

Soil respiration measurements and simple models for a tropical rain forest fragment in Rondônia, Southwest Amazonia

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Abstract

Soil respiration plays a significant role in the carbon cycle of Amazonian rain forests. Measurements of soil respiration have only been carried out at few locations and its dependence on soil temperature (T_s) and moisture content (θ) in Amazonian forests are not well understood yet. This study investigates the temporal variability of soil respiration efflux (R_s) measured with five automatic soil chambers, soil moisture content, soil temperature and litterfall in a tropical rain forest fragment near Ji-Paraná, Rondônia – Brazil, between April 2003 and January 2004. Mean half-hourly R_s values varied considerably between 0.6 and 17.0 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, with an average of $7.9 \pm 3.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ over a 247-day period. Soil respiration exhibited a seasonal trend, with lower values during the dry season (average 6.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than during the wet season (average 9.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). The general seasonal pattern corresponded with seasonal variations in soil temperature and moisture content. A soil respiration maximum (average 12.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was observed in the transition period from the dry to the wet season (September 2003), which coincided with increasing temperature, rainfall, sunlight, evapotranspiration and ecosystem productivity. Seasonal litterfall variations also seemed to contribute to creating favourable conditions for biomass decomposition early in the wet season, after a period of fresh litter accumulation on the forest floor during the dry season. We evaluated the performance of three soil respiration models over a range of time scales using our observed data. These models are based on soil temperature, soil moisture or both, and included the exponential Q_{10} model, the Reichstein model, and a newly developed log- θ model. Our analyses show that these models generally fail to predict the observed variation in R_s using short averaging periods (less than 7 days), but perform better when R_s is averaged over longer periods of time. The observations suggest a range of θ between 0.12 and 0.25 for which average R_s is at a maximum of about 11 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The Q_{10} quotient was high, which was attributed to the limited amplitude of T_s at this site. This would argue against using the Q_{10} or Reichstein model for simulations in this type of Amazonian rain forest as large errors would occur during periods with large anomalies in temperature. Soil temperature and moisture content are weakly correlated to soil respiration when using averaging periods of less than a day and

modelling the variation of R_s at such time scales for this Amazonian rain forest would require the development of more sophisticated models, which should include a range of environmental and biological factors.

1 Introduction

Soil respiration processes play an important role in the carbon cycle of Amazonian forests. Soil respiration interacts with water and energy cycles on both spatial and seasonal scales (Richey et al., 2002; von Randow et al., 2004), and shows a coupling to regional and global climate (Betts et al., 2004; Saleska et al., 2009). Various studies suggest that soil CO_2 emissions are between 60–80% of total primary production (Meir et al., 1996; Davidson et al., 1998; Janssens et al., 2001). The Amazonian rain forest carbon cycle is now studied by a combination of various techniques, including flux measurements with eddy-covariance systems (Grace et al., 1996; de Araújo et al., 2002; Saleska et al., 2003; Goulden et al., 2004; de Araújo, 2009), soil respiration measurements using chambers (Meir et al., 1996; Davidson et al., 2000; Sotta et al., 2004; Buchmann et al., 1997; Salimon et al., 2004), biomass assessments (Malhi et al., 2002, 2009), hydrological export studies (Richey et al., 2002; Waterloo et al., 2006), remote sensing and airborne flux studies (Lloyd et al., 2007).

Soil respiration measurements in Amazonian forests, and in particular those made over longer periods of time providing seasonal information, are still scarce. The available data also suggest considerable variation between locations in the Amazon Basin. Soil respiration measurements are essential to get a reliable understanding of the driving forces behind soil processes and to provide information on the sensitivities of model formulations to reduce uncertainties. There is a broad consensus about the necessity to validate models with observations in tropical regions, in view of strong climate anomalies, high carbon stocks and different local forcing variables. However, field research, especially in Amazonia, is still not in pace with the modeller's data requirements. Simple soil CO_2 efflux models may be used to assess the dependence of soil respiration rates on climate (*e.g.* temperature) and allow integration with *in situ* measurements (Meir et al., 1996; Davidson et al., 2000; Sotta et al., 2004). Such models that improve our

understanding of soil respiration processes may therefore contribute to improving the land surface parametrisation used in climate modelling studies to predict effects of land use and climate change in Amazonia.

Simple soil respiration models have been developed with soil temperature providing the functional relationships for particular ecosystems (Lloyd and Taylor, 1994; Davidson et al., 1998; Janssens et al., 2003). However, heterotrophic and root respiration in the soil is not only controlled by temperature, but also by other factors including soil moisture, soil texture and composition, chemical properties and biomass of leaf litter and roots and activity of the macro- and micro-fauna (Liski and Westma, 1997; Giardina and Ryan, 2000; Howard and Howard, 1993; Davidson et al., 1998; Irvine and Law, 2002; Janssens et al., 2003; Raich et al., 2002; Reichstein et al., 2003). Several studies also suggest an influence of seasonal variation in litterfall on soil respiration rates (Reichstein et al., 2003; Salimon et al., 2004; Valentini et al., 2008).

There is evidence that the soil respiratory Q_{10} quotient (*i.e.* the relative change in respiration due to a temperature change of 10 °C) may decrease when soil temperature increases because of the dependency of soil respiration on soil moisture content (Howard and Howard, 1993; Lloyd and Taylor, 1994; Janssens and Pilegaard, 2003). The mechanism was explained by Linn and Doran (1984), who observed that under very dry soil conditions the substrate diffusion through water films around soil particles to microbial active cells becomes limited. In contrast, under very wet soil conditions oxygen diffusion may inhibit gas production and the diffusion through pore spaces to the atmosphere also may become limited (Skopp et al., 1990; Davidson, 1993). Such non-linear dependence of soil respiration on temperature and soil moisture content can be minimised when the analysis is restricted to specific ranges of T_s and θ . Lloyd and Taylor (1994) reported that use of the Q_{10} factor in soil respiration models may lead to a systematic underestimation of soil respiration rates at low temperatures and overestimation at high temperatures.

The dependency of soil respiration on soil moisture seems to vary between different rain forest ecosystems in Amazonia. For example, in East Amazonia (Santarém) soil respiration rates appeared to decline over the entire dry season, despite higher litterfall early in the dry season. This suggests an increasing soil moisture limitation for these well-drained upland sites

over a 4–5 month period (Keller et al., 2004; Goulden et al., 2004; Saleska et al., 2009). Canopy photosynthesis appeared to increase at the same site from the middle of the dry season onwards due to a combination of increasing sunlight, a green-leaf flush and deep root activity (Saleska et al., 2003; Goulden et al., 2004; da Rocha et al., 2004). At another East Amazonian forest site with sandy soils (Caxiua), controlled drought experiments reduced soil respiration (Sotta et al., 2004), whereas similar drought conditions did not induce substantial changes in soil respiration of the more clayey soils in Santarém (Davidson et al., 2008). In Central Amazonia (Manaus) the plateau landscape is strongly dissected and consists of an alternation of well-drained plateaus and poorly drained valleys. The relationship between soil respiration and soil moisture content was here negatively correlated (Chambers et al., 2004), with higher respiration rates observed for the clayey plateau soil than for the moist sandy valley soils.

