high (Ewel et al. 1987). Our annual respiration estimate is also higher than might be predicted based on published relationships between soil respiration and litterfall. Average annual above-ground litterfall at the primary forest site is 0.45 kg C m^{-2} yr^{-1} (Trumbore et al. 1995), and this value can be used in the empirical function of Raich and Nadelhoffer (1989) to predict annual soil respiration of 1.5 kg C m^{-2} yr^{-1}, but this empirical function was also based on literature reports of soil respiration using soda lime techniques. It is possible that rates of soil respiration in tropical forests may have been underestimated in the past, although our study site in eastern Amazonia may also have higher soil respiration rates than many other moist tropical forests. The strong seasonality of precipitation in the eastern half of the Amazon Basin requires large below-ground allocation of carbon to a large root biomass in order to obtain sufficient water from a deep soil profile during the dry season (Nepstad et al. 1994). Both root respiration and microbial decomposition of dead roots would be expected to be high in this environment.

Effects of temperature

Seasonal variation in soil temperature at 10 cm depth is small in this environment. In the forest, it ranged from 22 °C to 24 °C (Figure 2(a)), and in the pasture, where there is less shade, the range was 23 °C to 31 °C (Figure 2(b)).

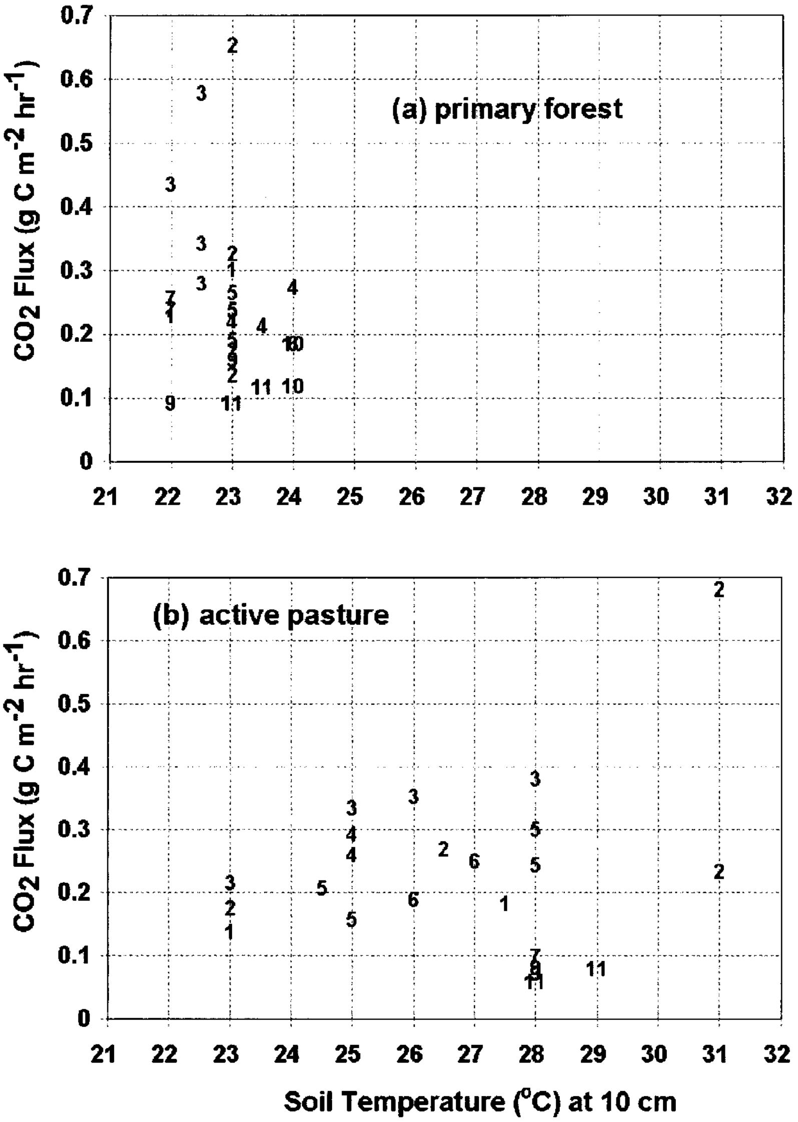

Figure 2. Relationship between seasonal variation in soil temperature and CO_2 flux for primary forest (a) and active pasture (b). Plotting symbols indicate the month of the year (Jan = 1, Dec = 12), and each symbol is a mean of 8 chamber measurements for a study site.

