

Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest

J. CURIEL YUSTE,^{1,2} I. A. JANSSENS,¹ A. CARRARA,¹ L. MEIRESONNE³ and R. CEULEMANS¹

¹ University of Antwerpen, Department of Biology, Research Group of Plant and Vegetation Ecology, Universiteitsplein 1, B-2610 Wilrijk, Belgium

² Author to whom correspondence should be addressed (jorge.curielyuste@ua.ac.be)

³ Institute for Forestry and Game Management (IBW), Ministry of the Flemish Community, Gaverstraat 4, B-9500 Geraardsbergen, Belgium

Received June 11, 2002; accepted May 17, 2003; published online November 17, 2003

Summary Soil respiration (SR) was monitored periodically throughout 2001 in a Scots pine (*Pinus sylvestris* L.) stand located in the Belgian Campine region. As expected for a temperate maritime forest, temperature was the dominant control over SR during most of the year. However, during late spring and summer, when soil water content (SWC) was limiting, SR was insensitive to temperature ($Q_{10} = 1.24$). We observed that during prolonged rain-free periods, when SWC was less than 15% (v/v), SR decreased dramatically (up to 50%) and SWC took over control of SR. During such drought periods, however, rain events sometimes stimulated SR and restored temperature control over SR, even though SWC in the mineral soil was low. We hypothesize that restoration of temperature control occurred only when rain events adequately rewetted the uppermost soil layers, where most of the respiratory activity occurred. To quantify the rewetting capacity of rain events, an index (I_w) was designed that incorporated rainfall intensity, time elapsed since the last rain event, and atmospheric vapor pressure deficit (a proxy for evaporative water losses). To simulate SR fluxes, a model was developed that included the effects of soil temperature and, under drought and non-rewetting conditions (I_w and SWC < threshold), an SWC response function. The model explained 95% of the temporal variability in SR observed during summer, whereas the temperature function alone explained only 73% of this variability. Our results revealed that, in addition to temperature and SWC, rain plays a role in determining the total amount of carbon released from soils, even in a maritime climate.

Keywords: drought stress, Q_{10} , Scots pine, soil temperature, soil water content.

Introduction

Soil respiration (SR) is an important component of forest ecosystem carbon (C) budgets. Forest soils contain large C stores, (Post et al. 1982) and it has been hypothesized that relatively small changes in SR induced by climate change could rival the

annual fossil fuel loading of atmospheric CO₂ (Jenkinson et al. 1992, Raich and Schlesinger 1992). On a global scale, SR is mainly controlled by temperature and precipitation (Raich and Schlesinger 1992, Raich et al. 2002). Because global temperatures and precipitation patterns are expected to change in the future (Borken et al. 1999), CO₂ fluxes from soils may be altered (Raich et al. 2002). Thus, it is important to understand which climatic factors control SR and, moreover, how these factors affect CO₂ emissions from soils. Where no severe drought stress occurs, soil temperature is typically a reliable predictor of SR (Moncrieff and Fang 1999). However, other biotic and abiotic factors have been reported to influence SR: soil water content (SWC) (Carlyle and Than 1988, Howard and Howard 1993, Keith et al. 1997, Epron et al. 1999, Law et al. 1999, Reichstein et al. 2002), soil organic matter quantity and quality (Taylor et al. 1989), root and microbial biomass, root nitrogen content (Ryan et al. 1996), soil acidity, soil texture and site productivity (Raich and Schlesinger 1992, Raich and Potter 1995). In the presence of a drought, the amount and distribution of precipitation has also been shown to be an important controlling factor of SR (Borken et al. 1999, Lee et al. 2002, Rey et al. 2002). Rain exerts control during dry periods either by controlling SWC fluctuations in surface layers where most of the biological activity occurs (Lee et al. 2002) or by strongly stimulating soil CO₂ emissions in what is called the "Birch effect" or "drying and rewetting effect" (Birch 1958, 1960, Andersson 1973, Orchard and Cook 1983, Russell and Voroney 1998, Borken et al. 1999, Davidson et al. 2000, Lee et al. 2002, Rey et al. 2002). Especially arid and semiarid regions may be more sensitive to changes in precipitation patterns (Rey et al. 2002). Furthermore, temperate ecosystems, where precipitation is evenly distributed over the year, may be sensitive to the amount and distribution of rainfall during drought (Borken et al. 1999, Longdoz et al. 2000, Lee et al. 2002).

Soil CO₂ efflux has been modeled using linear (Andersson 1973, Witkamp 1996), power (Kucera and Kirkham 1971) and sigmoid (Schlentner and van Cleve 1985, Janssens et al.

2000b, Matteucci et al. 2000) relationships with temperature. However, exponential relationships, especially the Q_{10} relationship (van't Hoff 1898), are more frequently used to predict respiration rates from temperature (Peterjohn et al. 1994, Raich and Potter 1995, Boone et al. 1998, Davidson et al. 1998, Epron et al. 1999, Buchmann 2000, Morén and Lindroth 2000). Although there has been no agreement on the best shape of the relationship (Lloyd and Taylor 1994), and it has been a matter of controversy whether a function developed to explain temperature effects at a molecular level could be extrapolated to larger scales such as organisms or ecosystems (Chai-Berlinck et al. 2002), Q_{10} functions often provide a good indication of the temporal variation in soil respiration. Most empirical models have used a constant Q_{10} ("annual Q_{10} ") to predict ecosystem respiratory responses to temperature. However, several authors have pointed out that Q_{10} is not constant during the year, but decreases as temperature increases (Paembonan et al. 1991, Rayment and Jarvis 2000, Tjoelker et al. 2001, Xu and Qi 2001b, Janssens and Pilegard 2002). Thus, at synoptic timescales, models with constant parameters may be less accurate than models with seasonally fluctuating parameters. The aims of this study were (1) to analyze which climatic factors control SR during different periods of the year and to determine the relationships between the controlling factors and SR; and (2) to analyze the seasonal changes in the temperature-sensitivity of SR and determine which factors may explain these seasonal changes.