In the present study we deployed five automatic soil chambers to measure half-hourly soil respiration rates in a pristine tropical rain forest fragment in Southwest Amazonia over a 10 month period. The objective was to investigate diurnal and seasonal soil respiration patterns in a climatic zone for which such data are lacking and to determine the feasibility of using simple models to simulate soil respiration rates from litterfall, soil moisture and temperature data, using different time-averaging periods.

2 Materials and methods

2.1 Study area and climate

The study area was at Fazenda Itapirema, a ranch located along the Urupá River in Southwest Amazonia (10°55.60' S, 62°01.27' W, 162 m a.s.l.) at about 15 km distance from Ji-Paraná in Rondônia State, Brazil. Measurements were made in a pristine rain forest fragment of about 500 m by 650 m, which was surrounded by 20-year old secondary forest and pasture. Tree height varied between 25 and 30 m, and crown diameters were typically 10 to 15 m. Palm trees (*e.g.* *Orbignya martiana*, locally called *Babaçus*) were abundant at the site. This type of forest fragments is typical for the landscape in Rondônia State, which has been deforested according

to a characteristic fishbone pattern. The size of the forest fragment is rather small, but edge effects on micro-climate and forest production do not extend to more than 100–150 m into such forest fragments (Vasconcelos and Luizão, 2004; Laurance, 2008). The measurements carried out in this study were in the center of the fragment, at least 175 m away from the forest edge.

The mean annual precipitation at this site is about 2000 mm, and the wet season is between October and April. During the dry season, coincident with the southern winter, rainfall often falls below 20 mm per month. Monthly average air temperature ranges from 24°C in July and 27°C in October (da Rocha et al., 2009). It is common for two to three cold spells to occur, usually between July and August, due to the passage of large-scale cold fronts. During these events the minimum temperature may drop to $\sim 10^{\circ}\text{C}$ at night for 1–3 consecutive days. The atmosphere in the winter season is generally drier than in the southern summer, with average specific humidity ranging from 11.9 g kg^{-1} in July to 17.2 g kg^{-1} in December (Culf et al., 1996; von Randow et al., 2004).

The soil in the study area is an Oxisol, with a typical particle size distribution of 58% sand, 9% silt and 33% clay in the top 15–20 cm of the soil (Ballester et al., 2003).

2.2 Soil respiration measurements

An automatic soil respiration chamber system, consisting of five chambers (C1, C2, . . . C5) a CO_2 gas analyser, pneumatic valves and a data logger system, was developed at the University of São Paulo. Each chamber had a volume of 16.4 l and was placed on fixed collars installed about 4 cm into the soil. All chambers sequentially closed at regular time intervals. An air pump then circulated air at 4 l min^{-1} through the chamber's head-space and through tubing connected via two pneumatic valves (Clippard, USA) to an infrared CO_2 gas analyser (Ciras-SC, PP Systems, Hitchin, UK) that also measured chamber air temperature. A CR10X data logger (Campbell Scientific, USA) controlled the sequential opening and closing of each chamber and corresponding pneumatic valves. Chamber lids were open at an angle of about 45° and an electrical motor with a cord and pulley was activated to close the lid. The opening of the chamber lid under a 45° angle was sufficient to allow rainfall (and leaf litter) to enter into the chamber (directly and through splash). After chamber closure, the data logger measured and

stored the output of the gas analyser at 5 s intervals over a 4 minute period, during which the chamber remained closed. Between measurements of different chambers the connecting tubes were allowed to flush over a 2 minute period before the next chamber would be closed. This procedure ensured that each of the five chambers would be measured once every 30 minutes. The system operated for 247 days between April 30, 2003, and January 6, 2004.

Linear regression was used to assess the rate of change of the CO₂ concentration in the chamber's head-space over time ($\frac{\Delta c}{\Delta t}$). The first 10 measurements after chamber closure were discarded to avoid any effect of recent chamber closure on CO₂ concentration in the head-space. The soil respiration flux was calculated as:

$$R_s = \frac{\Delta c}{\Delta t} \left(\frac{P}{T_s * R} \right) M_d \left(\frac{V}{A} \right) \quad (1)$$

where R_s is the soil respiration flux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), P is the air pressure (kPa), T_s is the chamber air temperature (K), R is the specific gas constant for ideal air ($287.053 \text{ J kg}^{-1} \text{ K}^{-1}$), V is the chamber volume (m^3), A is the chamber surface area (m^2) and M_d is the molar weight of dry air ($28.9645 \text{ g mol}^{-1}$).

2.3 Soil temperature, soil moisture, precipitation and litterfall

Soil moisture measurements were made between April 30, 2003, until February 2004, whereas soil temperature measurements were extended to June 2004. Soil temperature was measured at 10 cm depth using T107 temperature sensors (Campbell Scientific, USA) installed near each chamber. Soil moisture content was measured simultaneously with CS615 Frequency Domain Reflectometry sensors (Campbell Scientific, USA) inserted into the soil near each chamber under an angle to provide the average soil water content at 0–25 cm depth. Soil moisture sensor calibration was done according to the methodology of Bruno et al. (2006) on soil samples of similar texture and structure collected at the nearby Reserva Jarú experimental site. A rough estimate of the rainfall input below the canopy was obtained from a single tipping bucket rain gauge (ARG-100; Environmental Measurements Ltd., UK) to assess the impact of rainfall events and subsequent infiltration on soil respiration fluxes. All sensors were connected to the

CR10X data logger and measured at the same intervals given above.

Litterfall was measured with 15 litter traps (1 m^2) placed in a 150 m by 200 m area surrounding the set of soil respiration chambers. The collectors were installed at 30 cm above the soil surface to avoid the proximity of the ground surface influencing leaf litter decomposition in the traps (Newbould, 1967). Samples were collected twice a month, between September 19, 2003, and May 1, 2004, and leaf litter was weighed and then dried in an oven for three days at 50°C before being reweighed.

2.4 Statistics and data analysis

The average half-hourly site respiration was calculated from observations of the five automatic chambers. Data gaps occurred due to mechanical malfunctioning of the chamber mechanism, heavy rain storms and due to a tree falling down on the area surrounding chamber C4 in early November 2003, which locally increased litter standing stock and subsequent litter decomposition activity. As a result, the observed soil respiration flux of chamber C4 became three times higher between November and December 2003 than before the event and these data were excluded from the analysis.

Soil respiration flux measurements were very variable in time, with large spikes observed during and shortly after rainfall events. These spikes were attributed to the forced removal of pore-space gas in response to infiltration of rain water into the soil and were removed from the data set by excluding measurements done between 1 h before and 3 h after rainfall events.