In neither forest nor pasture was there a relationship between soil temperature and soil respiration across months. The variation in temperature shown in Figure 2 is probably due more to the time of day of sampling and the presence or absence of clouds on sampling dates rather than to a consistent seasonal trend in temperature.

The pasture soils also experience somewhat greater diel variation in soil temperature than do the forest soils, with a range of 24 °C to 28.5 °C in the pasture and 22 °C to 24.5 °C in the forest on the day that we did diel studies (Figure 3). In an earlier study (Trumbore et al. 1995), we found no significant diel variation in soil respiration in the same primary forest and degraded pasture sites during either the wet or dry season. In the present study, there was again no significant relationship between diel soil temperature and soil respiration in the primary forest and the degraded pasture at the end of the dry season (Figure 3(a,c)), but there was a relationship in the active pasture (Figure 3(b)). Soil respiration in the active pasture increased by a factor of 6 between 7 AM and 4 PM and then fell by a similar magnitude by 6 PM. Soil temperature did not fall as quickly between 4 and 6 PM as did soil respiration. Hence, the relationship between temperature and soil respiration is not a typical exponential function, and with only four time points across a rather narrow temperature range, fitting an empirical function was not possible. The sharp drop in soil respiration at the end of the daylight period suggests that this diel pattern may be related more to the response of grass metabolism to light than to a response of soil processes to soil temperature. Linkages between root respiration and responses of the entire plant to light probably vary among species and deserve more research attention. The degraded pasture obviously experienced the same diel pattern of light and temperature as did the active pasture, but it did not show the same diel pattern in soil respiration. The vegetation in the degraded pasture is less productive than in the active pasture and it includes a large component of woody species.

Effects of soil moisture

When soils are very dry (e.g., matric potential <-10 MPa), small differences in volumetric water content result in large differences in matric potential, and so the uncertainty in the matric potential estimates increases with decreasing water content. Despite uncertainty in the very low matric potential values, matric potential is a useful expression of the availability of free water to microorganisms and roots, thereby taking into account differences in the amount of water adsorbed to soil particles of different soil textures. In the present study, all land uses were on Belterra clays (Sombroek 1966), and clay content of the top 10 cm soil is between 76% and 82% on all sites. Despite the nearly uniform soil texture across land uses, it is still appropriate to report