Materials and methods

Plot description

This study was conducted in a 72-year-old Scots pine (*Pinus sylvestris* L.) stand located in Brasschaat, 20 km NE of Antwerpen in the Belgian Campine region (51°18' N and 4°31' E). The stand is part of De Inslag forest and is a level-II observation plot of the European Programme for Intensive Monitoring of Forest Ecosystems (EC regulation No. 3528/86 and UN/ECE), managed by the Institute for Forestry and Game Management (Flanders, Belgium). De Inslag is also part of the Carboeuroflux Research Network (<http://www.bgc-jena.mpg.de/public/carboeur/>), funded by the European Commission's Fifth Framework Programme. The site is almost flat (slope = 0.3%), with an elevation of 16 m. At the time of study (2001), stand density was 376 trees ha⁻¹, with a mean tree height of 21 m and a mean diameter at breast height of 0.29 m (Xiao et al. 2003). In the area where the SR measurements reported here were collected, understory vegetation was limited to a moss layer (Janssens et al. 1999).

The site has a temperate maritime climate, with a mean annual temperature of 9.8 °C (mean temperatures of the coldest and warmest months are 3 and 18 °C, respectively) (Janssens et al. 1999). Long-term (30 year) mean annual precipitation is 750 mm, and long-term mean annual potential evapotranspiration is 670 mm (Čermák et al. 1998). During the growing season (March to October), total precipitation averages around 433 mm, whereas potential evapotranspiration rates are much

higher: 619 mm (Čermák et al. 1998), suggesting that drought stress may occur in summer. The forest has a sandy soil (80–98% sand in upper 1 m; Janssens et al. 1999) with a distinct humus or iron B-horizon (Baeyens et al. 1993). The soil type is Psammentic Haplumbrept (USDA classification) or Umbric Regosol (FAO classification). In the uppermost 1 m, the mineral soil contains 115 Mg C ha⁻¹, and the surface litter layer contains 27 Mg C ha⁻¹ (Janssens et al. 1999).

The site has poor drainage as a result of a clay layer located at a depth of 1.5 to 2 m. The soil is moist, but rarely saturated, as a result of the high hydraulic conductivity in the upper layers (sand). Soil water content is typically above water holding capacity (WHC, 0.123 m³ m⁻³), except during summer when SWC frequently drops below WHC (Figure 2). More detailed information on soil and local climatic conditions can be found in Baeyens et al. (1993), Janssens et al. (1999) and Kowalski et al. (2000).

Soil respiration measurements

A closed dynamic system (IRGA: CIRAS-1 soil chamber: SRC-1, both PP-Systems, Hitchin, U.K.) was used to measure soil respiration. To mitigate spatial variability, we enlarged the surface area sampled by the chamber by attaching a PVC rim to the base of the chamber. The bottom side of the PVC rim had a slot in which a rubber joint provided an airtight seal for the soil collars (Janssens et al. 2000a). Modification of the chamber did not alter the measured fluxes (Janssens et al. 2000a).

Ten PVC collars (diameter = 20 cm, height = 16 cm) were installed randomly within the experimental plot during November 2000. The lowest 6 cm of each collar were perforated with 5-mm holes to allow fine roots to recolonize the space within the collar, thus recreating natural conditions similar to those of undisturbed soil. Collars were inserted in the soil, leaving 4 cm exposed. The sparse ground vegetation (mosses) was carefully removed from within the collars just after installation to avoid bias due to their respiratory activity. The meteorological parameters used in this study were logged continuously in the vicinity of a meteorological tower, 50 m from the experimental plot. Precipitation (tipping-bucket rain gauge, Didcot DRG-51, U.K.) and air relative humidity (psychrometer, Didcot DTS-5A, U.K.) measurements were collected at the top of the tower (40 m), whereas air temperature was measured at 1.5 m above the forest floor and soil temperature at depths of 2 and 9 cm in the mineral soil. Precipitation, relative humidity and air and soil temperature were continuously measured and stored as half-hourly means or totals on a data logger (CSI CR10, Campbell Scientific, Logan, UT). Soil water content was measured at two locations, one with a shallow clay layer (1 m) and one with a deeper clay layer (2 m), at 25 and 30 cm in the mineral soil, respectively, using two 50 cm long, horizontally-installed time domain reflectometry (TDR) probes (Meiresson and Overloop 1999). We averaged SWC from both locations because the depth of the clay layer was extremely variable (Meiresson and Overloop 1999). Measurements were taken about twice a week (cable tester Tectronix 1502B) and were linearly interpolated.

Measurements of SR were made frequently over the course of 1 year beginning in early January 2001 (2 months after collars were inserted) until the end of December 2001 (Figure 2a). Each measurement was duplicated and the mean was used in the calculations. No significant differences were found between consecutive measurements (data not shown). Soil respiration was pooled over all 10 collars. The data set was then subdivided into three subsets, each representing a different period of the year (winter/early spring, late spring/summer and fall; Figure 2a and Table 1).