Three soil respiration models were evaluated in this study. The first Q_{10} exponential model (Lloyd and Taylor, 1994; Davidson et al., 2005) is based on a relation between R_s and T_s . The second model is that developed by Reichstein et al. (2003), which is based on the model of Lloyd and Taylor (1994), but also incorporates a dependency on soil water content. The third empirical model has been developed in this study and is based on a polynomial log- θ function to simulate R_s and does not incorporate T_s . The three models will be discussed more extensively below and were tested by fitting to our observations using a non-linear least-square fitting procedure. Root mean square errors (RMSE) and coefficients of determination were calculated as indicators for the goodness of fit. All calculations were made with Matlab (Software version 6.5.0.1, The

3 Results

3.1 Temporal variation

The mean average diurnal patterns of R_s during the dry (28 July – 1 August 2003) and wet (25 – 30 December 2003) seasons, and corresponding soil temperature patterns, are shown in Figure 1. During the dry period R_s averaged $5.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and showed a variation of about $2.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ over the day. Average R_s reached a minimum of $4.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at dawn (6:30 h) and then gradually increased during the day to a maximum of $6.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ around 15:00 h. R_s remained rather constant in the late afternoon and during the night at $6.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, before decreasing to its daily minimum after 4:00 h. The corresponding diurnal cycle of T_s showed a different pattern. T_s averaged 23.9°C and varied in a sinusoidal fashion between a minimum of 23.6°C at 8:30 h and a maximum of 24.2°C at 19:00 h.

A different diurnal pattern of R_s was observed during the wet season (Figure 1). The daily average R_s was significantly higher at $8.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and the diurnal variation larger at $4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. R_s was high from the late afternoon until about 3:00 h, reaching a maximum of about $11.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ between 18:00 h and 22:00 h. Soil respiration started to decrease earlier in the morning (around 4:00 h) and reached its minimum of $4.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at about 8:00 h, 1.5 h later than in the dry season. R_s remained low during the morning hours and increased again from noon onwards. As expected, soil temperature was higher in the wet period with an average of 26.5°C and again varied less than 1°C over the day with minimum (26.2°C) and maximum (26.9°C) values occurring about 3 h earlier than during the dry season (Figure 1).

Soil respiration exhibits a pronounced seasonal variation at this site as demonstrated in Figure 2, which shows the variation in half-hourly R_s values over the full measurement period. Soil CO_2 emissions during the dry season averaged at $6.4 \pm 1.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, whereas those

during the wet season averaged at $9.9 \pm 1.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Corresponding T_s values averaged at $23.9 \pm 0.5^\circ\text{C}$ and $26.3 \pm 0.5^\circ\text{C}$, whereas corresponding θ values averaged at 0.11 ± 0.02 and 0.26 ± 0.08 , respectively.

The lowest mean R_s of around $1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was observed at the height of the dry season in August, when soil temperature (23°C) and soil moisture content (0.10) were also at their annual minimum, as shown in Figure 2. From the onset of the wet season in September 2003 onwards, soil temperature and moisture content increased gradually (Figure 2). Maximum values of soil temperature ($\sim 28^\circ\text{C}$) and moisture ($0.55 \text{ m}^3 \text{ m}^{-3}$) were reached in January. Peak values for half-hourly R_s of up to $17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ occurred regularly from September onwards, even though both T_s and θ had not increased to their annual maximum values yet. Figure 2 clearly illustrates the coupling between T_s and θ at this site.

Litterfall also showed a maximum of about 76 g m^{-2} in the dry season (August 2003 and in March 2004, Figure 3a) and remained approximately constant during the ensuing wet season at approximately 40 g m^{-2} . A similar seasonal pattern was observed by Luizão and Schubart (1987), who report that litterfall usually remains low during the wet season and reaches a maximum during the dry season in tropical rain forests.

Monthly litterfall totals correlated poorly with corresponding R_s values (Figure 3a, $R^2 = 0.14$). However, when monthly litterfall totals were shifted ahead in time by one month with respect to monthly average R_s values, *i.e.* by introducing a time lag of one month for $R - s$ to respond to litterfall, a good relation was observed ($R^2 = 0.62$; Figure 3b). Introducing such time lags may be required for some biological parameters in a heterotrophic soil respiration model, allowing time for the bio-community to respond to changed environmental conditions.

If we look at the onset of the wet season more in detail, it is clear that soil respiration responds sharply to increases in temperature and soil water content after the first rainfall events in September 2003 (Figure 4a, ellipses). These events caused θ to increase from 0.09 in the first week of September to $0.25 \text{ m}^3 \text{ m}^{-3}$ (Figure 4b) at the end of the month. A corresponding increase in R_s from $2\text{--}8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ before rainfall to $8\text{--}17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ during and after these rainfall events. Sudden increases in R_s were observed during and shortly after rainfall events. These could be explained by the percolation of rain water into the soil pore

spaces driving high $[\text{CO}_2]$ air out of the pore spaces, as was also observed by Matteucci et al. (2000). Higher R_s rates can also be caused by biological controls, such as fine-root regrowth, an increase in microbial activity with a fresh supply of moisture following drought, and the release of organic solutes from live and dead organic matter following wetting (Kieft et al., 1987; Howard and Howard, 1993; Davidson et al., 2000, 2005). September 2003 had the highest soil respiration, reaching an average of $12.6 \pm 3.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Corresponding monthly averages of T_s and θ amounted to $24.7 \pm 1.0^\circ\text{C}$ and 0.19 ± 0.04 , respectively.

3.2 Soil respiration efflux modelling

The dependence of R_s on T_s at 10 cm depth was assessed by the empirical soil heterotrophic respiratory quotient (Q_{10}) approach (Equations 2 and 3). The Q_{10} model is formulated as

$$R_s = R_0 * e^{(\beta_0 * T_s)} \quad (2)$$

where R_0 and β_0 are parameters obtained through fitting of observational R_s and T_s data. Q_{10} , the sensitivity parameter describing the change in R_s due to a 10°C change in T_s , is then determined as

$$Q_{10} = e^{10 * \beta_0} \quad (3)$$

This exponential model does not incorporate soil water content or other factors affecting R_s , and therefore does not limit respiration explicitly (Lloyd and Taylor, 1994; Fang and Moncrieff, 2001; Janssens and Pilegaard, 2003; Reichstein et al., 2003; yuste et al., 2004). The Q_{10} quotient has been used in several climate models, including the Hadley Centre coupled model HadCM3LC (Jones and Cox, 2004).