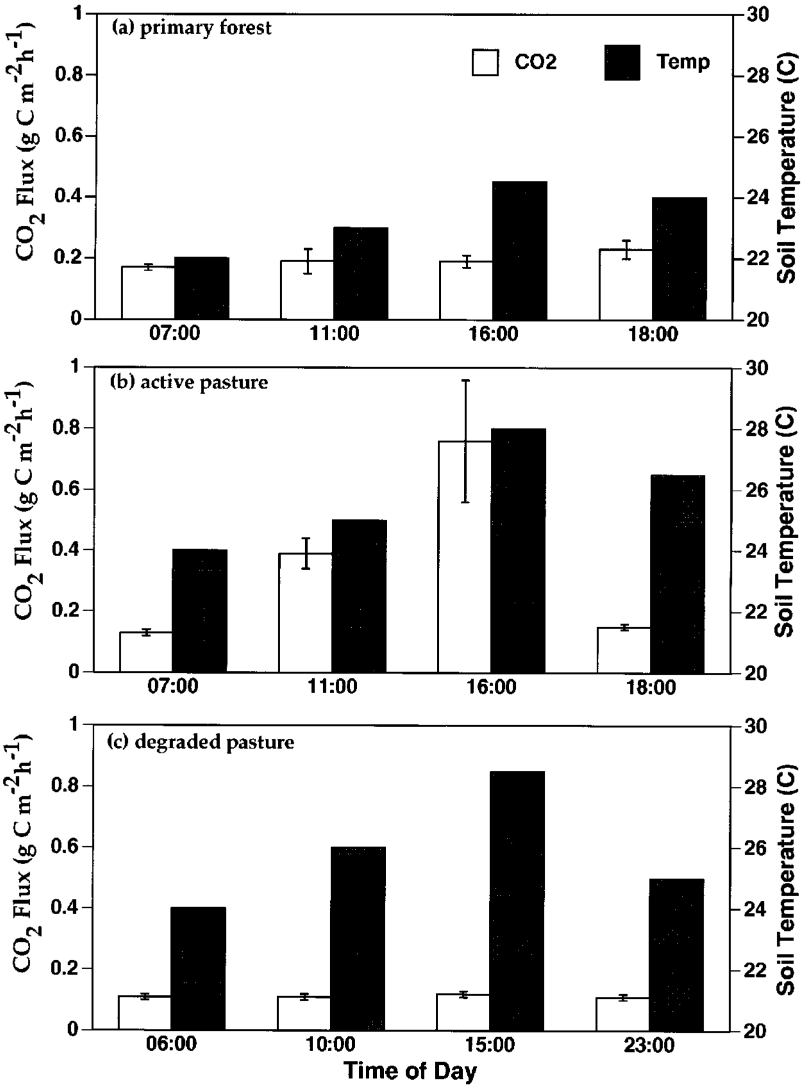

Figure 3. Relationship between diel variation in soil temperature at 10 cm depth (shaded bars) and CO_2 fluxes (open bars) in primary forest (a), active pasture (b), and degraded pasture (c) on 4–5 December 1995. Fluxes are means of 8 chamber measurement per site and time. Standard errors of the mean are shown for fluxes.

matric potential so that the results of this study can be compared to other studies on other soil types with different soil textures.

Respiration rates generally decreased with decreasing water content in both pasture and forest soils (Figure 4). Some of the soil respiration rates early in the rainy season were higher than would be expected based only on a matric potential function (e.g., the February and March measurements with respiration rates >0.5 g C m^{-2} hr^{-1}; Figure 4). These high rates may have been due to wet-up effects, which have been demonstrated to produce pulses of microbial activity and CO_2 production (Birch 1958; Bottner 1985; Kieft et al. 1987). Although the rainy season was already well underway, the surface layers of the soil may dry between rainfall events, causing wetting and drying cycles near the soil surface that are not apparent in our TDR data.

Only on two occasions, when measurement dates fell soon after large rainfall events, did we observe matric potential >-0.005 MPa, where soil respiration appeared to be inhibited by near saturated water contents (January and February datapoints in Figure 4(b)). Although these soils have high clay content, they also have good structure and porosity and high infiltration rates, which result in infrequent saturated conditions (Jipp et al. 1998). For the regressions shown in Figure 4, the presumed wet-up events were excluded (respiration >0.5 g C m^{-2} hr^{-1}), as were the near saturated events (matric potential >-0.005 MPa).

In agreement with the function derived by Orchard and Cook (1983; Table 1), soil respiration was correlated with the logarithm of matric potential (appearing as a straight line when matric potential is plotted on a log scale; Figure 4). Also plotted in Figure 4 (broken lines) are functions based on the cube of the volumetric water content, which Papendick and Campbell (1981) show is the appropriate theoretical expression of water content in equations predicting rates of diffusion of soluble organic substrates through water films in dry soils. If soil respiration were predominantly microbial, then this might be the best formulation. Because roots are also present and because scatter in the data about both sets of regression lines precludes identifying one or the other as providing a clearly superior statistical fit, either the logarithm of the matric potential or the cube of the volumetric water content appears to be a suitable predictor of the general effect of water content on soil respiration.