Temperature responses

The temperature response of SR was estimated by means of a Q_{10} function:

$$SR = SR_{10} Q_{10}^{(T-10)/10} \quad (1)$$

where SR is predicted soil respiration, SR_{10} is simulated SR at 10 °C, Q_{10} is temperature sensitivity of SR (the respiratory flux at one temperature over the flux at a temperature 10 °C lower), and T is measured soil temperature at 2 cm depth in the mineral soil. The function was first fitted to the entire annual data set and finally to each of the three periods to test for seasonal changes in Q_{10} . To avoid confounding effects of drought on the temperature response, the following observations were removed from the data sets. (1) Measurements taken during a drought, defined as SWC below the WHC ($0.123 \text{ m}^3 \text{ m}^{-3}$). (2) Measurements taken more than 30 h after the last significant rain event ($> 1 \text{ mm h}^{-1}$). These data were excluded because the upper layers, containing most of the organic matter and fine roots (Janssens et al. 2002b), dried out rapidly, with the result that drought occurred in these upper layers, even if SWC at 25 cm was above the WHC. (3) Measurements taken immediately after a rain event. These data were excluded to avoid possible stimulative effects as a result of rewetting of the upper soil layers (Birch 1958, 1960, Anderson 1973, Kelliher et al. 1999, Lee et al. 2002, Rey et al. 2002). Thus, SR_{10} and Q_{10} were estimated when water availability was not limiting and avoided the confounding effects of rain. Only in Period 3, corresponding to late spring and summer, were data excluded.

Drought and rain effects

When SWC was below WHC, the following model was fitted to the data:

$$SR = f(T)f(\text{SWC}) \quad (2)$$

where SR is soil respiration, $f(T)$ is a Q_{10} function and $f(\text{SWC})$ is a linear function depending on SWC:

$$f(\text{SWC}) = a\text{SWC} + b \quad (3)$$

where SWC is soil water content in $\text{m}^3 \text{ m}^{-3}$, and a and b are parameters (5.2 and -0.05 , respectively).

However, we often observed that, under limited SWC conditions, SR was enhanced by significant rain events to such a degree that temperature control over SR was restored. Hence,

application of Equation 3 was restricted to those measurements where no rewetting occurred. To define where rewetting was significant and where it was not, we needed to quantify the rewetting potential of rain events. We assumed that rewetting capacity would be positively related to water input (amount of precipitation) and negatively related to water loss (evaporation, uptake by roots and percolation). Because percolation and uptake by roots were impossible to estimate, we used time since the last rain event as a proxy for these water losses. Evaporation was also not measured. Because vapor flux density is positively related to atmospheric vapor pressure deficit (VPD_a ; Penman-Monteith equation), we used VPD_a as a proxy for the evaporative water losses from the soil surface.

Thus, quantification of the rewetting capacity by rain events was simulated with a rewetting index (I_w) that included the absolute amount of precipitation during the rain event, VPD_a , and time since the last rain in Equation 4. We obtained the best fit with a logarithmic function of the form:

$$I_w = \alpha + \log \left(\frac{\sqrt{R}}{VPD_a t^2} \right) \quad (4)$$

where α is a constant (2.5), R represents amount of precipitation during the last rainfall event (mm), t is time since the last rain event (h), and VPD_a is mean vapor pressure deficit of the atmosphere at 1.5 m above the forest floor (kPa) averaged over the last 24 h. We observed that the effect of rain was relatively independent of its intensity (Figures 1a and 1c). Therefore, we minimized its contribution by using the square root of the rain intensity in Equation 4. Time, in contrast, was critical because the rain stimulation was highly ephemeral (Figures 1b and 1c). We therefore maximized the contribution of time by using the square of the elapsed time in Equation 4.

Thus, I_w was intended to be a rough representation of the rewetting intensity in the upper soil layers where no soil water sensors were installed. Because we observed that, when I_w was above 0.3, temperature resumed control over the measured fluxes, we applied the SWC correction only when I_w was below 0.3. Figure 1 shows bidimensional representations of the relationship among the three variables controlling I_w . Even relatively small rain events ($< 4 \text{ mm}$) rewetted the uppermost layers sufficiently to restore temperature control ($I_w > 0.3$, Figures 1a and 1c). The value of I_w decreased rapidly with time, especially during the first hours (Figure 1c). Furthermore, Figures 1a and 1b show that, even at the highest values of VPD_a , I_w may be greater than 0.3 for extended time periods when precipitation exceeded 3–4 mm.

Results and discussion

Temperature control over SR

Seasonal differences in SR rates were large, with fluxes ranging between $0.3 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in January and $2.3 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in late July (Figure 2a). Temperature was the main controlling factor over SR during most of the year (Table 1, Figure 3).

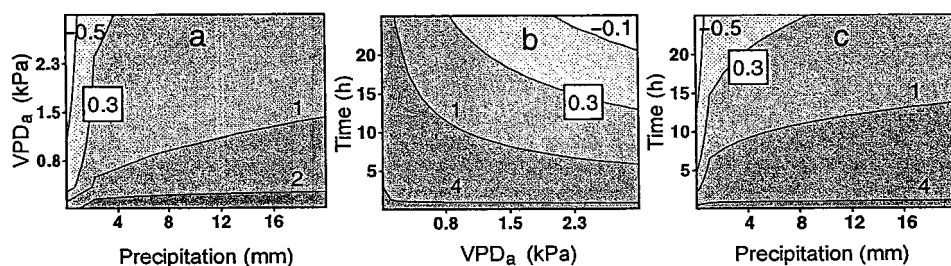


Figure 1. Contour graphs illustrating the influence of different parameters on the rewetting index (I_w). (a) Effect of atmospheric vapor pressure deficit (VPD_a) and amount of precipitation during the last rain event 10 h after that rain event. (b) Time since the last rain event and VPD_a .

following 10 mm of precipitation. (c) Time since the last rain event and precipitation during the last rain event at a VPD_a of 0.75 kPa. The white box indicates the rewetting threshold (0.3).