The Reichstein et al. (2003) is based on the Lloyd and Taylor (1994) model, but adds a soil water dependency to the soil temperature dependency of R_s . This is achieved through the use of a Relative Soil Water Content (RSWC) parameter, defined as:

$$\text{RSWC} = \frac{\theta}{\theta_{\text{FC}}} \quad (4)$$

where θ_{FC} is the soil moisture content at field capacity approximated by θ after three days of drainage following saturation. R_s is modelled according to:

$$R_s = R_{\text{ref}} * f(T_s, \text{RSWC}) * g(\text{RSWC}) \quad (5)$$

with R_{ref} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) being the soil respiration flux at the reference temperature $T_{\text{ref}} = 25^\circ\text{C}$, which is approximately equal to the annual mean soil temperatures at our site. The temperature and soil moisture functions in the model are described by the following set of equations:

$$f(T_s, \text{RSWC}) = e^{E_0(\text{RSWC}) \left(\frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T_s - T_0} \right)} \quad (6)$$

$$g(\text{RSWC}) = \frac{\text{RSWC}}{\text{RSWC}_{1/2} + \text{RSWC}} \quad (7)$$

where T_0 (-46°C) represents the lower temperature limit for soil respiration from the original model of Lloyd and Taylor (1994) and $\text{RSWC}_{1/2}$ (dimensionless) the soil moisture content where 50% of the maximum R_s at a certain temperature is observed. Reichstein et al. (2003) proposed that the temperature sensitivity of soil respiration be exponentially dependent on RSWC (Equation 6) and that for a first approximation the activation energy E_0 (K^{-1}) would be depending linearly on RSWC (a and b are linear regression coefficients of E_0 versus RSWC):

$$E_0(\text{RSWC}) = a + b * \text{RSWC} \quad (8)$$

The third, alternative model is based on θ only, and may be appropriate for tropical rain forest areas where diurnal and seasonal variations in T_s are small and θ is coupled to T_s . This $\log\text{-}\theta$ model exhibits a nonlinear dependence of R_s on the natural logarithm of θ through a polynomial function:

$$R_s = a + b * \ln(\theta) + c * \ln^2(\theta) \quad (9)$$

where the regression coefficient a represents a minimum R_s for dry soils, b a parameter for intermediately wet conditions and c parameter that becomes important when θ falls outside

certain upper and lower limits, which in the present study are defined as outside the range 0.15–0.25.

Both Q_{10} and Reichstein et al. (2003) models were fitted to the entire half-hourly data set (Figure 5, Table 1). Correlations between R_s and T_s were weak for the Q_{10} model ($R^2=0.17$, $Q_{10}=3.9$ and $RMSE=3.88$). Including θ in the analysis with the Reichstein et al. (2003) model did not improve the significantly ($R^2=0.17$ and $RMSE=2.77$). We noticed that R_s increased at soil temperatures between 23.0 °C and about 26.3 °C, but tended to decrease when T_s exceeded 26.3 °C. However, such high soil temperatures are normally also coupled to high soil moisture contents in SW Amazonia (see Figure 2), which makes it difficult to say if this is a negative response of R_s to high T_s or high θ values. This interdependency of T_s and θ complicates the interpretation of the results of fitting such simple models to the data.

The half-hourly observations of R_s were also fitted against θ for the log- θ model (Figure 5b, Table 1), which again gave a poor correlation ($R^2=0.29$; $RMSE=2.57$; $p<0.05$). However, this does indicate that R_s reaches a maximum with θ varying around an optimum range of 0.15 and 0.25 $m^3 m^{-3}$, which is near field capacity for these oxisols.

To better understand the dependence of R_s to T_s under different θ conditions, the Q_{10} and Lloyd and Taylor models were fitted to three different classes of θ , *i.e.* dry conditions with $0.09<\theta<0.115$, moderately moist conditions with $0.115<\theta<0.25$ and wet conditions with $\theta>0.30$. The results are shown in Figure 6.

During dry conditions (Figure 6a) R_s shows a clear exponential pattern against T_s with moderate scatter, which can be modelled by both exponential models, albeit with low coefficients of determination (Table 1). Coincidentally, dry season T_s was low and rather constant at this time, which limits the range of T_s (Figure 6a). The Q_{10} parameter was estimated at 11.3, which is relatively high. This could be explained by the low amplitude of T_s in these forest soils, which forces the Q_{10} parameter to be higher than normally observed in studies where the variation in soil temperature is much more pronounced.

Under moderately wet conditions (Figure 6b), R_s also shows an exponential increase with T_s but with a very high scatter in the data, again causing low coefficients of determination for the models, although the Lloyd and Taylor model performed slightly better than the Q_{10} model

(Table 1). Under this moisture condition, Q_{10} was lower at 7.88.

For very wet conditions the scatter in the half-hourly T_s - R_s data pairs was such (Figure 6c) that no correlation could be established (Table 1). Hence R_s seemed not sensitive to either T_s or θ under very wet soil conditions and different processes must be active to cause the large variation in R_s .

We also fitted the log- θ model (Equation 9) for the same sets of moisture conditions (Figure 7). Under dry conditions (Figure 7a) R_s appeared to be rather constant at about $6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ until θ reaches a value of 0.105 and then shows a gradual increase to $8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at $\theta = 0.115$. The coefficient of determination for this model remains low at 0.37. Under moderately wet conditions (Figure 7b) the model predicts a maximum R_s of about $11 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at θ between 0.14 and 0.20 (Figure 7b), with R_s at about $6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at the class boundaries of θ (0.115 and 0.30). As for the previous models, no clear pattern could be discerned under moist soil conditions with the log- θ model due to the large scatter in the θ - R_s data with R_s ranging between 0.4 and $16.95 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Other processes than soil moisture or temperature apparently control soil CO_2 emissions. Determination of the responsible processes may be difficult as this would require a separation of the autotrophic and heterotrophic emissions.

The three soil respiration models were also applied to mean R_s , T_s and θ for periods with variable lengths, *i.e.* of 1, 5, 7, 10, 14 and 21 days and on monthly averages (Figure 8). This considerably reduces the variation that is present in the half-hourly data and therefore improves the model fit. The results are shown in Table 2 and indicate the fit gets better progressively when averages are used over longer periods of time.

Finally, a 30-days time lag was introduced between monthly averages of R_s and those of T_s and θ , followed by fitting of the models. Under these conditions both Q_{10} and Reichstein et al. (2003) models explained over 55% of the variance in monthly R_s (Figure 8a,c), with Q_{10} now lower at 4.53, which must still be considered high. The log- θ model performed even better under the same conditions, explaining over 79% of the monthly variation (Figure 8).

4 Discussion

4.1 Temporal patterns in soil respiration

Soil respiration in our *terra firme* rain forest in Southwest Amazonia averaged at $7.94 \pm 3.10 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ over a 8-month period, which covered both dry and wet seasons. Mean half-hourly R_s observations showed large variation, ranging from 0.6 to $17.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Several studies have reported on the correlation of R_s and T_s , measured at 2–10 cm depth (e.g. Meir et al., 1996). Davidson et al. (1998) reported maximum T_s and R_s values to occur late in the afternoon, around 18 h, in a primary forest in East Amazonia. This is similar to our observations in the dry period (Figure 1).