This relationship between matric potential and soil respiration holds when all monthly means from all four land uses and all dates are included, although once again, there is considerable scatter (Figure 5(a)). In order to facilitate comparisons across sites with different productivity, we normalized emissions to the month with the highest observed mean CO_2 flux (excluding presumed wet-up periods) for each of the eight study plots, so that the highest value was unity and all other monthly means for that study plot were <1

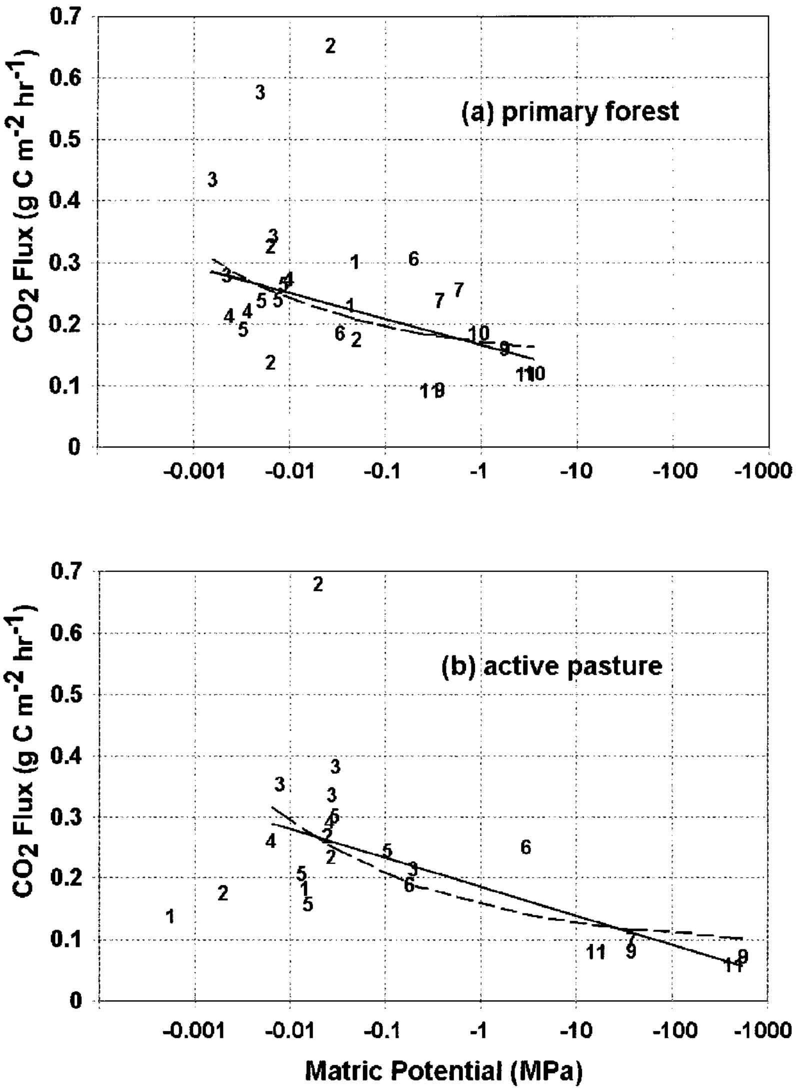

Figure 4. Correlation between seasonal variation in water content and CO_2 flux in primary forest (a) and active pasture (b). Plotting symbols indicate the month of measurement of the mean of 8 chambers in each of two study sites for each land use. Least squares regressions (excluding values where $\Psi > -0.005$ MPa or where CO_2 fluxes >0.5 gC m^{-2} hr^{-1} – see text) are shown for matric potential (Ψ, solid lines) and volumetric water content (θ, in cm^3 H_2O cm^{-3} soil; broken lines) as independent variables:

primary forest: $CO_2 = -0.0431\text{Log}(-\Psi) + 0.16$; $R^2 = 0.31$ $CO_2 = 1.902(\theta^3) + 0.14$; $R^2 = 0.30$
active pasture: $CO_2 = -0.0472\text{Log}(-\Psi) + 0.19$; $R^2 = 0.62$ $CO_2 = 3.461(\theta^3) + 0.09$; $R^2 = 0.54$
All regressions are significant at $\alpha = 0.01$.