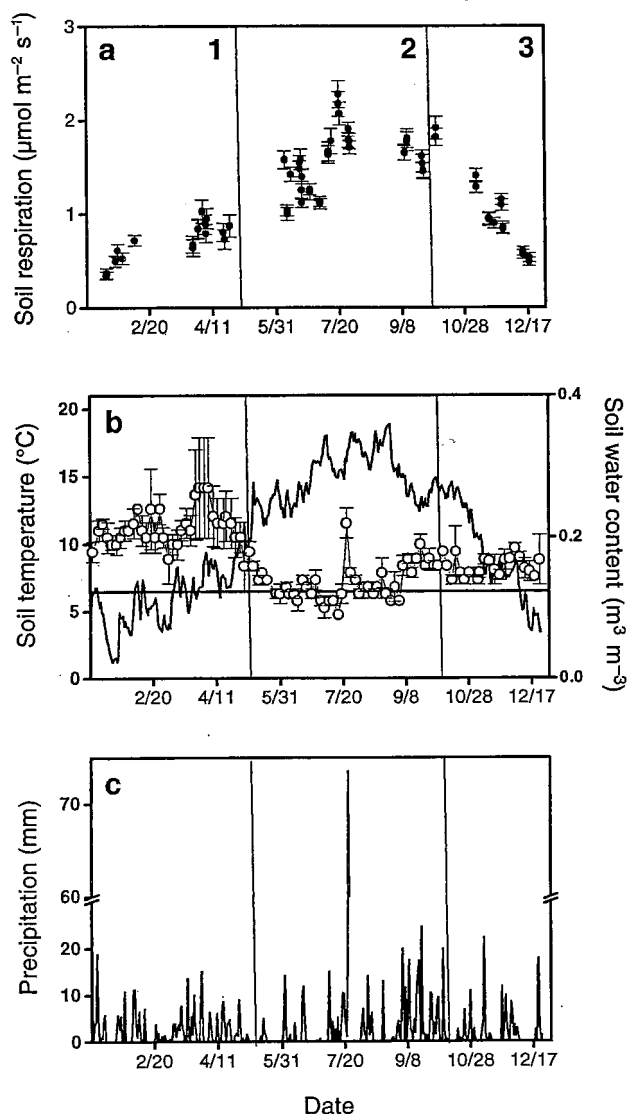


Figure 2. (a) Soil respiration under Scots pine overstory during 2001. Vertical bars represent standard error of the mean. (b) Daily mean soil temperature at 2 cm depth in the mineral soil (solid line) and soil water content at 25 cm depth in mineral soil (line + \circ) during 2001. Vertical bars represent standard error of the mean. The horizontal bar represents the water holding capacity ($0.123 \text{ m}^3 \text{ m}^{-3}$). (c) Time series of daily total precipitation during 2001. In each graph, vertical bars separate Periods 1, 2 and 3 assessed in this study.

Only during the growing season was temperature control over SR limited (Table 1, Figure 3), suggesting that other factors may exert a strong influence on SR during this season. When all potentially drought-affected data were excluded, a tight relationship between temperature and SR was also observed in summer (see Period 2 in Figure 3).

The annual Q_{10} function explained a large proportion of the temporal variation in SR ($R^2 = 0.68$; Table 1). When drought-affected data were excluded from the analysis, the annual Q_{10} increased from 1.93 to 2.9 (Table 1), a value well within the range (2.0–6.3) reported for European and North American forest ecosystems (Davidson et al. 1998, Janssens et al. 2001). The increase in Q_{10} and the significant improvement of the fit after exclusion of drought-affected data (R^2 from 0.68 to 0.95), emphasizes the confounding effect of drought on the sensitivity of SR to temperature. The annual SR_{10} , however, was unaltered by the exclusion of drought-affected measurements (Table 1), because most of our measurements were taken at soil temperatures around 10°C , and none of these measurements at moderate temperatures were drought-affected. Exclusion of a limited number of water-stressed data at higher temperatures therefore had no effect on the mean SR at 10°C , although it did change the Q_{10} .

Seasonal analysis of SR indicated that, even when rain- and drought-affected data were excluded, Q_{10} and SR_{10} varied considerably (Table 1). The SR_{10} was maximal during the growing season, but had similar values during winter and fall. This summer increase in basal soil respiration might have been related to the typical peak in root growth and biomass that occurs in the growing season (Lyr and Hoffmann 1967). The highest Q_{10} value (3.2) occurred in the fall, and the lowest in the summer (2.0). In our study, the highest Q_{10} did not coincide with lowest temperature or highest SWC (Table 1). The weak relationship between Q_{10} and SWC was expected, because drought-affected data were removed to avoid confounding effects in the Q_{10} estimates. However, the absence of a relationship between Q_{10} and temperature observed in this study conflicts with much evidence that the temperature sensitivity of respiration decreases as temperature increases (de Jong and Schappert 1972, Paembonan et al. 1991, Howard and Howard 1993, Lloyd and Taylor 1994, Sprugel et al. 1995, Rayment and Jarvis 2000, Tjoelker et al. 2001, Xu and Qi 2001b, Janssens and Pillegard 2002). On the other hand, some of these

Table 1. Mean flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$), standard deviation (SD), Q_{10} , soil respiration at 10 °C (SR_{10}), number of observations (n), proportion of variability explained by temperature (R^2), P -value, mean soil temperature (ST; °C) and mean soil water content (SWC; $\text{m}^3 \text{m}^{-3}$) for each period. Numbers with an asterisk represent Q_{10} , SR_{10} , R^2 and P -values before excluding the drought-affected data. The standard error of the mean (SE) was calculated by the curve-fitting program. Abbreviation: GS = growing season.

Period	Season	Mean flux	SD	Q_{10}	SE	SR_{10}	SE	n	R^2	P -value	Mean ST	Mean SWC
1-3	Whole year	1.22	0.48	1.93*/2.9	0.12*/0.12	1.06*/1.08	0.04*/0.01	67*/43	0.68*/0.95	< 0.0001	11.38	0.17
1	Winter	0.73	0.20	2.74	0.27	1.02	0.03	18	0.89	< 0.0001	6.35	0.24
2	GS	1.60	0.32	1.24*/1.98	0.20*/0.4	1.38*/1.23	0.14*/0.1	32*/10	0.06*/0.59	0.184*/0.001	15.45	0.13
3	Fall	1.02	0.44	3.21	0.21	1.15	0.03	15	0.96	< 0.0001	8.39	0.16

field studies may have included drought-affected data (Sprugel et al. 1995, Rayment and Jarvis 2000, Xu and Qi 2001b, Janssens and Pillegard 2002) that may have exacerbated the decrease in Q_{10} at higher temperatures (Xu and Qi 2001a). Inclusion of drought-affected data in this study significantly decreased Q_{10} in summer from 2.0 to 1.2 (Table 1, Figure 3). Because temperature and SWC are often correlated (Davidson et al. 1998), care should be taken when relating changes in Q_{10} to temperature.