The climate in Rondônia exhibits a strong seasonal variation with relatively low temperatures and rainfall during the dry season (June – August) and high temperatures and rainfall in the wet season (October – April). This affects both T_s and θ and a clear seasonal pattern was therefore observed for R_s . A similar seasonal pattern of R_s , albeit at much lower values ($2\text{--}4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was observed by Chambers et al. (2004) for a site in Central Amazonia, where the dry season was much shorter than at the present site. Chambers et al. (2004) also observed a spatial pattern related to topography, with the highest R_s values on the well-drained clayey plateaus and lowest in poorly drained sandy valleys.

Soil respiration reached a maximum during the dry-to-wet season transition period in September 2003 and showed a positive response to the sudden increase in temperature and soil moisture content after the first rainfall events. The moisture provided by the first rainfall events also may have led to increased activity of the decomposer community in the high litter standing stock, caused by high litterfall and subsequent litter accumulation during the dry season (Luizão and Schubart, 1987; Selva et al., 2007). Furthermore, the combination of higher solar radiation (da Rocha et al., 2009) and a wetting of the soil may have increased forest productivity and transpiration rates (Saleska et al., 2009), which would affect root respiration positively, especially that by fine roots in the shallow soil layers. Finally, the infiltration of water into pore spaces may have forced pore space air with high CO_2 concentrations out of the soil, generating high peaks of CO_2 emission. This has been observed earlier in chamber experiments (Matteucci et al.,

2000). All these factors may have contributed to the high R_s observed in the dry-to-wet season transition period. The increase of soil respiration following rainfall and a sudden increase in θ early in the wet season agrees with observations in East Amazonian forests (Davidson et al., 2000; Sotta et al., 2004) and in a rain forest in Acre, Southwest Amazonia (Salimon et al., 2004).

Davidson (1993) and Chambers et al. (2004) showed that increases in θ led to decreases in R_s at their sites, which could be caused by inhibition of respiratory activity due to inadequate oxygen supply in near-saturated soils (Linn and Doran, 1984). Our measurements also suggest that above a threshold for θ of 0.20 no further increase in R_s occurred, although high half-hourly values of R_s were still observed at θ values up to 0.40. Recently, Savage et al. (2009) and Penga et al. (2009) suggested that soil respiration tends to become more sensitive to temperature changes with increasing soil moisture content, before reaching a threshold. But in the present study the sensitivity of R_s to T_s decreases under high soil moisture conditions, presumably in response to reduced oxygen diffusion. The direct reaction of R_s to changes in θ in the dry-to-wet season transition could be partly explained by the heterotrophic component, as decomposition of accumulated organic matter is activated by an increase of the micro-organism population following the first rains after a long dry period. In seasonal climates, this mechanism could be responsible for 25% of primary productivity (Lankreijer et al., 2002). Our observations most closely resemble the increase of R_s observed at the Santarém East Amazonian forest site during the wet season (December; Goulden et al., 2004), although our R_s observations were again somewhat higher.

4.2 Modelling of soil respiration

Three simple empirical models were explored to derive R_s from T_s , θ or both. The Q_{10} exponential model was fitted on observations of T_s , measured at 10 cm below the soil surface, and R_s . This resulted a high heterotrophic respiratory Q_{10} quotient of 3.9 over the whole period, based on half-hourly data, and even higher values for the dry (11.3) and wet (4.8) periods (Table 1). When averages were used over longer periods of time (1–30 days), Q_{10} ranged between 2.8 (21 days) and 4.5 (30 days). Several authors have reported correlations between R_s and

T_s , measured at depths between 2 and 25 cm below the mineral soil surface (Meir et al., 1996; Davidson et al., 1998, 2000; Irvine and Law, 2002; Sotta et al., 2004). The diurnal and annual amplitudes of T_s were small at less than 2 °C (Figure 1 and 4 °C, Figure 2), respectively. Similar low-amplitude soil temperature patterns were observed by Alvalá et al. (2002) and Meir et al. (1996) in Amazonian rain forests. In the present soils under a closed rain forest canopy, soil temperature gradients and heat flux remain very small as radiation hardly penetrates the closed canopy, causing only small diurnal variations in soil temperature (Figure 1 Alvalá et al., 2002).

The choice of depth for the T_s measurements is important because of the increasing lag and decreasing amplitude with depth of the temperature signal with respect to the air temperature signal. When correlating synchronous observations of T_s and R_s , as for the Q_{10} model, a shift in time in T_s with respect to R_s due to T_s measurements at a non-ideal depth would decrease the correlation. In addition, a low diurnal amplitude of the T_s signal, in combination with a high amplitude of the R_s signal, may lead to high apparent sensitivity to temperature expressed in a high Q_{10} (Graf et al., 2008). Such high apparent sensitivity to temperature may also be obtained if the sensitivity of R_s to T_s is small because of other factors regulating R_s . From Figure 1 it is not obvious that the observed T_s measured at 10 cm exhibited a substantial lag with respect to R_s . Davidson et al. (1998) reported maximum soil temperature and respiration around 18:00 h in a primary forest in East Amazonia, which is also observed in our observations for the dry period. In fact, comparison of the diurnal patterns of R_s and T_s suggests that R_s seems to respond to other factors more than to T_s (or θ), especially during the wet period (Figure 1). This would support the observation by Davidson et al. (2005) that Q_{10} values significantly above 2.5 are a sign of different factors than T_s impacting on R_s . We suspect that the low sensitivity of R_s to T_s in this environment would explain the high values of Q_{10} , also because the T_s measurement depth of 10 cm is generally regarded as appropriate for assessing the dependence of R_s on T_s (Graf et al., 2008; Savage et al., 2009; Penga et al., 2009).

Inclusion of θ in the model of Reichstein et al. (2003) did not improve the goodness of fit of the average half-hourly R_s , T_s and θ observations (Table 1). This model performed slightly better than the Q_{10} model when averages were made over longer periods of time, but the highest R^2 was still low at 0.44 for an averaging period of 10 days. This may be attributed to the

strong coupling that exists between T_s and θ , both reaching a minimum in the dry season and a maximum in the wet season.

The log- θ model does not perform better than the other models on the half-hourly data set (Table 1). However, it does seem to capture the variation better than the models discussed above when longer averaging periods are used (Table 2). Again due to the coupling between T_s and θ in Southwest Amazonia, this approach suffers from the same drawbacks as the previous approaches.

We did not find an optimal temperature at which biological processes are maximum (other environmental factors being constant) (Fang and Moncrieff, 2001). However the observations and application of the log- θ model clearly suggested an optimum soil moisture range. Linn and Doran (1984) and Davidson (1993) have suggested that an optimum would be found over a large θ -range of 0.20 to 0.70, including both low-porosity sands and high-porosity clay soils. We observed a maximum R_s to coincide with a soil moisture range of 0.12 to 0.25 for a soil with a porosity of about 0.52.