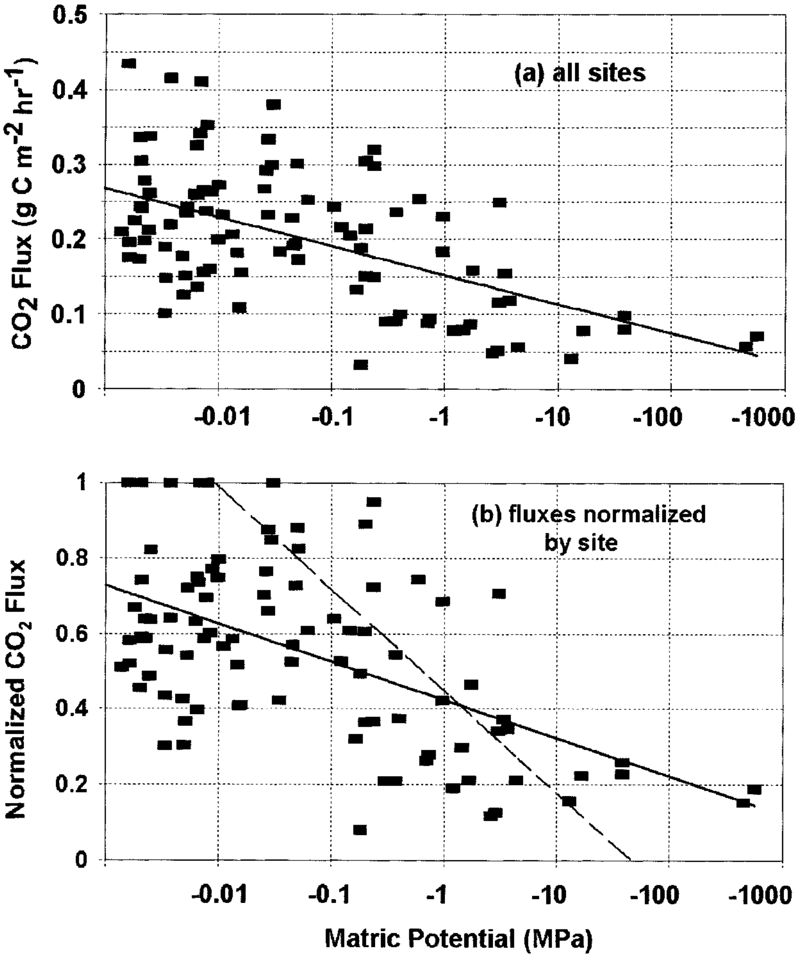

Figure 5. Soil matric potential and CO_2 fluxes for all study sites of all land uses and all dates (a) and for the same data normalized by the maximum (non-wet-up – see text) flux observed at each study site (b). The solid least squares regression lines are significant at $\alpha = 0.01$:
(a): $CO_2 = -0.039 \mathrm{Log}(-\Psi) + 0.15$; $R^2 = 0.31$
(b): normalized $CO_2 = -0.10 \mathrm{Log}(-\Psi) + 0.42$; $R^2 = 0.29$
The broken line shows the function for the Harvard Forest, Massachusetts from Davidson et al. (1998) and unpublished data: normalized $CO_2 = -0.27 \mathrm{Log}(-\Psi) + 0.45$.

(Figure 5(b)). Included in this comparison is a function originally developed by Davidson et al (1998) and since updated (unpublished data) that relates soil matric potential to soil respiration measured in a temperate forest on a sandy loam soil during a summer drought. The function for the shallower glacial soils of the New England forest is steeper than the function for the deep tropical soils. We speculate that water stress develops more quickly in shallower soils and is affected not only by matric potential of the surface soils but also by the total amount of water held in the soil profile. Significant CO_2 production has been demonstrated below 1 m depth in the tropical soils (Davidson & Trumbore 1995), and below 20 cm depth in the New England soil (unpublished data). If production of CO_2 occurs below the depth at which water and temperature are measured in the soil, and if the depth of production varies among sites and seasons, then functions based on surface measurements of temperature and water are likely to yield inconsistent results.

We conclude that soil respiration can be expressed as a function of matric potential, but it is premature to offer an empirical function that would be universally applicable. Perhaps this is not a surprise, given that soil respiration is a combination of plant and microbial metabolism, each of which may respond differently to temperature and water content. The depth of biological activity in soils must also be considered, as it varies with climate, soil type, and vegetation type. Relating rates of soil respiration to water and temperature measurements made at some arbitrarily chosen depth of the surface horizons is simplistic. Further progress in defining temperature and moisture functions will probably require isolation of root and microbial processes and measurements of temperature, water content and CO_2 production for each soil horizon.

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