Another factor that may explain the weak correlation between temperature and Q_{10} is the temporal scale used in this study. Because of the relatively long periods (3–5 months), other factors or processes, e.g., seasonality of root growth/mortality or litter inputs during fall, could have confounded the relationship between SR and temperature in some periods, making Q_{10} no longer a measure of temperature sensitivity only. Different temporal scales have recently been used to study the temperature dependence of SR. Rayment and Jarvis (2000) used a daily timescale basis to calculate Q_{10} , whereas Janssens and Pillegard (2002) usually chose subsets of 4 to 7 days, and Xu and Qi (2001b) used approximately 1-month periods. However, none of these studies have attempted an in-depth investigation into the relationship between the temporal scale and the resulting Q_{10} of SR. Short temporal scales would minimize the probability that other factors confound the observed temperature dependence, but are not always realistic because the smaller temperature ranges and the smaller number of flux measurements increase the uncertainty in the calculated Q_{10} values.

Drought and rain responses

Even within the maritime climate at our site, SWC became a limiting factor in summer. This was a result of the combination of the limited water storage capacity typical of sandy soils (Kelliher et al. 1999) and the relatively long rain-free periods (Figure 2) and high evapotranspiration rates in early summer (Meiresonne et al. 2002). Under conditions of decreasing SWC, it might be expected that the upper soil layers would suffer even more severe drought stress, because evaporation and maximum fine root density (and thus water extraction by roots) occur mainly in these surface layers.

After correcting the entire annual data set for temperature, three different subsets of soil fluxes became distinguishable (Figure 4). A first subset of data corresponded to measurements taken with SWC greater than $0.15 \text{ m}^3 \text{m}^{-3}$ (solid circles in Figure 4). Data included in this subset were obtained mostly outside of summer, with generous and evenly distributed rainfall (Figure 2) and lower evapotranspiration rates (Meiresonne et al. 2002). These SR rates were not significantly affected by SWC or post-rainfall effects, and therefore increased exponentially with temperature (fluctuated around 1 after correction for temperature; Figure 4).

A second group comprised data obtained when soil water availability at 25 cm in mineral soil was low (SWC < $0.15 \text{ m}^3 \text{m}^{-3}$), but with an I_w above the rewetting threshold of 0.3 (solid triangles in Figure 4). Similar to the first, unstressed group of measurements, SR rates in this subset were well explained by the Q_{10} function. These measurements were taken just a few hours after heavy rain events (I_w above the threshold of 0.3).

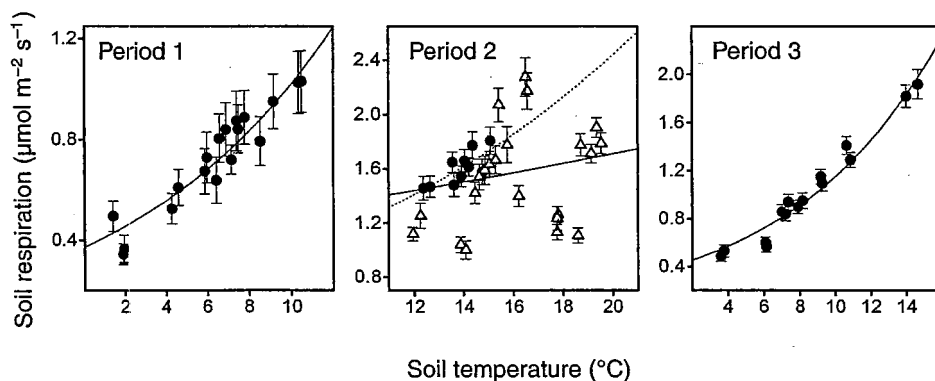


Figure 3. Soil respiration as a function of soil temperature at a depth of 2 cm in mineral soil for each of the periods defined in Table 1 and its corresponding Q_{10} function (solid line). The dashed line in Period 2 corresponds with Q_{10} fitted to non-drought-affected data only. Symbols: Δ = drought-affected data; and \bullet = non-drought-affected measurements. Vertical bars represent standard error of the mean.

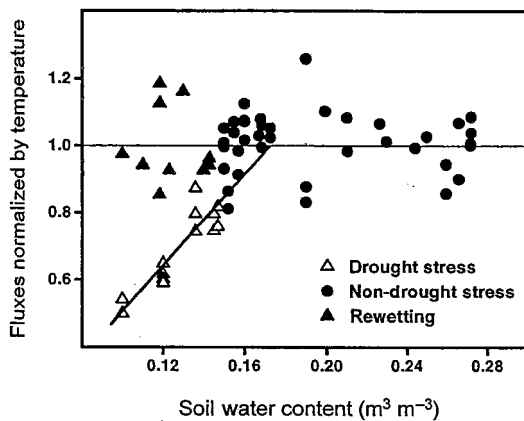


Figure 4. Soil respiration (SR) data were normalized for temperature (measured SR was divided by SR predicted from the temperature response under non-water-stress conditions) and plotted against soil water content (SWC). Fluxes of each period were normalized based on their corresponding Q_{10} function. Symbols: \blacktriangle = SWC < 0.15 mm and rewetting index (I_w) > 0.3; \triangle = SWC < 0.15 mm and I_w < 0.3; and \bullet = SWC > 0.15. The solid line represents the linear correction for drought stress.