The model analysis suggests that the Q_{10} , Reichstein et al. (2003) and log- θ approaches are not capable to explain the variance in the half-hourly soil respiration observations. This is partly due to the high variation in these observations. However, it is clear from Figures 5–Fig.8 that these models do represent the mean R_s values, and therefore do not contradict the observations entirely. The performance of the regression improves when the data means are calculated over longer periods of up to one month, (Figure 8), which allows the models to represent the seasonal cycle in R_s . The log- θ model then outperforms the others. Finally, provided that a lag of one month was introduced between litterfall and subsequent R_s , monthly litterfall also showed a moderate correlation with average monthly R_s (Figure 3). By classifying the data according to low, intermediate or high moisture content

The apparent importance of other factors than soil temperature or moisture for regulating soil respiration over short periods of time periods in this Southwest Amazonian rain forest environment suggests that the Q_{10} , Reichstein et al. (2003) and log- θ approaches can be considered inappropriate for modelling R_s , especially over small time scales (*e.g.* less than a week).

5 Conclusions

Half-hourly soil respiration rates show a large variation over short periods of time. These variations cannot satisfactorily be captured by simple models based on temperature and/or soil moisture data. R_s also shows a seasonal variation, with relatively high values during the wet season and low values in the dry season when temperatures also reach their annual minimum. This variation can be captured by simple models, but care should be taken with the interpretation of the high Q_{10} values that are distilled from the observations. Soil respiration efflux is highest during the transition from the dry to the wet season, when soil moisture increases from a minimum after the first rainfall events and litter has accumulated on the forest floor during the preceding dry period.

Classification of the data in different soil moisture classes provided better fits of the models to the R_s data. Due to the high rainfall in Amazonia, soil moisture may be above field capacity for extended periods of time, especially during the dry season. The classification assisted in determining dependencies of R_s on T_s and θ during the wet and dry seasons. Application of the log- θ model also identified an optimum soil moisture range for R_s .

During the dry period soil respiration was controlled more by soil moisture (log- θ model) than by temperature. The range of soil moisture in this season was very limited, but over this small range R_s showed an exponential increase (Figure 7). The intermediate moisture class (0.115 to 0.25) is where the highest soil temperature and moisture variation occurs and here the Reichstein et al. (2003) model performed best, indicating that soil respiration responded to variations in both T_s and θ . However, the large scatter in the data also indicates that other processes were acting to drive R_s .

In the Amazon Basin in general, and in this region in particular, there seems not to be a single factor that can serve as a reliable parameter for modelling soil respiration. This study showed that soil temperature and/or moisture were not the dominant drivers of soil respiration. The log- θ model applying a 30 days lag time showed the best predictive power, with an $R^2 = 0.79$. However, this is likely to be restricted to application to this particular region and would fail if used in global soil respiration models, where soil temperature may be a better indicator.

Simple models using T_s and/or θ all fail at time scale of less than a week. However, there is a need to be able to model R_s over shorter periods of time. This suggests that for capturing the half-hourly variation in the Amazon rain forests, more sophisticated models should be developed that incorporate additional factors affecting soil respiration, such as soil nutrient and carbon composition, microbial activity, decomposition processes, root respiration, photosynthetic activity and forest productivity. As there is a general paucity of the most basic data, including soil temperature and moisture, for the Amazon Basin, and even more so for data concerning the additional factors listed above, providing such data and developing a better model will pose a challenge to both experimental and modelling communities.

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Table 1. Regression coefficients and statistical data describing the goodness of fit of R_s to various classes of half-hourly observational data (n= 11537) for three selected models.

Models							
Exponential Q_{10}	Parameters / coefficients				Statistics		
	R_0	b_0	Q_{10}	R_s mean \pm std	Model mean \pm std	R^2	RMSE
Dry class	0.01	0.24	11.27	5.96 \pm 1.45	5.95 \pm 0.76	0.27	1.24
Intermediate	0.05	0.20	7.88	8.21 \pm 2.93	8.22 \pm 1.48	0.27	2.51
Wet class	0.13	0.15	4.83	8.61 \pm 3.57	8.69 \pm 0.68	0.04	3.50
Whole period	0.27	0.14	3.88	8.09 \pm 3.05	7.82 \pm 1.28	0.19	2.77
Reichstein et al. (2003)	Parameters / coefficients				Statistics		
	R_{ref}	RSWC	E_0	R_s mean \pm std	Model mean \pm std	R^2	RMSE
Dry class	10.50	0.41	1066	5.96 \pm 1.45	6.10 \pm 0.75	0.28	1.28
Intermediate	11.63	0.51	796.88	8.21 \pm 2.93	8.25 \pm 1.50	0.33	2.40
Wet class	7.93	1.23	663.16	8.61 \pm 3.57	8.61 \pm 0.74	0.04	3.50
Whole period	10.49	0.62	316.80	8.09 \pm 3.05	8.01 \pm 1.21	0.17	2.79
Log- θ	Parameters / coefficients				Statistics		
	a_0	b_0	c_0	R_s mean \pm std	Model mean \pm std	R^2	RMSE
Dry class	2165.10	1891.40	414.10	5.96 \pm 1.45	6.17 \pm 1.50	0.37	1.10
Intermediate	-41.20	-60.00	-17.00	8.21 \pm 2.93	8.82 \pm 1.58	0.28	2.57
Wet class	12.40	8.17	6.14	8.61 \pm 3.57	9.14 \pm 0.46	0.01	3.69
Whole period	-9.72	-26.02	-8.30	8.09 \pm 3.05	8.09 \pm 1.64	0.29	2.57

Table 2. Coefficients and statistics for the three models when applied to different averaging periods, ranging from daily average values to those for a 30-day period.