following a period of drought. It is therefore likely that, although the mineral soil was still dry, SR of the surface layers was no longer water-limited. Because most SR originates from these upper layers, temperature control of SR was restored. Only in three measurements, taken less than 5 h after relatively heavy rain events, was the rewetting-induced stimulation of SR not captured well by the model. Davidson et al. (2000) also reported post-rainfall increases in SR under dry conditions, above those expected by a simple matrix potential function. There is an extensive literature discussing these post-rainfall pulses of CO_2 (Birch 1958, 1960, Andersson 1973, Orchard and Cook 1983, Russell et al. 1998, Borken et al. 1999, Davidson et al. 2000, Lee et al. 2002, Rey et al. 2002). It has been hypothesized that stimulation of SR after rainfall results from the displacement of CO_2 -rich air from within the soil (Rey et al. 2002), rapid decomposition of microbial biomass during drought (Borken et al. 1999) and an increase in surface area of palatable organic substrates (Birch 1959) due to desorption of organic molecules in the soil matrix (Serevinatne and Wild 1985). To date, no consensus has been reached about the actual causes, duration and magnitude of these post-rainfall stimulative effects. In the maritime climate of our study site, rewetting effects were restricted to measurements taken shortly after rain events during a limited number of drought-stress periods. Hence, there were insufficient data to assess quantitatively the relationship between I_w and the magnitude of the post-rainfall effects. However, in general, we observed that a sufficiently large I_w restored the temperature control over SR. Therefore, I_w was not used directly in the model, but only to determine if drought reduced SR.

A third subset (open triangles in Figure 4) comprised data with SWC < 0.15 $\text{m}^3 \text{m}^{-3}$ and I_w < 0.3. Here, rewetting was absent or marginal, and SR declined linearly with decreasing

SWC. The strong control exerted by SWC at 25 cm during periods of scarce rain events and low SWC may suggest that, during these periods, a major fraction of the fluxes came from deeper layers in the soil profile, and a lesser part from the upper layers. As in most forests, the upper layers of the soil profile at our site are by far the richest in fine roots and organic matter (Janssens et al. 1999). Most of the respiratory potential is therefore located in these upper layers, which may explain why fluxes fell dramatically when rain was scarce for long periods and the soil surface started to dry out. Similar results were obtained by Rey et al. (2002), who showed SR to be strongly limited when SWC of the upper 10 cm of soil fell below a certain threshold. Longdoz et al. (2000) also ascribed an observed summer decrease in SR to water limitations in the organic layer. Lee et al. (2002) suggested that the SWC of the surface layers may be a better predictor of SR rates because microbial biomass and activity is likely to be greater in these layers than in deeper ones. Moreover, the amplitude of fluctuations in SWC is larger near the soil surface (Lee et al. 2002). Therefore, modeling the responses of SR to SWC measured at one depth only may be too simplistic to understand the relationship between SR and SWC (Davidson et al. 2000).

The model combining the responses of temperature and drought (when SWC < 0.15 $\text{m}^3 \text{m}^{-3}$ and I_w < 0.3) simulated SR rates significantly better than Equation 1 alone ($R^2 = 0.95$, $P < 0.0001$ versus $R^2 = 0.72$, $P < 0.0001$, Figure 5). Thus, even in temperate maritime climates, drought can affect total soil C losses significantly during summer periods. The good fit of our model indicates that our approach to quantifying the rewetting capacity may be a good and simple solution to modeling drought responses when no SWC measurements are available in the most active layers.

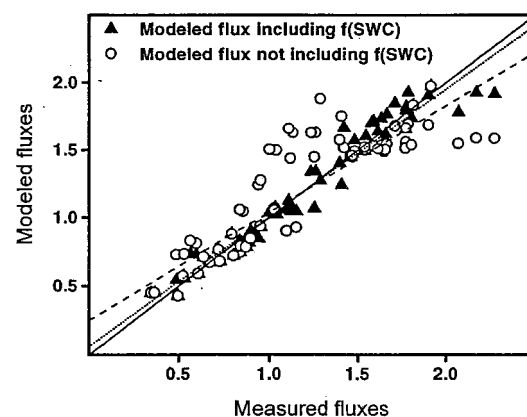


Figure 5. Measured versus modeled fluxes for 2001. Symbols: \blacktriangle = fluxes modeled with both temperature and soil water content (SWC) correction ($f(T):f(\text{SWC})$ in the figure legend); \circ = fluxes modeled using the temperature function only ($f(T)$). Fluxes of each period were modeled based on their corresponding Q_{10} function. Correlation coefficients (R^2) for each model are also shown. The solid line represents the 1:1 line; the dotted and dashed lines represent, respectively, the linear fit for measured fluxes versus fluxes modeled with temperature and SWC and versus fluxes modeled using the temperature function only.

Conclusions

Soil temperature exerted dominant control over SR during most of the year. Sensitivity of SR to temperature changed significantly during the year. However, we found no evidence for control of the temperature sensitivity of SR by temperature or SWC. When SWC decreased to less than $0.15 \text{ m}^3 \text{ m}^{-3}$, water became the limiting factor, and SWC in the mineral soil as well as the amount and distribution of rainfall strongly influenced SR rates. Our results suggest that, although most of the metabolic activity occurs in the upper few centimeters of the soil profile most of the time, deeper soil layers may become important during severe drought. Therefore, at our site, SR should preferably be modeled using SWC measurements obtained at different depths.

Acknowledgments

This study was supported financially in part by the Fifth Framework Programme of the European Commission (R&TD programme) through the CARBOEUROFLUX (Contract EVK2-CT-1999-00032) and the MEFYQUE Research Contract (QLKS-CT-2001-00345). This study contributes to the Global Change and Terrestrial Ecosystems (GCTE) Core Project of the International Geosphere-Biosphere Programme (IGBP). The authors gratefully acknowledge F. Kockelbergh for technical assistance, the Institute for Forestry and Game Management for logistic support at the site and Marc Schuurmans for his help and advice. I.A.J. is indebted to the Fund for Scientific Research-Flanders (F.W.O.) for a post-doctoral fellowship.

References

- Anderson, J.M. 1973. Carbon dioxide evolution from two temperate deciduous woodland soils. *J. Appl. Ecol.* 10:361–378.
- Baeyens, L., J. Van Slycken and D. Stevens. 1993. Description of the soil profile at Brasschaat. Institute for Forestry and Game Management, Geraardsbergen, Belgium, 17 p.
- Birch, H. 1958. The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* 10:9–31.
- Birch, H. 1960. Nitrification of soil after different periods of dryness. *Plant Soil* 12:81–96.
- Boone, R.D., K.J. Nadelhoffer, J.D. Canary and J.P. Kaye. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396:570–572.
- Borken, W., Y.-J. Xu, R. Brumme and N. Lamersdorf. 1999. A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: drought and rewetting effects. *Soil Sci. Soc. Am. J.* 63:1848–1855.
- Buchmann, N. 2000. Biotic and abiotic factors regulating soil respiration rates in *Picea abies* stands. *Soil Biol. Biochem.* 32:1625–1635.
- Carlyle, J.C. and U.B. Than. 1988. Abiotic controls of soil respiration beneath an eighteen-year-old *Pinus radiata* stand in south-eastern Australia. *J. Ecol.* 76:654–662.
- Čermák, J., F. Riguzzi and R. Ceulemans. 1998. Scaling up from the individual tree to the stand level in Scots pine. I. Needle distribution, overall crown and root geometry. *Ann. Sci. For.* 55:63–88.
- Chau-Berlinck, J.G., L.H. Alves Monteiro, C.A. Navas and J.E.P.W. Bicudo. 2002. Temperature effects on energy metabolism: a dynamic system analysis. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 269:15–19.
- Davidson, E.A., E. Belk and R.D. Boone. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol.* 4:217–227.
- Davidson, E.A., L.V. Verchot, J.H. Cattanio, I.L. Ackerman and J.E.M. Carvalho. 2000. Effects of soil water content on soil respiration in forest and cattle pastures of eastern Amazonia. *Biogeochemistry* 48:53–69.
- de Jong, E. and H.J.V. Schappert. 1972. Calculation of soil respiration and activity from CO₂ profile in the soil. *Soil Sci.* 113:328–333.
- Epron, D., L. Farque, E. Lucot and P.-M. Badot. 1999. Soil CO₂ efflux in a beech forest: dependence on soil temperature and soil water content. *Ann. For. Sci.* 56:221–226.
- Howard, D.M. and P.J.A. Howard. 1993. Relationships between CO₂ evolution, moisture content and temperature for a range of soil types. *Soil Biol. Biochem.* 25:1537–1546.
- Janssens, I.A. and K. Pilegaard. 2003. Large seasonal changes in Q₁₀ of soil respiration in a beech forest. *Global Change Biol.* 9:911–918.
- Janssens, I.A., D.A. Sampson, J. Čermák, L. Meiresonne, F. Riguzzi, S. Overloop and R. Ceulemans. 1999. Above- and below-ground phytomass and carbon storage in a Belgian Scots pine stand. *Ann. For. Sci.* 56:81–90.
- Janssens, I.A., A.S. Kowalski, B. Longdoz and R. Ceulemans. 2000a. Assessing forest soil CO₂ efflux: an in situ comparison of four techniques. *Tree Physiol.* 20:23–32.
- Janssens, I.A., L. Meiresonne and R. Ceulemans. 2000b. Mean soil CO₂ efflux from a mixed forest: temporal and spatial integration. *In* Forest Ecosystem Modelling, Upscaling and Remote Sensing. Eds. R. Ceulemans, F. Veroustraete, V. Gond and J. Van Rensbergen. SPB Academic Publishing, The Hague, pp 19–33.
- Janssens, I.A., S. Dore, D. Epron, H. Lankreijer, N. Buchmann, B. Longdoz, J. Brossaud and L. Montagnani. 2001. Climatic influences on seasonal and spatial differences in soil CO₂ efflux. *In* Canopy Fluxes of Energy, Water and Carbon Dioxide of European Forests. Ed. R. Valentini. Springer-Verlag, Berlin, pp 233–253.
- Jenkinson, D.S., D.D. Harkness, E.D. Vance, D.E. Adams and A.F. Harrison. 1992. Calculating net primary production and annual input of organic matter to soil from the amount and radiocarbon content of soil organic matter. *Soil Biol. Biochem.* 24:295–308.
- Keith, H., K.L. Jacobsen and R.J. Raison. 1997. Effects of soil phosphorus availability, temperature and moisture on soil respiration in *Eucalyptus pauciflora* forest. *Plant Soil* 190:127–141.
- Kelliher, F.M., J. Lloyd, A. Arneth et al. 1999. Carbon dioxide efflux density from the floor of a central Siberian pine forest. *Agric. For. Meteorol.* 94:217–232.
- Kowalski, A.S., S. Overloop and R. Ceulemans. 2000. Eddy fluxes above a Belgian, Campine forest and their relationship with predicting variables. *In* Forest Ecosystem Modelling, Upscaling and Remote Sensing. Eds. R. Ceulemans, F. Veroustraete, V. Gond and J. Van Rensbergen. SPB Academic Publishing, The Hague, pp 3–17.
- Kucera, C.L. and D.L. Kirkham. 1971. Soil respiration studies in tall grass prairies in Missouri. *Ecology* 52:912–915.
- Law, B.E., D.D. Baldocchi and P.M. Anthoni. 1999. Below-canopy and soil CO₂ fluxes in a ponderosa pine forest. *Agric. For. Meteorol.* 94:171–188.
- Lee, M.-S., K. Nakane, T. Nakatsubo, W.-H. Mo and H. Koizumi. 2002. Effects of rainfall events on soil CO₂ flux in a cool temperate deciduous broad-leaved forest. *Ecol. Res.* 17:401–409.
- Lloyd, J. and J.A. Taylor. 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8:315–323.