Average period	Log- θ		Q_{10}			Reichstein et al. (2003)	
	R^2	RMSE	R^2	Q_{10}	RMSE	R^2	RMSE
1 day	0.37	1.86	0.29	3.28	1.96	0.29	2.09
5 days	0.42	1.79	0.30	3.40	1.96	0.32	2.04
7 days	0.44	1.88	0.35	3.91	2.03	0.37	2.00
10 days	0.61	1.56	0.34	3.85	2.05	0.44	1.90
14 days	0.42	1.92	0.37	3.87	2.02	0.40	1.96
21 days	0.46	1.80	0.25	2.82	2.13	0.30	2.06
30 days	0.79	1.20	0.57	4.53	1.71	0.55	1.74

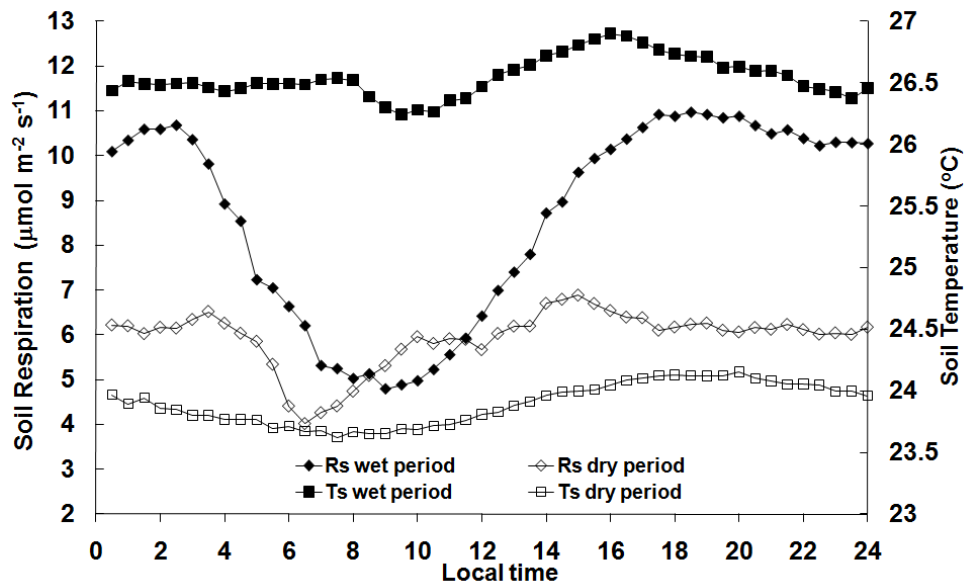


Fig. 1. Diurnal patterns of soil respiration efflux and soil temperature for dry (28 July – 1 August 2003) and wet (25–30 December 2003) periods.

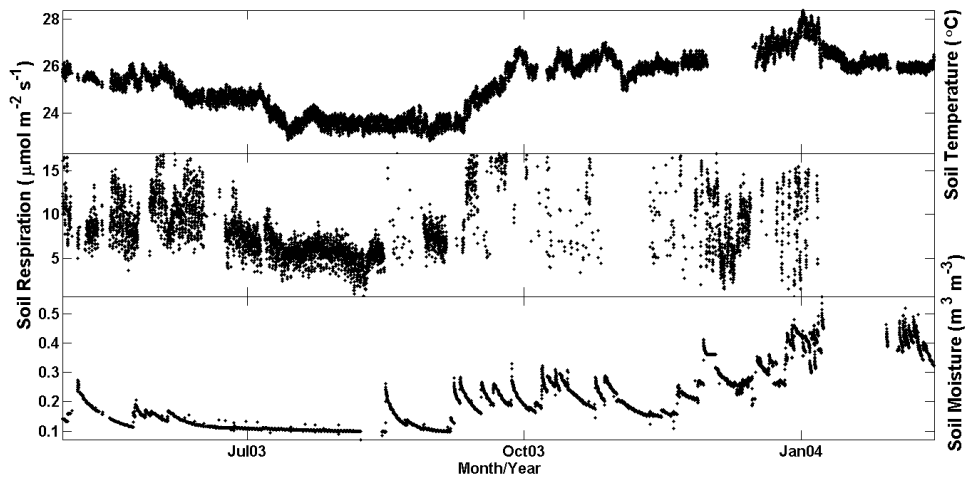


Fig. 2. Half-hourly values of a) soil temperature, b) soil respiration efflux and c) soil moisture content over the period 30 April 2003 – 26 January 2004.

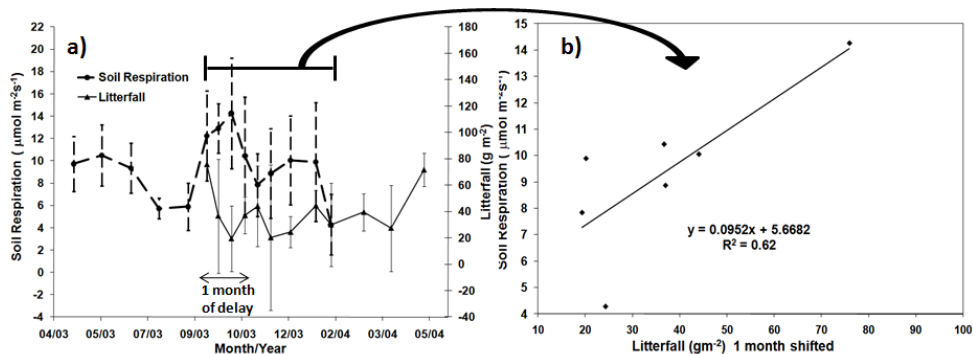


Fig. 3. Seasonal variation of a) soil respiration efflux and litterfall, showing similar patterns during the season, but the soil respiration efflux has on delay of one month latter in relation to the litterfall onset. b) and correlation between monthly average of soil respiration efflux and litterfall, using a time lag of one month. The linear model had a better fit (62%) compared to the non-lag time correlation (14%).

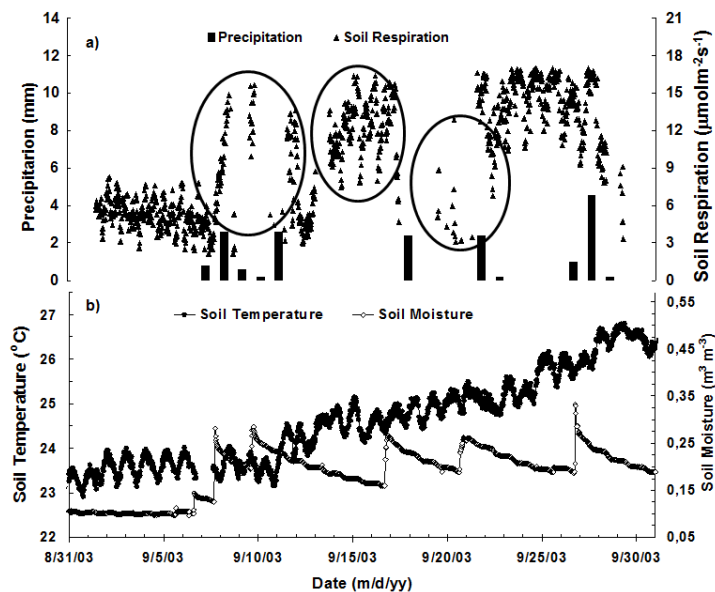


Fig. 4. Daily values of below canopy precipitation and half-hourly R_s values (a) in relation to changes in half-hourly T_s and θ (b) during the transition to the wet season in September 2003.