- Longdoz, B., M. Yernaux and M. Aubinet. 2000. Soil CO₂ efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution. *Global Change Biol.* 6: 907–917.
- Lyr, H. and G. Hoffmann. 1967. Growth rates and growth periodicity of tree roots. *Int. Rev. For. Res.* 2:181–236.
- Matteucci, G., S. Dore, C. Rebmann, S. Stivanello and N. Buchmann. 2000. Soil respiration in beech and spruce forests in Europe: trends, controlling factors, annual budgets and implications for the ecosystem carbon balance. *In Carbon and Nitrogen Cycling in European Forest Ecosystems*. Ed. E.-D. Schulze. Springer-Verlag, Berlin, pp 217–236.
- Meiresonne, L. and S. Overloop. 1999. Transpiratiebegroting van een Grove dennenbestand: een eerste modelmatige benadering. *Comm. Inst. For. Game Manage., Belgium*, No. 1999/1, pp 103–119.
- Meiresonne, L., D.A. Sampson, A.S. Kowalski, I.A. Janssens, N. Nadezhdina, J. Čermák, J. Van Slycken and R. Ceulemans. 2002. Water flux estimates from a Belgian Scots pine stand: a comparison of different approaches. *J. Hydrol.* 270:230–252.
- Moncrieff, J.B. and C. Fang. 1999. A model for soil CO₂ production and transport. 2. Application to a Florida *Pinus elliottii* plantation. *Agric. For. Meteorol.* 95:237–256.
- Morén, A.-S. and A. Lindroth. 2000. CO₂ exchange at the floor of a mixed boreal pine and spruce forest. *Agric. For. Meteorol.* 101: 1–14.
- Orchard, V. and F. Cook. 1983. Relationship between soil respiration and soil moisture. *Soil Biol. Biochem.* 15:447–453.
- Paembonan, S.A., A. Hagihara and K. Hozumi. 1991. Long-term measurement of CO₂ release from the aboveground parts of a hinoki forest tree in relation to air temperature. *Tree Physiol.* 8: 399–405.
- Peterjohn, W.T., J.M. Melillo, P.A. Steudler and K.M. Newkirk. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecol. Appl.* 4:617–625.
- Post, W.M., W.R. Emanuel, P.J. Zinke and A.G. Stangenberger. 1982. Soil carbon pools and world life zones. *Nature* 298:156–159.
- Raich, J.W. and C.S. Potter. 1995. Global patterns of carbon dioxide emissions from soils. *Global Biogeochem. Cycles* 9:23–36.
- Raich, J.W. and W.H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B:81–99.
- Raich, J.W., C.S. Potter and D. Bhagawati. 2002. Interannual variability in global soil respiration, 1980–94. *Global Change Biol.* 8: 800–812.
- Rayment, M.B. and P.G. Jarvis. 2000. Temporal and spatial variation of soil CO₂ efflux in a Canadian boreal forest. *Soil Biol. Biochem.* 32:35–45.
- Reichstein, M., J.D. Tenhunen, O. Roupsard and J.M. Ourcival. 2002. Severe drought effects on ecosystem CO₂ and H₂O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? *Global Change Biol.* 8:999–1017.
- Rey, A., E. Pegoraro, V. Tedeschi, I. De Parri, P.G. Jarvis and R. Valentini. 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. *Global Change Biol.* 8:851–866.
- Russell, C.A. and R.P. Voroney. 1998. Carbon dioxide efflux from the floor of a boreal aspen forest. I. Relationship to environmental variables and estimates of C respired. *Can. J. Soil Sci.* 78:301–310.
- Ryan, M.G., R.M. Hubbard, S. Pongracic, R.J. Raison and R.E. McMurtrie. 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiol.* 16:333–343.
- Schlentner, R.E. and K. van Cleve. 1985. Relationships between soil CO₂ evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. *Can. J. For. Res.* 15:97–106.
- Seneviratne, R. and A. Wild. 1985. Effect of mild drying on the mineralization of soil nitrogen. *Plant Soil* 84:175–179.
- Sprugel, D.G., M.G. Ryan, J.R. Brooks, K.A. Vogt and T.A. Martin. 1995. Respiration from the organ level to the stand. *In Resource Physiology of Conifers. Acquisition, Allocation, and Utilization*. Eds. W.K. Smith and T.M. Hinckley. Academic Press, San Diego, CA, pp 255–291.
- Taylor, B.R., D. Parkinson and W.F.J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70:97–104.
- Tjoelker, M.G., J. Oleksyn and P.B. Reich. 2001. Modelling respiration of vegetation: evidence for a general temperature-dependent Q_{10} . *Global Change Biol.* 7:223–230.
- van't Hoff, J.H. 1898. Lectures on theoretical and physical chemistry. Part I. Edward Arnold, London, pp 224–229.
- Witkamp, M. 1966. Decomposition of leaf litter in relation to environment, microflora and microbial respiration. *Ecology* 47: 194–201.
- Xiao, C.-W., J. Curiel Yuste, I.A. Janssens, P. Roskams, L. Nachtergale, A. Carrara, B.Y. Sanchez and R. Ceulemans. 2003. Above- and belowground biomass and net primary production in a 73-year-old Scots pine forest. *Tree Physiol.* 23:505–516.
- Xu, M. and Y. Qi. 2001a. Soil-surface CO₂ efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biol.* 7:667–677.
- Xu, M. and Y. Qi. 2001b. Spatial and seasonal variations of Q_{10} determined by soil respiration measurements at a Sierra Nevada Forest. *Global Biogeochem. Cycles* 15:687–696.