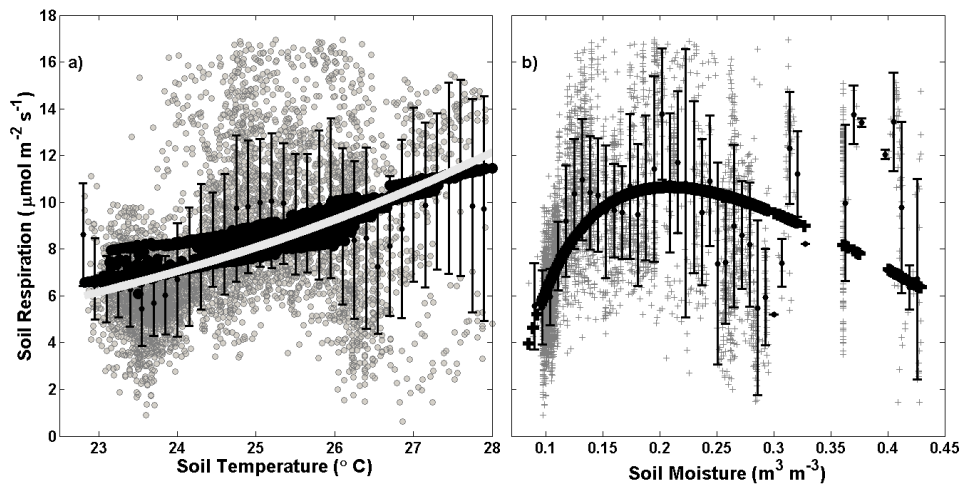


Fig. 5. Plot of half-hourly R_s data (grey circle) and their means and standard deviations (error bars) against T_s (a) and θ (b). The lines in a) represent modelled R_s values according to the Q_{10} model (solid grey line) and the Reichstein model (scattered black line), whereas that in b) represents the modelled values with the log- θ model (Solid black line).

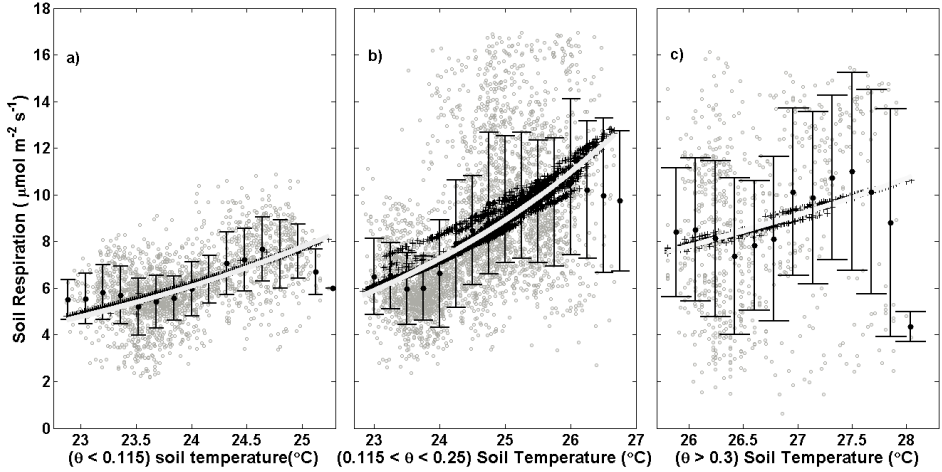


Fig. 6. Plot of half-hourly R_s data (grey circle) and their means and standard deviations (error bars) against T_s for three classes of θ . Lines represent modelled R_s values according to the Q_{10} model (solid grey line) and the Reichstein model (scattered black line). Soil moisture classes were a) $0.09 < \theta < 0.115$, b) $0.115 < \theta < 0.25$ and c) $\theta > 0.30$.

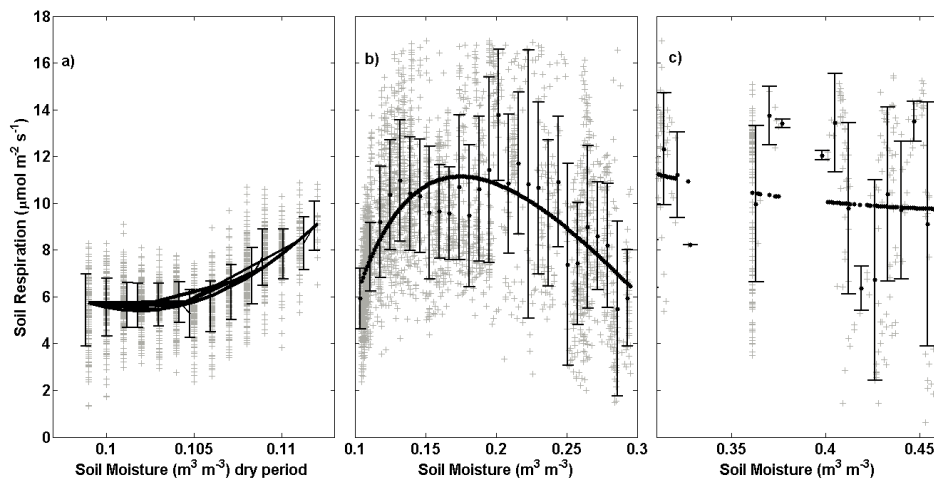


Fig. 7. Mean half-hourly values (grey circle) and standard deviations of soil respiration and soil moisture content for three classes of soil moisture. The solid black line represents the fit of the model to the experimental data.

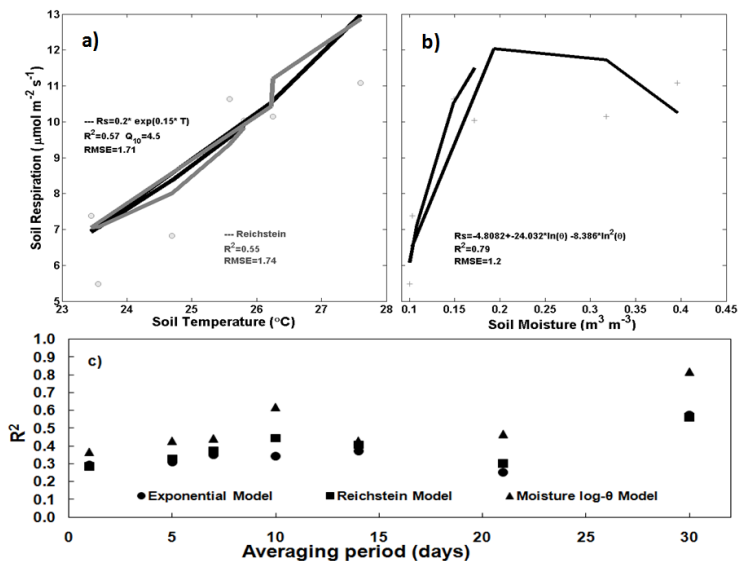


Fig. 8. Mean monthly soil respiration and a) soil temperature, b) soil moisture over the whole period. The lower plot c) provides information about how well the three models performed for various periods of averaging of the half-hourly data.